Goodheart et al. Marine Biodiversity Records (2016) 9:56
DOI 10.1186/s41200-016-0048-z

Marine Biodiversity Records

MARINE RECORD Open Access

Identification guide to the heterobranch sea slugs (Mollusca: Gastropoda) from Bocas del Toro, Panama

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Abstract

Background: The Bocas del Toro Archipelago is located off the Caribbean coast of Panama. Until now, only 19 species of heterobranch sea slugs have been formally reported from this area; this number constitutes a fraction of total diversity in the Caribbean region.

Results: Based on newly conducted fieldwork, we increase the number of recorded heterobranch sea slug species in Bocas del Toro to 82. Descriptive information for each species is provided, including taxonomic and/or ecological notes for most taxa. The collecting effort is also described and compared with that of other field expeditions in the Caribbean and the tropical Eastern Pacific.

Conclusions: This increase in known diversity strongly suggests that the distribution of species within the Caribbean is still poorly known and species ranges may need to be modified as more surveys are conducted.

Keywords: Heterobranchia, Nudibranchia, Cephalaspidea, Anaspidea, Sacoglossa, Pleurobranchomorpha

Introduction

The Bocas del Toro Archipelago is located on the Caribbean coast of Panama, near the Costa Rican border. The major islands of the archipelago include Isla Colón, Bastimentos, Solarte, Cristóbal, Popa and Cayo Aqua. The archipelago has a predominantly wet climate, receiving an average precipitation of 2870 mm per year (Gordon, 1982) and a maximum of 7000 mm (Rodríguez *et al.*, 1993). The primary marine ecosystems in the archipelago consist of mangroves (dominated by red mangroves), seagrass beds and coral reef patches (Wysor & Kooistra, 2003; Lovelock *et al.*, 2004; Collin, 2005).

The Bocas del Toro Research Station, a well-known marine station of the Smithsonian Tropical Research Institute (STRI), is located on Isla Colón. Numerous researchers at this station, both past and present, have utilized the waters surrounding the archipelago for various studies. However, this research has often been hampered by a lack of accurate and updated identification/field guides. This is particularly problematic for researchers studying heterobranch sea slugs, for which the taxonomy and systematics have changed dramatically in recent years. The only available field guide for Caribbean heterobranch sea slugs (Valdés *et al.*, 2006) is outdated and in need of revision.

Although the Caribbean Sea is inhabited by hundreds of heterobranch sea slug species (Valdés *et al.*, 2006), only 19 species have been formally identified and documented in the Bocas del Toro Archipelago (Collin *et al.*, 2005), representing only a fraction of the total diversity of sea slugs in the Caribbean.

In this paper we present an updated record of the diversity of heterobranch sea slugs in the Bocas del Toro Archipelago, resulting from several research trips to the area and a field course organized by STRI in July and August of 2015. We report new records for Bocas del Toro and provide updated information for previous records

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from the overall area, increasing the total number of observed heterobranch sea slug species in the region to 82.

Materials and methods

The STRI course on the taxonomy of sea slugs took place from July 24th to August 5th, 2015 in the Bocas del Toro Archipelago, Panama. Collecting effort for this expedition was documented and completed by a total of 16 observers with various levels of experience in searching for sea slugs (the minimum and maximum number of observers at any given time was 7 and 15, respectively). Although the amount of substrata collected was not measured, search time and the number of observers in each location were recorded. Therefore, "collecting effort" refers to the total searching time through direct observations for all observers. The results below represent an estimation of the species found using both direct and indirect methods.

Records from two previous field expeditions in Bocas del Toro are reported here as well, the first occurring in December 2004 and the second in July 2006. Collecting effort during these trips was not quantified, thus is not documented in this paper.

Eleven sites in Bocas de Toro were explored, exclusively during the daytime (Fig. 1). Specimens were documented via: (1) direct observation in the field (mainly snorkeling, but also SCUBA diving), or (2) substrate collection (primarily various species of algae and hydroids). After the substrate was collected and searched, materials were separated into trays with fresh seawater and left to rest overnight to allow for further examination and collection of sea slugs the following day.

Most specimens were identified in the field using the field guide by Valdés *et al.* (2006) or in the laboratory using primary literature from the Caribbean region. A few problematic specimens were identified based on unpublished sequence data. Some specimens were collected and preserved for further study.

Results

After approximately 307.5 person-hours of field searching, a total of 82 species belonging to five clades of heterobranch sea slugs were found, some of which have not yet been described (Table 1). The clade Nudibranchia had the highest number of species ($n = 40$, ~49 % of total) and was present in all eleven localities, followed by Sacoglossa ($n = 28$, ~34 % of total), which was present in all localities but one. In contrast, Pleurobranchomorpha had the lowest number of species ($n = 2$, <3 % of total) and was found in only three localities (Table 1).

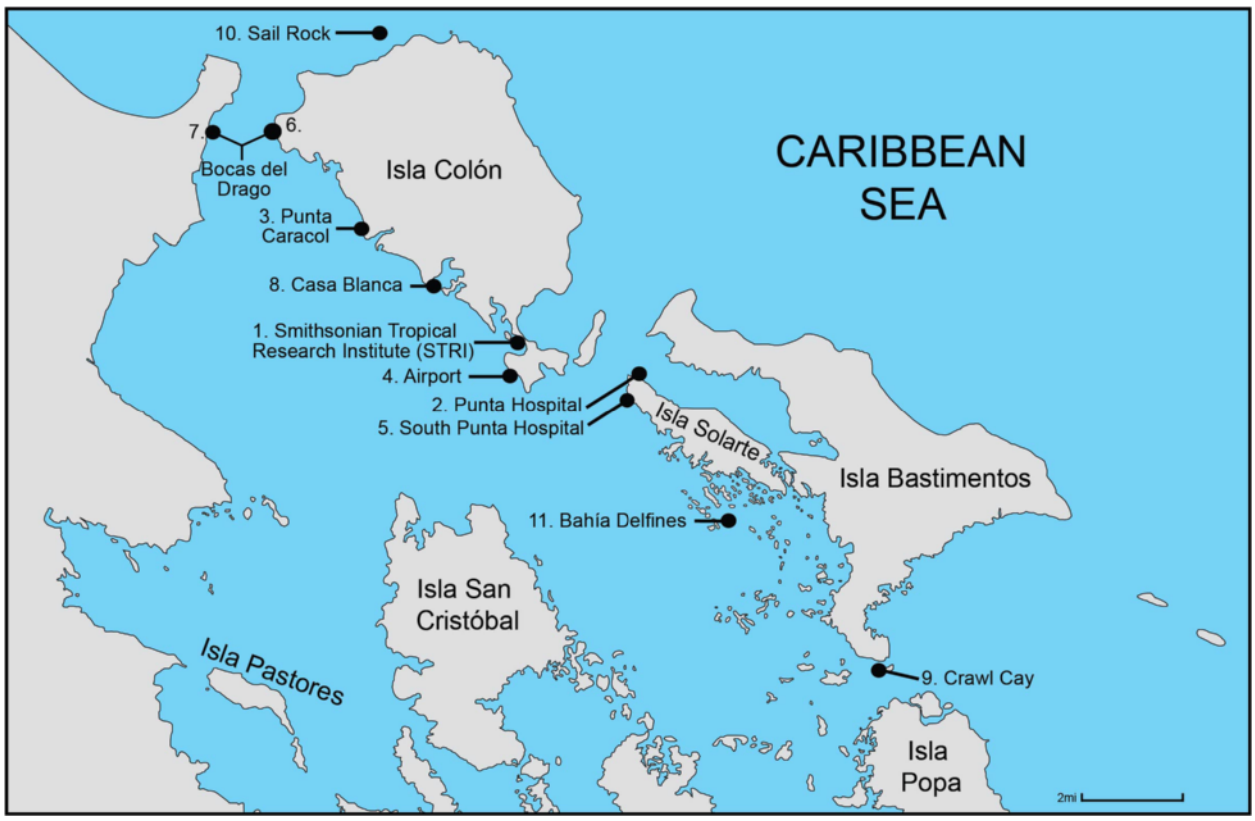

Fig. 1 Map of localities sampled in Bocas del Toro, Panama

Table 1 Number and proportion of species found per clade in Bocas del Toro, Panama

Order	Number of species	Percentage of total	Localities
Cephalaspidea	6	7.3	1, 8–11
Anaspidea	6	7.3	1, 6, 10
Sacoglossa	28	34.1	1–10
Pleurobranchomorpha	2	2.4	2, 4, 9
Nudibranchia	40	48.8	1–11

The highest number of species ($n = 22$) was found at STRI (locality 1), followed by Crawl Cay (locality 9) and Sail Rock (locality 10), and the lowest overall species number ($n = 2$) was recorded in the Panamanian mainland side of Bocas del Drago (locality 7) (Table 2). All sites had species belonging to the clades Nudibranchia and Sacoglossa, except for Little Cay in Bahía Delfines (locality 11), in which sacoglossans were not found. The average search time and number of nudibranch species found per locality were almost 28 h and $n = 5$, respectively. The locality with the highest collecting effort was STRI (locality 1) and the lowest was the Panamanian mainland side of Bocas del Drago (locality 7) (Table 2), which might explain the highest and lowest number of species found. It is also important to note that locality 7 was the only collecting site located off the Panamanian mainland, which contains numerous rivers and is strongly influenced by terrestrial runoff and turbidity in the water. These factors likely reduced the overall abundance of heterobranch sea slugs and impeded attempts to find them. In Sail Rock (locality 10) all the species were found by indirect methods.

In the systematics section below, summarized descriptions and illustrations are provided for described species as well as for those species previously recognized as distinct in other studies. For most species the habitat information (substrate or food source on which specimens were found) is provided. In cases in which the food source is important for field collection or identification, but the animals were not found in association with specific substrates, this information is provided with references. Several sacoglossan species were kept in captivity and the egg masses obtained and examined; brief descriptions of the egg masses are also included. For some species egg mass information is provided with references meaning that these data were not obtained in the course of this study.

Systematics

Clade Nudipleura Wägele & Willan, 2000
Order Pleurobranchomorpha Pelseneer, 1906
Suborder Pleurobranchoidea Gray, 1827
Family Pleurobranchidae Gray, 1827
Genus *Pleurobranchus* Cuvier, 1804
Pleurobranchus areolatus Mörch, 1863
(Fig. 2a)

Synonyms

Pleurobranchus crossei Vayssière, 1896; *Pleurobranchus atlanticus* Abbott, 1949; *Pleurobranchus reesi* White, 1952; *Susania gardineri* White, 1952; *Pleurobranchus evelinae* Thompson, 1977; *Pleurobranchus emys* Ev. Marcus, 1984.

Description

Body oval. Rhinophores rolled and fused at the base, with horizontal striations from base to tip. Dorsum with numerous small, polygonal and flat tubercles. Shell internal. Background color ranges from light brown to deep violet, with varying degrees of opaque white pigment on the tubercles. In some cases the opaque white pigment is arranged in a symmetrical pattern across the body. Up to 150 mm long.

Table 2 Search time and number of species found in each of the 11 sites explored in Bocas del Toro, Panama

Site	Search time (h)	Nudibranchia	Anaspidea	Pleurobranchomorpha	Cephalaspidea	Sacoglossa	Total
1	75.25	10	3	0	1	8	22
2	34.75	3	0	1	0	5	9
3	36	3	0	0	0	1	4
4	25.5	7	0	2	0	2	11
5	18.42	1	0	0	0	4	5
6	21.42	6	1	0	0	2	9
7	2.67	1	0	0	0	1	2
8	22.5	3	0	0	1	2	6
9	44.5	13	0	1	1	3	18
10	4.5	9	2	0	2	3	16
11	22	4	0	0	2	0	6

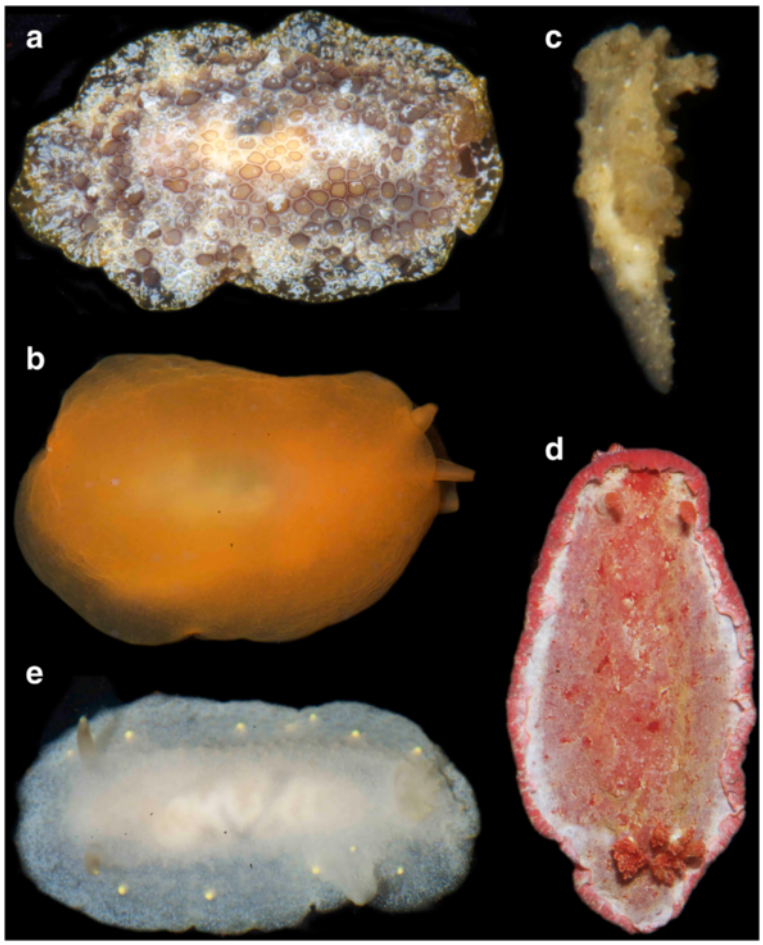

Fig. 2 Nudipleura: Pleurobranchidae, Hexabranchidae, Aegiridae and Cadlinidae. **a** *Pleurobranchus areolatus* Mörch, 1863; **b** *Berthellina quadridens* (Mörch, 1863); **c** *Aegires ortizi* Templado, Luque & Ortea, 1987; **d** *Hexabranchus morsomus* Ev. Marcus & Er. Marcus, 1962; **e** *Cadlina rumia* Er. Marcus, 1955

Distribution

Mexico, Costa Rica, Venezuela, Brazil, Jamaica, Puerto Rico, St. Thomas, Aruba, St. Maarten/St Martin, Bahamas, Bermuda (Valdés *et al*., 2006; Goodheart *et al.,* 2015) and Panama (Collin *et al*., 2005).

Notes

This species is found under rocks and coral rubble and probably feeds on ascidians (Willan, 1984; Valdés *et al.,* 2006). Although there were believed to be six species of *Pleurobranchus* in the Caribbean, the other five (*Pleurobranchus atlanticus* Abbott, 1949, *Pleurobranchus evelinae* Thompson, 1977, *Pleurobranchus crossei* Vayssière, 1896, *Susania gardineri* White, 1952, *Pleurobranchus reesi* White, 1952 and *Pleurobranchus emys* Ev. Marcus, 1984) were recently synonymized with *P. areolatus,* based on molecular and morphological evidence (Goodheart *et al.,* 2015).

Genus *Berthellina* Gardiner, 1936
Berthellina quadridens (Mörch, 1863)
(Fig. 2b)

Description

Body oval, inflated. Dorsum smooth covering the internal shell, which is located over the anterior portion of the viscera. Anterior end of the body with a large oral veil, rhinophores rolled emerging between the veil and the dorsum. Color yellow to orange, semi-translucent. Up to 25 mm long.

Distribution

Mexico, Belize, Colombia, Costa Rica, Panama, Venezuela, Aruba, Curaçao, Haiti, Jamaica, Puerto Rico, Virgin Islands, St. Maarten/St. Martin, St. Lucia, Guadeloupe, Martinique, Barbados, St. Vincent and the Grenadines, Grenada,

Trinidad and Tobago, Brazil (Valdés *et al*., 2006; Camacho-García *et al*., 2014).

Notes
Possibly feeds on sponges (Willan, 1984) and likely on the corals *Orbicella faveolata* (Ellis & Solander, 1786) and *Orbicella annularis* (Ellis & Solander, 1786) (see Vermeij, 2010) as well as on anemones (Marcus & Marcus 1967).

Order Nudibranchia Odhner, 1984
Infraorder Anthobranchia Wägele & Willan, 2000
Family Aegiridae P. Fischer, 1883
Genus *Aegires* Lovén, 1844
Aegires ortizi Templado, Luque & Ortea, 1987
(Fig. 2c)

Description
Body elongate. Tubercles large, varying from conical to mushroom-shaped, with flat tops in some individuals. Gill leaves forming a semicircle on the posterior portion of the dorsum. Background color usually mottled white, sometimes with noticeable brown spots. Up to 8 mm long.

Distribution
Cayman Islands, Bahamas, Venezuela, Cuba (Valdés *et al*., 2006; Caballer Gutiérrez *et al*., 2015) and Panama (present study).

Notes
A single specimen was found on cyanobacteria over coral rubble and sand patches. In the Bahamas this species has been found on algae of the genera *Cladophora* Kützing, 1843 and *Sargassum* Agardh, 1820 (see Redfern, 2001).

Family Hexabranchidae Bergh, 1891
Genus *Hexabranchus* Ehrenberg, 1828
Hexabranchus morsomus Ev. Marcus & Er. Marcus, 1962
(Fig. 2d)

Description
Body oval to elongate. Dorsum with small conical tubercles. Rhinophores club shaped. Gill large, composed of several multi-pinnated leaves. Background color reddish with mottled white and yellow patches on the dorsum. Mantle margin usually curled up over small portion of dorsum covering white areas. Up to 400 mm long.

Distribution
Honduras, Costa Rica, Venezuela, Aruba, Puerto Rico, Virgin Islands, St. Maarten/St. Martin, St. Lucia, Martinique, Antigua, Grenada, St. Vincent and the Grenadines, Trinidad and Tobago (Valdés *et al.*, 2006) and Panama (Collin *et al.*, 2005).

Notes
Found under rocks or coral rubble, primarily on living reefs (Valdés *et al.,* 2006). Defensive behavior consists of the unrolling of the mantle margins to expose bright white areas followed by swimming by contracting the body and mantle margin (Collin *et al.,* 2005). Species of the genus *Hexabranchus* prey on a variety of sponges (McDonald & Nybakken, 1997).

Family Cadlinidae Bergh, 1891
Genus *Cadlina* Bergh, 1879
Cadlina rumia Er. Marcus, 1955
(Fig. 2e)

Description
Body oval, flat, covered with numerous small tubercles. Background color usually translucent white with a few yellow spots (mantle glands). Rhinophores and gill often yellowish brown. Up to 15 mm long.

Distribution
Amphiatlantic. Western Atlantic: Florida, Belize, Panama, Venezuela, Bahamas, Dominican Republic, Jamaica, Puerto Rico, Curaçao, St. Maarten/St. Martin, St. Lucia, St. Vincent & the Grenadines, Grenada, Brazil (Valdés *et al*., 2006; Caballer Gutiérrez *et al*., 2015) and Panama (Collin *et al*., 2005).

Notes
This is the only species of *Cadlina* in the tropical western Atlantic (Edmunds, 1981; Valdés *et al*., 2006, García-García *et al*., 2008). The genus *Cadlina* was recently transferred from the Chromodorididae to the Cadlinidae (Johnson & Gosliner, 2012). In our study *C. rumia* was found under rocks and on various sponges. This species feeds on several types of sponges from different orders (including spiculate and non-spiculate species), exhibiting a not specialized diet preference among the spongivorous dorid nudibranchs (Belmonte *et al*., 2015).

Family Chromodorididae Bergh, 1891
Genus *Tyrinna* Bergh, 1898
Tyrinna evelinae (Er. Marcus, 1958)
(Fig. 3a)

Synonyms
Cadlina burnayi Ortea, 1988.

Description
Body oval to elongate. Background color usually translucent white with a number of orange spots. Mantle margin edged by an opaque white line and white mantle glands with orange tips. Rhinophores and branchial leaves translucent white with opaque white tips. Up to 30 mm long.

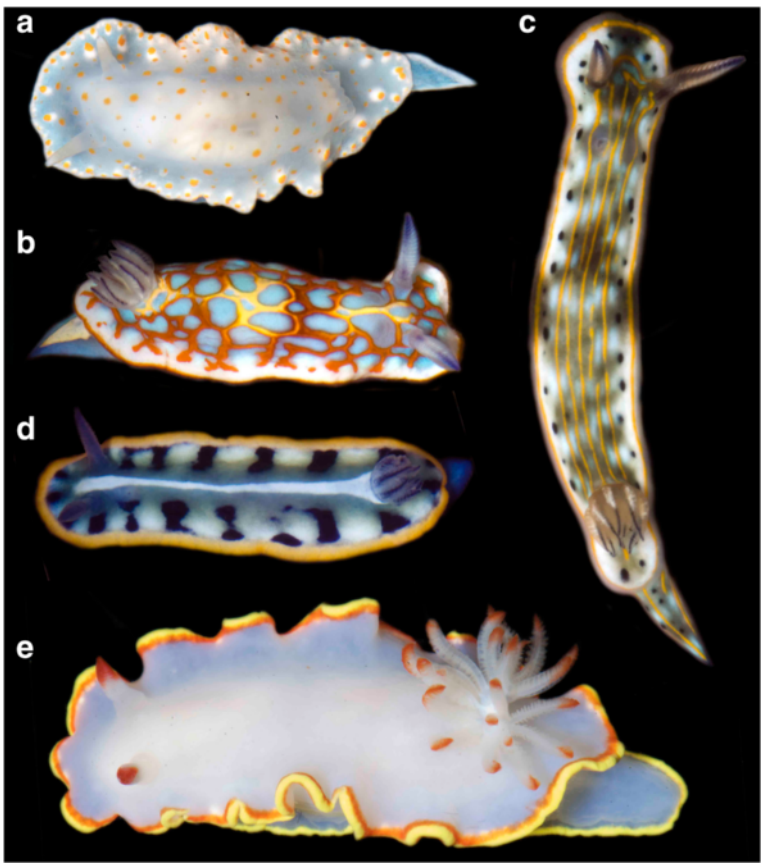

Fig. 3 Nudipleura: Chromodorididae. **a** *Tyrinna evelinae* (Er. Marcus, 1958); **b** *Felimida clenchi* (Russell, 1935); **c** *Felimare fregona* (Ortea & Caballer *in* Ortea *et al*., 2013); **d** *Felimare kempfi* (Ev. Marcus, 1971); **e** *Doriprismatica sedna* (Ev. Marcus & Er. Marcus, 1967)

Distribution

Eastern Atlantic, Eastern Pacific, and Western Atlantic: Costa Rica, Venezuela, Jamaica, Puerto Rico, Dominican Republic, Brazil (Valdés *et al*., 2006; Caballer Gutiérrez *et al*., 2015) and Panama (present study).

Notes

Found under rocks and on various sponges in this study. Belmonte *et al*. (2015) found that *Tyrinna evelinae* in Brazil feeds primarily on dysideid sponges, but also upon an unidentified chalinid species of the order Haplosclerida. This species has planktotrophic development. Caribbean populations are morphologically indistinguishable from Eastern Pacific and Eastern Atlantic populations (Valdés *et al*., 2006).

Genus *Felimida* Ev. Marcus, 1971
Felimida clenchi (Russell, 1935)
(Fig. 3b)

Description

Body oval. Dorsum smooth. Background color pale blue with a dense pattern of red covering the dorsum, but leaving small circular uncovered areas. The red becomes yellow near the rhinophores and gill. Mantle margin with a submarginal white band edged with a red line. Rhinophores and gill white with purple rachises. Up to 30 mm long.

Distribution

Florida, Costa Rica, Panama, Colombia, Venezuela, Bermuda, Cayman Islands, Jamaica, Curaçao, St. Lucia, St. Vincent and the Grenadines (Valdés *et al*., 2006; Caballer Gutiérrez *et al*., 2015).

Notes

Found under rocks or on sponges in this study. Originally a member of the genus *Chromodoris* Alder & Hancock, 1855, this species was recently transferred to *Felimida* by Johnson & Gosliner (2012). This species is part of a complex that comprises *Felimida binza* (Ev. Marcus & Er. Marcus, 1963), *Felimida britoi* (Ortea & Pérez, 1983) and *Felimida neona* (Er. Marcus, 1955). All these species share a similar reticular pattern of yellow and red pigment and morphology (Ortea *et al*., 1994; Valdés *et al*., 2011; Camacho-García *et al*., 2014).

Felimare fregona (Ortea & Caballer *in* Ortea *et al*., 2013)
(Fig. 3c)

Description
Body elongate, narrow, with the posterior portion of foot extending beyond the mantle margin. Background color white with irregular shades of pale blue and gray. Dorsum with three longitudinal yellow lines. Mantle margin edged by an opaque white line with a narrow submarginal band of yellow and a series of black circular spots. Rhinophores white with a purple longitudinal line up from the base. Up to 40 mm long.

Distribution
Venezuela, Puerto Rico, Virgin Islands, Curaçao (Valdés *et al*., 2006), Guadeloupe (Ortea *et al*., 2013), and Panama (present study).

Notes
Feeds on a blue sponge (Valdés *et al.,* 2006). Recently described by Ortea & Caballer *in* Ortea *et al*. (2013) from Guadeloupe. Appears to be the same morphotype illustrated by Valdés *et al*. (2006) as *Hypselodoris* sp. 3.

Genus *Felimare* Ev. Marcus & Er. Marcus, 1967
Felimare kempfi (Ev. Marcus, 1971)
(Fig. 3d)

Description
Body elongate, narrow, with the posterior portion of foot extending slightly beyond the mantle margin. Background color bright blue with a thick yellow line around the mantle margin. A central white line and a series of large black and white spots extend down the dorsum. Rhinophores and gills blue, branchial leaves with black rachises. Up to 20 mm long.

Distribution
Florida, Mexico, Costa Rica, Venezuela, Brazil, Puerto Rico (Valdés *et al*., 2006; Caballer Gutiérrez *et al*., 2015) and Panama (Collin *et al*., 2005)

Notes
This species has previously been placed in the genera *Chromodoris* Alder & Hancock, 1855 (see Collin *et al.,* 2005) and *Mexichromis* Bertsch, 1977. It was recently transferred to *Felimare* by Johnson & Gosliner (2012).

Genus *Doriprismatica* d'Orbigny, 1839
Doriprismatica sedna (Ev. Marcus & Er. Marcus, 1967)
(Fig. 3e)

Synonyms
Chromodoris fayae Lance, 1968.

Description
Body oval. Mantle margin ruffled. Background color white with two colored bands (inner red and outer yellow) bordering the foot and mantle. Upper half of the rhinophoral clubs and tips of the branchial leaves of the gill red. Up to 65 mm long.

Distribution
Eastern Pacific: from the Gulf of California to the Galapagos Islands (Bertsch, 1988) and Western Atlantic: Florida, Belize, Bahamas (Valdés *et al*., 2006) and Panama (present study).

Notes
Found on mangrove roots covered with sponges in this study. The diet of *Doriprismatica sedna* was studied by Padilla-Verdín et al. (2010) on the Pacific coast of Mexico. By examining the stomach content and feces, they found that this species feeds exclusively on spiculated sponges and exhibits a variable diet, which includes 16 different species. Originally described from the Eastern Pacific, records from the Caribbean are considered the result of a recent introduction, presumably human-induced. This species has previously been placed in the genus *Glossodoris* Ehrenberg, 1831 (see Valdés *et al*., 2006), but was recently transferred to *Doriprismatica* by Johnson & Gosliner (2012).

Family Discodorididae Bergh, 1891
Genus *Discodoris* Bergh, 1877
Discodoris branneri MacFarland, 1909
(Fig. 4a–b)

Synonyms
Discodoris evelinae Er. Marcus, 1955; *Discodoris hedgpethi* Ev. Marcus & Er. Marcus, 1960.

Description
Body oval, moderately rigid. Dorsum covered by numerous conical tubercles. Background color variable, from cream to purplish brown, sometimes with black or white patches and spots. Rhinophores and gill usually the same color as the dorsum with white tips. Up to 110 mm long.

Distribution
Florida, Texas, Costa Rica, Honduras, Panama, Colombia, Venezuela, Bahamas, Cayman Islands, Puerto Rico, Jamaica, Barbados, Martinique, St. Lucia, Guadeloupe, St. Vincent and the Grenadines, Brazil (Valdés *et al*., 2006).

Notes
Found under rocks in this study. Members of this family feed on sponges. When disturbed, this species autotomizes parts of the mantle (Valdés *et al*., 2006). This species previously identified as *Discodoris evelinae* Er. Marcus 1955,

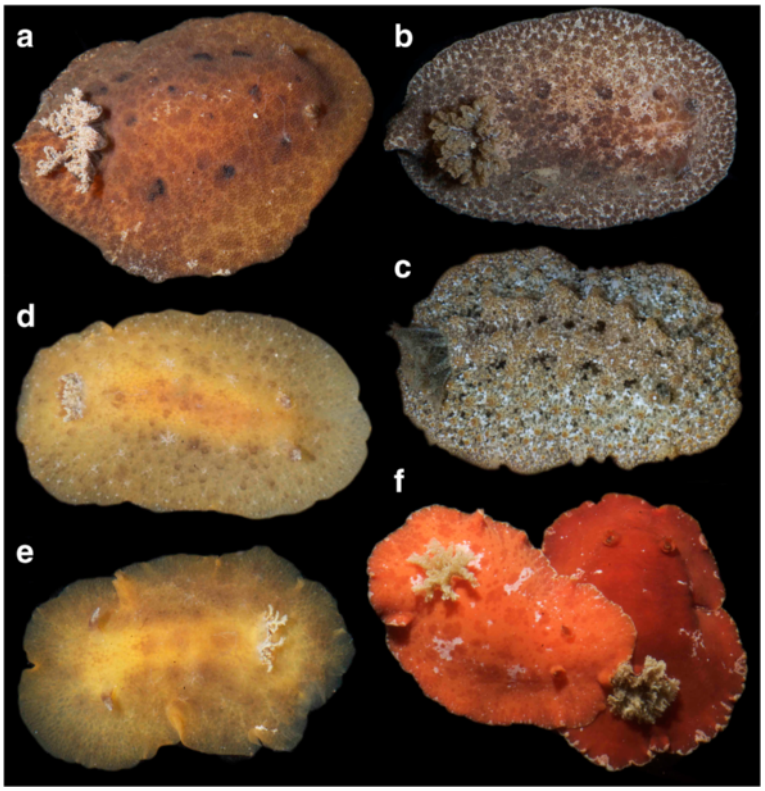

Fig. 4 Nudipleura: Discodorididae. **a**–**b** *Discodoris branneri* MacFarland, 1909; **c** *Sclerodoris prea* (Ev. Marcus & Er. Marcus, 1967); **d** *Geitodoris* cf. *planata* (Alder & Hancock, 1846); **e** *Geitodoris immunda* Bergh, 1894; **f** *Platydoris angustipes* (Mörch, 1863)

but is now accepted as *Discodoris branneri* (see Alvim & Pimenta, 2013).

Genus *Sclerodoris* Eliot, 1904
Sclerodoris prea (Ev. Marcus & Er. Marcus, 1967)
(Fig. 4c)

Description

Body oval, mantle rigid. Dorsum covered with numerous caryophyllidia. Larger tubercles arranged in two rows along the visceral hump, with a longitudinal depression in the center. Rhinophores elongate, gill composed of multipinnate branchial leaves. Background color cream-brown with numerous dark brown spots. Black patches present along the center of the visceral hump. Rhinophores cream with dark spots and gill gray with opaque white spots. Up to 40 mm long.

Distribution

Florida, Venezuela, Bahamas, Jamaica and Barbados (Valdés *et al*., 2006; Caballer Gutiérrez *et al*., 2015) and Panama (present study).

Notes

Found under rocks in this study. This species probably feeds on sponges.

Geitodoris cf. *planata* (Alder & Hancock, 1846)
(Fig. 4d)

Synonyms

Doris testudinaria Risso, 1826; *Doris complanata* Verrill, 1880.

Description

Body oval, mantle rigid. Dorsum covered by rounded, stalked tubercles. Background color grayish-brown with some dark brown irregular patches. The color fades and becomes more translucent towards the mantle margin. Larger tubercles surrounded with opaque white pigment. Rhinophores and gill usually the same color as the dorsum with white tips. Up to 65 mm long.

Distribution

Mediterranean Sea, North Atlantic Ocean, North Sea (Whittaker, 2013); Western Atlantic: New Jersey, St. Lucia (Valdés *et al*., 2006) and Panama (present study).

Notes
Found in coral rubble in a predominately sea grass habitat in this study. Feeds on sponges (McDonald & Nybakken, 1997). Originally described from Europe, Caribbean populations are morphologically similar but almost certainly distinct. Alvim & Pimenta (2013) regarded Caribbean animals as *Geitodoris pusae* (Er. Marcus, 1955), but no molecular studies have been conducted to compare animals from both sides of the Atlantic Ocean. Further research is necessary to clarify the status of this species.

Genus *Geitodoris* Bergh, 1891
Geitodoris immunda Bergh, 1894
(Fig. 4e)

Description
Body oval, mantle moderately rigid. Dorsum with a complex network of low ridges covering the entire surface, with some conical tubercles at the intersections. Branchial sheaths with characteristic wavy edges. Background color grayish-brown with numerous opaque white dots and some darker brown areas. Rhinophores and gill brown with white tips. Up to 43 mm long.

Distribution
Gulf of Mexico, Costa Rica, Venezuela, Brazil (Valdés *et al*., 2006, Moretzsohn *et al.*, 2011) and Panama (present study).

Notes
Found under coral rubble in a reef habitat in this study. This species as well as the preceding one are similar to *Geitodoris pusae* (Er. Marcus, 1955), redescribed by Alvim & Pimenta (2013). Further review is necessary to clarify the taxonomic status of these taxa.

Genus *Platydoris* Bergh, 1877
Platydoris angustipes (Mörch, 1863)
(Fig. 4f)

Synonyms
Platydoris alaleta Bergh, 1877; *Platydoris rubra* White, 1952.

Description
Body oval, mantle rigid. Dorsum flattened, covered with caryophyllidia. Background color ranges from reddish-brown to red or orange with scattered white specks often clustered in 3–4 dense groups. Mantle margin often darker or lighter than the rest of the mantle with proportionally more white patches. Rhinophores dark brown with cylindrical apex. Gill translucent straw-colored often with numerous opaque white spots. Up to 150 mm long.

Distribution
Central American mainland, from Florida to Panama, also Greater Antilles, Cayman Islands, Lesser Antilles, Turks and Caicos, and Brazil (Valdés *et al*., 2006; Camacho-García *et al*., 2014; Caballer Gutiérrez *et al*., 2015).

Notes
Found under rocks in this study. This species possibly has lecithotrophic development. Additional information and descriptions provided by Alvim & Pimenta (2013).

Genus *Diaulula* Bergh, 1878
Diaulula phoca (Ev. Marcus & Er. Marcus, 1967)
(Fig. 5a)

Description
Body oval, mantle rigid. Dorsum covered with small caryophyllidia. Body, rhinophores, and gill dark purplish brown with numerous small opaque white dots. Up to 50 mm long.

Distribution
Florida, Honduras, Costa Rica, Brazil (Valdés *et al*., 2006, García-García *et al*., 2008) and Panama (present study).

Notes
Feeds on sponges (Marcus & Marcus 1967). Originally named *Discodoris phoca* Marcus & Marcus 1967 it is considered a member of *Diaulula* because of the presence of caryophyllidia.

Genus *Jorunna* Bergh, 1876
Jorunna cf. *spazzola* (Er. Marcus, 1955)
(Fig. 5b–c)

Synonyms
Discodoris mortenseni Ev. Marcus & Er. Marcus, 1963.

Description
Body oval, mantle rigid. Dorsum flattened, covered with small caryophyllidia. Branchial leaves very short. Background color translucent gray with a few darker gray or brown patches over the dorsum. Mantle margin surrounded by small opaque white glands. Rhinophores and gill the same color as the rest of the body. Up to 18 mm long.

Distribution
Florida, Honduras, Costa Rica, Venezuela, Cuba, Curaçao, Barbados, Virgin Islands, Turks and Caicos, Brazil (Valdés *et al*., 2006; Camacho-García *et al*., 2014; Caballer Gutiérrez *et al*., 2015) and Panama (present study).

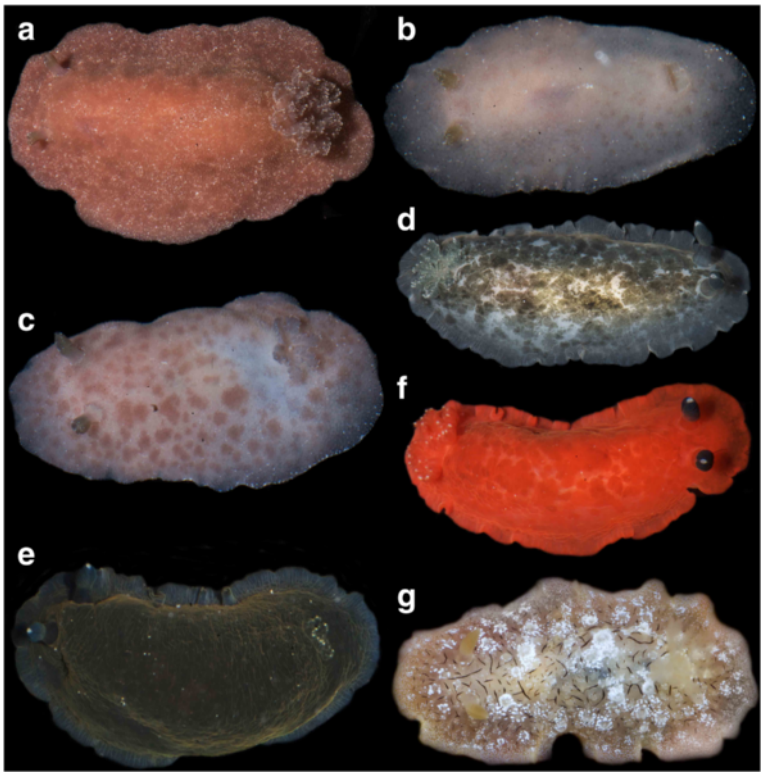

Fig. 5 Nudipleura: Discodoridae and Dendrodoridae. **a** *Diaulula phoca* (Ev. Marcus & Er. Marcus, 1967); **b**–**c** *Jorunna* cf. *spazzola* (Er. Marcus, 1955); **d**–**f** *Dendrodoris krebsii* (Mörch, 1863) **g** *Doriopsilla nigrolineata* Meyer, 1977

Notes

Found under rocks in this study. Known to feed on sponges of the order Haplosclerida (Belmonte *et al.*, 2015) on which it is well camouflaged. This species is able to quickly change colors as a response to unknown environmental cues (Valdés *et al.,* 2006). Camacho-García *et al.* (2014) suggested Caribbean animals identified as *Jorunna spazzola* could constitute a distinct species, because they display external differences with the original description from southern Brazil.

Family Dendrodoridae O'Donoghue, 1924
Genus *Dendrodoris* Ehrenberg, 1831
Dendrodoris krebsii (Mörch, 1863)
(Fig. 5d–f)

Description

Body oval to elongate, dorsum soft, lacking tubercles. Background color extremely variable, white, black, orange, red or light green, with or without spots of red, black, gray or white. Rhinophores and gill usually the same color as the rest of the body with white tips. Up to 150 mm long.

Distribution

North and south American mainland from Georgia to Brazil, Bahamas, Cuba, Cayman Islands, Jamaica, Dominican Republic, Virgin Islands, St. Martin, Antigua, Guadeloupe, Martinique, St. Lucia, St. Vincent and the Grenadines, Barbados, Aruba, Curaçao, Bonaire, Grenada (Valdés *et al.*, 2006; Camacho-García *et al.*, 2014).

Notes

Found under coral rubble or rocks in this study. This is one of the most common species of Nudibranchia in the Caribbean. Members of this family are suctorial sponge feeders. Belmonte *et al.* (2015) recorded active feeding of *Dendrodoris krebsii* upon a haplosclerid sponge.

Genus *Doriopsilla* Bergh, 1880
Doriopsilla nigrolineata Meyer, 1977
(Fig. 5g)

Synonyms

Doriopsilla areolata nigrolineata Meyer, 1977.

Description

Body oval to elongate. Dorsum rigid, covered with rounded tubercles. Background color translucent white to orange, with a series of irregular black lines over the entire dorsum. Bases of tubercles densely spotted with white, rhinophores and gill yellow. Up to 30 mm long.

Distribution
Panama, Honduras (Valdés *et al*., 2006).

Notes
Found in 3–6 m of water. Previously considered a subspecies of *Doriopsilla areolata* Bergh, 1880 by Valdés & Ortea (1997), but Valdés & Hamann (2008) confirmed that it is a distinct species.

Infraorder Cladobranchia Willan & Morton, 1984
Family Tritoniidae Lamarck, 1801
Genus *Tritonia* Cuvier, 1798
Tritonia hamnerorum Gosliner & Ghiselin, 1987
(Fig. 6a)

Description
Body elongate and narrow. Rhinophoral sheaths elevated with an irregular edge. Cerata short and branched. Edge of the oral veil with relatively long appendages, rhinophores long, branched. Background color translucent gray with a series of irregular, longitudinal, thin white lines that run along the length of the dorsum. Up to 15 mm long.

Distribution
Florida, Mexico, Belize, Bahamas, Cayman Islands (Valdés *et al*., 2006) and Panama (present study).

Notes
Found on gorgonian sea fans in dense aggregations in this study. This species reportedly feeds on the octocorals *Gorgonia ventalina* Linnaeus, 1758 and *Gorgonia flabellum* Linnaeus, 1758. It sequesters chemicals from the sea fans and stores them for its own defense (Cronin *et al*., 1995).

Tritonia bayeri Ev. Marcus & Er. Marcus, 1967
(Fig. 6b)

Synonyms
Tritonia bayeri misa Ev. Marcus & Er. Marcus, 1967.

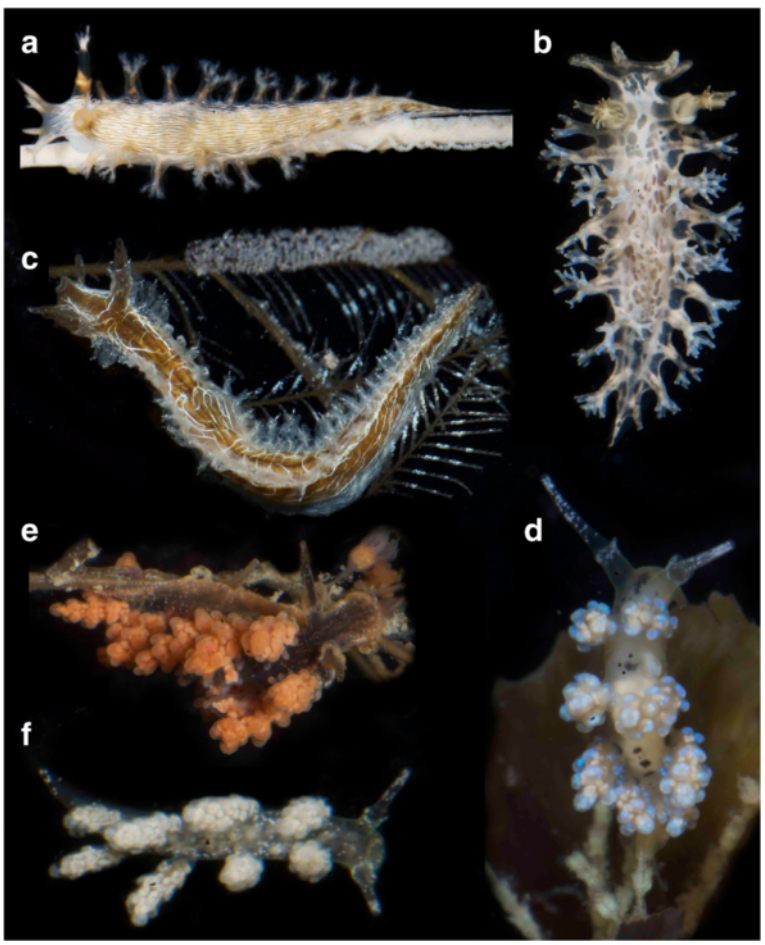

Fig. 6 Nudipleura: Tritoniidae, Lomanotidae and Dotidae. **a** *Tritonia hamnerorum* Gosliner & Ghiselin, 1987 on substrate with egg mass; **b** *Tritonia bayeri* Ev. Marcus & Er. Marcus, 1967. **c** *Lomanotus vermiformis* Eliot, 1908, on substrate with egg mass; **d** *Doto escatllari* Ortea, Moro & Espinosa, 1998, on substrate; **e** *Doto chica* Ev. Marcus & Er. Marcus, 1960, on substrate; **f** *Doto* cf. *wildei* Er. Marcus & Ev. Marcus, 1970

Description
Body elongate and narrow. Rhinophoral sheaths elevated with an irregular edge. Cerata relatively short and branched. Edge of the oral veil with relatively long appendages, rhinophores long, branched. Background color translucent gray with a distinctive reticulate network of opaque white across the dorsum. Up to 11 mm long.

Distribution
Georgia, Florida, Belize, Honduras, Cayman Islands, Virgin Islands, Guadaloupe, Barbados (Valdés *et al*., 2006) and Panama (present study).

Notes
Found on gorgonians and coral rubble in this study. Inhabits reefs down to 77 m depth. This species feeds on the octocorals *Briareum asbestinum* (Pallas, 1766), *Leptogorgia virgulata* (Lamarck, 1815) and *Pseudopterogorgia* sp. (McDonald & Nybakken, 1999).

Family Lomanotidae Bergh, 1890
Genus *Lomanotus* Vérany, 1844
Lomanotus vermiformis Eliot, 1908
(Fig. 6c)

Synonyms
Lomanotus stauberi Clark & Goetzfried, 1976.

Description
Body very elongate and narrow. Rhinophoral sheaths with papillae and elevated to cover three quarters of the rhinophores. Cerata very short and pointed. Background color brown with dark brown spots and opaque yellow lines. Opaque white reticulations also present across the body. Up to 40 mm long.

Distribution
Circumtropical. Western Atlantic: Florida, Bahamas (Valdés *et al*., 2006) and Panama (Collin *et al*., 2005).

Notes
This species feeds on hydroids of the genus *Macrorhynchia* Kirchenpauer, 1872 (McDonald & Nybakken, 1999). In this study was found feeding on an unidentified species of hydroid (illustrated), on which it is extremely cryptic. This species can swim with lateral flexions of the body when disturbed (Valdés *et al*., 2006).

Family Dotidae Gray, 1853
Genus *Doto* Oken, 1815
Doto escatllari Ortea, Moro & Espinosa, 1998
(Fig. 6d)

Description
Body short and narrow. Rhinophores smooth. Rhinophoral sheaths with small frontal extensions. Cerata large with rounded tubercles; apical tubercles much larger than the rest. Background color translucent gray with a series of dark brown spots on the dorsum. Cerata with dark brown branches of the digestive gland and bluish tubercles, rhinophores with opaque white dots. Up to 5 mm long.

Distribution
Costa Rica, Barbados (Valdés *et al*., 2006) and Panama (present study).

Notes
Found on hydroids in this study.

Doto chica Ev. Marcus & Er. Marcus, 1960
(Fig. 6e)

Synonyms
Doto fragilis umia Ev. Marcus & Er. Marcus, 1969.

Description
Body narrow and elongate. Rhinophores smooth, rhinophoral sheaths with small posterior extensions. Cerata large, with rounded tubercles; apical tubercles much larger than the rest. Background color translucent gray with a dense series of dark brown spots and a less dense set of opaque white spots on the dorsum. Cerata with orange extensions of the digestive gland. Up to 5 mm long.

Distribution
Florida, Mexico, Costa Rica, Venezuela, Puerto Rico, Curaçao, Cuba, Brazil (Valdés *et al*. 2006; García-García *et al*., 2008; Crescini *et al*., 2013) and Panama (present study).

Notes
Found on hydroids in this study. Known to feed on hydroids of the genus *Eudendrium* Ehrenberg, 1834 (Ev. Marcus, 1972).

Doto cf. *wildei* Er. Marcus & Ev. Marcus, 1970
(Fig. 6f)

Synonyms
Doto caramella wildei Er. Marcus & Ev. Marcus, 1970.

Description
Body narrow and elongate. Rhinophores smooth with tight rhinophoral sheaths. Cerata with rounded tubercles; apical tubercles much larger than the rest. Cerata spaced out along the dorsum. Background color translucent gray with a series of opaque white spots on the dorsum. Cerata

with cream or white extensions of the digestive gland. Up to 4 mm long.

Distribution

Curaçao (Valdés *et al*., 2006) and Panama (present study).

Notes

Found on hydroids. The identification of this specimen is uncertain; it looks most similar to *Doto wildei* but lacks pseudogills on the cerata. The systematics of *Doto* in the Caribbean region is in need of major revision and until the taxonomy is clarified many species identifications remain tentative.

Family Flabellinidae Bergh, 1889
Genus *Flabellina* Gray, 1833
Flabellina engeli Ev. Marcus & Er. Marcus, 1968
(Fig. 7a)

Description

Body elongate, narrowing posteriorly. Rhinophores lamellate, club-shaped, oral tentacles long. Cerata arranged into clusters in two rows along the dorsum. Background color translucent gray with thick white or yellow patches running between the cerata clusters, on the margin of the dorsum. A submarginal row of opaque white spots present along the sides of the body. Three white or yellow patches on the head. Oral tentacles translucent, white at the tips; rhinophores with white bands. Cerata translucent with a brown or orange band about a third of the way down from the tip. Up to 25 mm long.

Distribution

Florida, Costa Rica, Colombia, Venezuela, Barbados, Cuba, Puerto Rico, Curaçao, St. Lucia, Martinique, Granada, Brazil (Valdés *et al*., 2006; García-García *et al*., 2008; Caballer Gutiérrez *et al*., 2015) and Panama (present study).

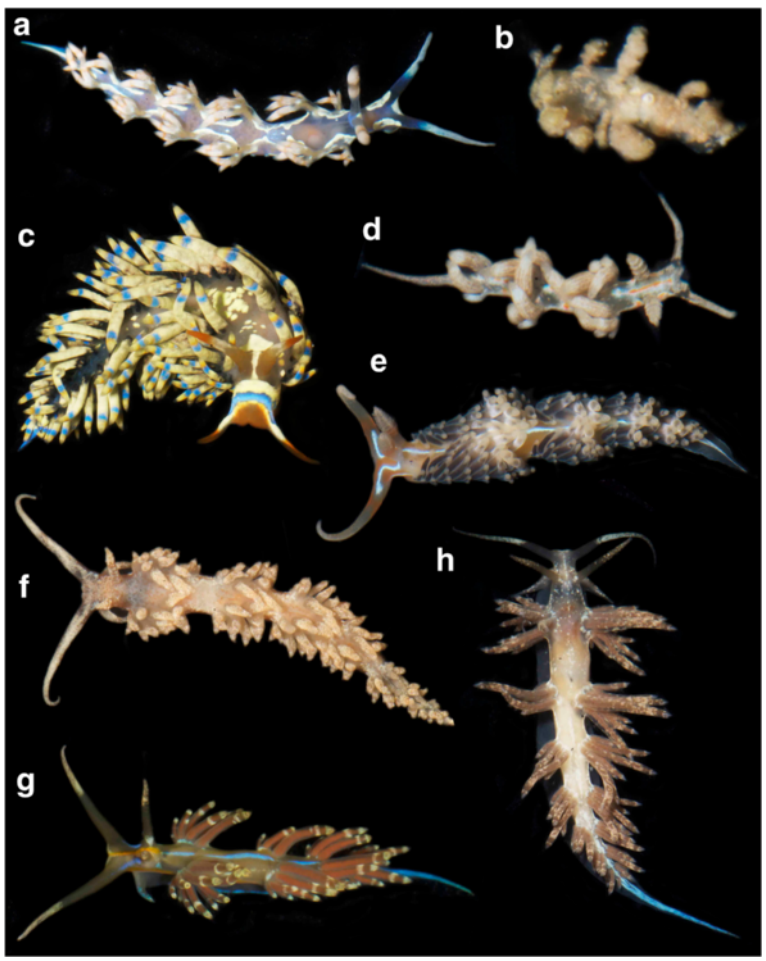

Fig. 7 Nudipleura: Flabellinidae, Eubranchidae, Tergipedidae, and Facelinidae. **a** *Flabellina engeli* Ev. Marcus & Er. Marcus, 1968; **b** *Eubranchus conicla* (Er. Marcus, 1958); **c** *Cuthona* cf. *caerulea* (Montagu, 1804); **d** *Nanuca sebastiani* Er. Marcus, 1957; **e** *Phidiana lynceus* Bergh, 1867; **f** *Palisa papillata* Edmunds, 1964; **g** *Dondice occidentalis* (Engel, 1925); **h** *Dondice parguerensis* Brandon & Cutress, 1985

Notes
One specimen found on a living blade of sea grass in 1 m of water.

Family Eubranchidae
Genus *Eubranchus* Forbes, 1838
Eubranchus conicla (Er. Marcus, 1958)
(Fig. 7b)

Synonyms
Eubranchus convenientis Ortea & Caballer, 2002.

Description
Body elongate. Rhinophores smooth, oral tentacles short. Cerata tuberculate, few in number, arranged in two simple rows. Background color translucent gray or brown with numerous white dots. Rhinophores and oral tentacles sometimes ringed with brown. Cerata white, sometimes with brown or green spots. Up to 4 mm long.

Distribution
Florida, Honduras, Costa Rica, Venezuela, Jamaica, Barbados, Tobago, Brazil (Valdés *et al*., 2006; Caballer Gutiérrez *et al*., 2015) and Panama (present study).

Notes
Found on *Sargassum* in less than 3 m of water.

Family Tergipedidae Bergh, 1889
Genus *Cuthona* Alder & Hancock, 1855
Cuthona cf. *caerulea* (Montagu, 1804)
(Fig. 7c)

Synonyms
Eolidia bassi Vérany, 1846; *Eolis glotensis* Alder & Hancock, 1846; *Eolis deaurata* Dalyell, 1853; *Eolis molios* Herdman, 1881.

Description
Body elongate. Rhinophores smooth, oral tentacles relatively short. Cerata numerous on both sides of the dorsum with a small empty space down the middle of the dorsum. Background color translucent gray with a bright blue patch, and sometimes a yellow patch, on the head. Oral tentacles yellow at the base, orange at the tips. Rhinophores with a translucent base, a central white or yellow area and orange-brown tips. Cerata translucent white, gray or yellow, with a blue band followed by a bright yellow band near the apex. Up to 25 mm long.

Distribution
Possibly amphiatlantic. Western Atlantic: Florida to Brazil (Valdés *et al*., 2006) including Panama (present study).

Notes
The animals here illustrated are tentatively identified as the European species *Cuthona caerulea*, but the coloration of the head, with a conspicuous blue patch, is different; they probably constitute an undescribed species. Found on hydroids in this study. This species has been recorded feeding upon hydroids of several different genera (McDonald & Nybakken, 1999).

Family Facelinidae Bergh, 1889
Genus *Nanuca* Er. Marcus, 1957
Nanuca sebastiani Er. Marcus, 1957
(Fig. 7d)

Description
Body elongate. Rhinophores annulate; oral tentacles long. Cerata arranged in two rows of clusters (with 3–5 cerata each) on the dorsum. Background color translucent green with numerous opaque white spots and a series of areas with blue and/or white with orange spots forming a cross-like pattern. Cerata with longitudinal opaque white lines with a white, narrow tip. Up to 12 mm long.

Distribution
Mexico, Costa Rica, Venezuela, Curaçao, Bonaire, Martinique, Cuba, Cayman Islands, Virgin Islands, Barbados, Bermuda, Brazil (Valdés *et al*., 2006; Caballer Gutiérrez *et al*., 2015) and Panama (present study).

Notes
This species was found in *Sargassum* algae with sertularid hydroids in this study.

Genus *Phidiana* Gray, 1850
Phidiana lynceus Bergh, 1867
(Fig. 7e)

Synonyms
Phidiana selencae Bergh, 1879; *Phidiana brevicauda* Engel, 1925.

Description
Body elongate and narrow. Rhinophores annulate, oral tentacles long. Cerata elongate densely covering the dorsum, except for the dorsal mid-line. Background color translucent gray with a dorsal white line that splits on the head and continues into the oral tentacles. The line can be narrow, broad or absent. Cerata with white apices. Orange pigment on the oral tentacles and rhinophores. Up to 45 mm long.

Distribution
Florida, Mexico, Costa Rica, Panama, Colombia, Venezuela, Curaçao, Aruba, Bonaire, Jamaica, Bahamas, Virgin Islands,

Guadeloupe, Martinique, St. Maarten/St. Martin, St. Lucia, Barbados, St. Vincent and the Grenadines, Brazil. Ghana, Canary Islands (Valdés *et al*., 2006; García-García *et al*., 2008).

Notes

Found under rocks in this study. Known to feed on hydroids (McDonald & Nybakken, 1997). Shows intraspecific variation in rhinophores and head morphology (Valdés *et al*., 2006).

Genus *Palisa* Edmunds, 1964
Palisa papillata Edmunds, 1964
(Fig. 7f)

Description

Body elongate. Rhinophores tuberculate; oral tentacles long. Cerata arranged in clusters forming a single row along each side of the dorsum. Background color translucent gray with numerous opaque white spots on both the dorsum and cerata. Cerata with a pale blue digestive gland and characteristic black or dark brown spots at the base. Up to 15 mm long.

Distribution

Florida, Jamaica (Valdés *et al*., 2006) and Panama (present study).

Notes

Found among algae in this study, probably feeding on epiphytic hydroids.

Genus *Dondice* Er. Marcus, 1958
Dondice occidentalis Engel, 1925
(Fig. 7g)

Description

Body elongate, tapering toward the posterior end. Rhinophores annulate, long; oral tentacles longer than the rhinophores. Cerata arranged in clusters along two rows on the dorsum. Background color translucent gray with a yellow or orange median line of variable width, running from the head to the anterior end, between the rhinophores. A white or blue broken line down the dorsal mid-line from behind the rhinophores to the posterior end of the body is sometimes present. Opaque white spots sometimes present on the dorsum. Oral tentacles translucent or light blue at the base, becoming white towards the tips. Cerata translucent gray, often with large blue or white bands covering the upper two-thirds of each ceras. Up to 50 mm long.

Distribution

Florida, Mexico, Belize, Costa Rica, Colombia, Venezuela, Curaçao, Bonaire, Venezuela, Bermudas, Bahamas, Cayman Islands, Jamaica, Turks and Caicos, Grenada, St. Maarten/St. Martin, Martinique, Trinidad, Brazil (Valdés *et al*., 2006; Caballer Gutiérrez *et al*., 2015) and Panama (present study).

Notes

Found on hydroids in this study. This species feeds on hydroids of the genus *Eudendrium* and *Amathia* Lamouroux, 1812 (see McDonald & Nybakken, 1999). It easily sheds the cerata when disturbed. According to Gonzalez *et al*. (2013), *Dondice occidentalis* and *Dondice parguerensis* probably represent an example of incipient sympatric speciation. Molecular analyses support partially the differentiation of these species, but are inconclusive. Further research is needed in order to resolve this species complex.

Dondice parguerensis Brandon & Cutress, 1985
(Fig. 7h)

Description

Body elongate, tapering toward the end. Rhinophores annulate, oral tentacles long. Cerata abundant, arranged in clusters along two rows on the dorsum. Background color translucent brown with a white median line from the head that extends posteriorly. Oral tentacles and rhinophores both translucent brown at the base and white on the distal half. Cerata translucent brown with white tips. Up to 48 mm long.

Distribution

Puerto Rico, Panama, Venezuela, Guadeloupe (Collin *et al*., 2005; Valdés *et al*., 2006; Mariño *et al*., 2011; Ortea *et al*., 2013).

Notes

This species is found exclusively on the tentacles of the upside-down jellyfish *Cassiopea* Péron & Lesueur, 1810 in shallow mangrove areas. The divergence of this species from the close relative *Dondice occidentalis* was recently investigated by Gonzalez *et al.,* 2013 (see above). Previously reported from Panama as *D. occidentalis* (Collin *et al*., 2005).

Family Aeolidiidae Gray, 1827
Genus *Berghia* Trinchese, 1877
Berghia rissodominguezi Muniain & Ortea, 1999
(Fig. 8a)

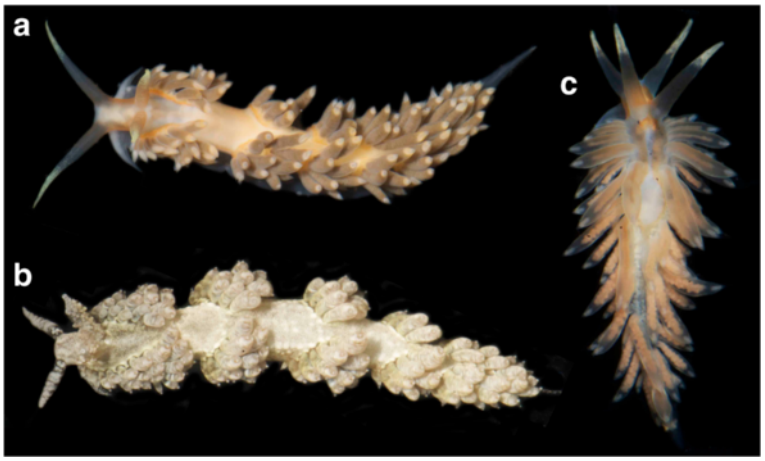

Fig. 8 Nudipleura: Aeolidiidae. **a** *Berghia rissodominguezi* Muniain & Ortea, 1999; **b** *Berghia creutzbergi* Er. Marcus & Ev. Marcus, 1970; **c** *Anteaeolidiella lurana* (Ev. Marcus & Er. Marcus, 1967)

Description

Body narrow and elongate. Oral tentacles longer than the rhinophores. Cerata moderately elongate, cylindrical, with round apices and constant diameter throughout most of their length. Rhinophores densely papillate on the posterior side. Background color translucent white with oblique orange lines on the borders of the insertion of the cerata. Cerata translucent with reddish brown diverticula and white to yellow apices. Rhinophores bright orange with yellow or cream pigmentation on the apical portion. Up to 52 mm long.

Distribution

Florida, Venezuela, Curaçao, Jamaica, St. Lucia, Guadeloupe, Brazil, Argentina (Valdés *et al.*, 2006; Carmona *et al.*, 2014b; Ortea *et al.*, 2013; Caballer Gutiérrez *et al.*, 2015) and Panama (present study).

Notes

Found under rocks in intertidal areas in this study. Feeds on anemones. It can autotomize the cerata when being handled. Carmona *et al.* (2014b) clarified the misidentifications that had been published for the western Atlantic.

Berghia creutzbergi Er. Marcus & Ev. Marcus, 1970
(Fig. 8b)

Synonyms

Milleria ritmica Ortea, Caballer & Espinosa, 2003.

Description

Body elongate. Rhinophores tuberculate. Cerata arranged in two rows of clusters along the dorsum. Background color translucent gray or brown with numerous opaque white spots covering the majority of the dorsum and cerata. Cerata with longitudinal opaque white lines and white, narrow tips. Up to 30 mm long.

Distribution

Tropical western Atlantic, Florida, Costa Rica, Venezuela, Cuba, Barbados, Bahamas, Cayman Islands, Curaçao, Brazil (Valdés *et al.*, 2006; Carmona *et al.*, 2014b) and Panama (present study).

Notes

The single specimen in this study was found under a rock in a seagrass bed. The cerata of this species rock from side to side distinctively while the animal is in motion (Valdés *et al.*, 2006). The genus *Berghia* was recently confirmed as the correct placement for this species (Carmona *et al.*, 2014b).

Genus *Anteaeolidiella* M.C. Miller, 2001
Anteaeolidiella lurana (Ev. Marcus & Er. Marcus, 1967)
(Fig. 8c)

Description

Body elongate. Rhinophores smooth, about the same length as the oral tentacles. Cerata covering most of the dorsum except for the dorsal mid-line. Background color translucent gray with orange pigmentation on the head, behind the rhinophores, and along the edges of the dorsum. Rhinophores and oral tentacles with cream or yellow tips. Cerata translucent with orange digestive diverticula and white cnidosacs. Up to 10 mm long.

Distribution

Amphiatlantic. Western Atlantic: Caribbean Sea, Brazil, Bermuda (Carmona *et al.* 2014a; Caballer Gutiérrez *et al.*, 2015) and Panama (present study).

Notes

Carmona *et al.* (2013) recently confirmed the validity of the genus *Anteaeolidiella*. Additional information on this species can be found in Carmona *et al.* (2014a).

Clade Euopisthobranchia Jörger, Stöger, Kano, Fukuda, Knebelsberger & Schrödl, 2010
Order Cephalaspidea P. Fischer, 1883
Family Haminoeidae Pilsbry, 1895
Genus *Haminoea* Turton & Kingston, 1830
Haminoea elegans (Gray, 1825)
(Fig. 9a)

Synonyms

Bulla guildinguii Swainson, 1840; *Bulla diaphana* Gould, 1852; *Haminoea taylorae* Petuch, 1987.

Description

Shell external, thin, translucent. Body wide and elongate, with large parapodia covering the anterior part of the shell. Shell with numerous and conspicuous spiral grooves crossed by growth lines. Cephalic shield deeply notched with reduced tentacles. Background color translucent yellowish gray with numerous black and opaque white. Up to 35 mm long.

Distribution

Florida to Brazil, Greater and Lesser Antilles, Bermuda and Bahamas (Valdés *et al.*, 2006; Camacho-García *et al.*, 2014).

Notes

Found on dense bacterial mats in shallow water, about 1 m depth.

Haminoea succinea (Conrad, 1846)
(Fig. 9b)

Synonyms

Haminoea solidor Vanatta, 1901.

Description

Shell external, rounded, translucent white. Body elongate, with a short and broad cephalic shield having two lateral, very short and wide extensions. Parapodia very short, not covering any portion of the shell. Posterior end of the foot broad and rounded. Background color

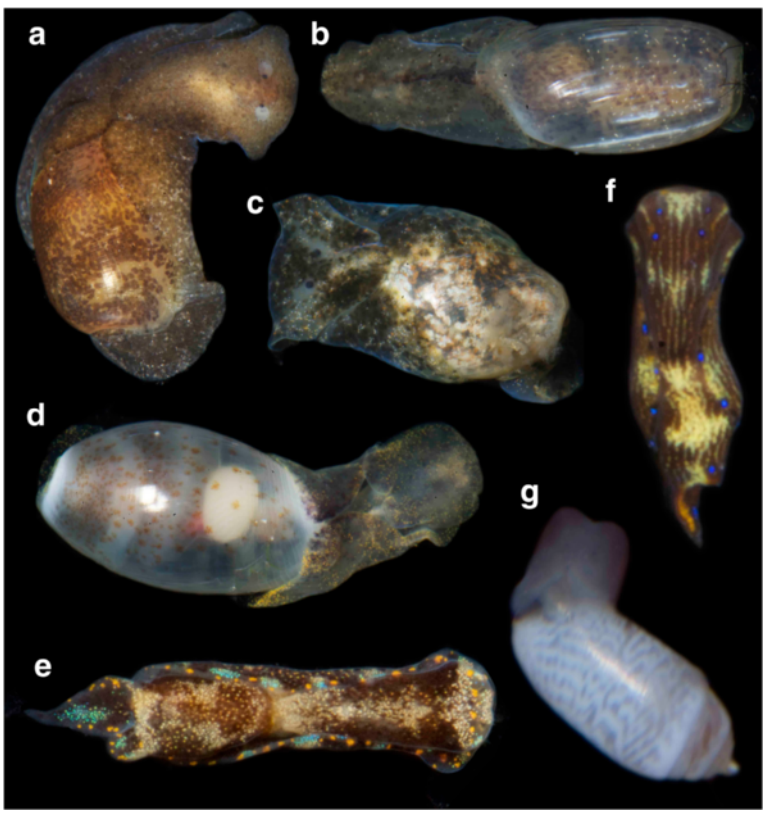

Fig. 9 Euopisthobranchia: Haminoeidae, Aglajidae and Acteocinidae. **a** *Haminoea elegans* (Gray, 1825); **b** *Haminoea succinea* (Conrad, 1846); **c** *Haminoea antillarum* (d'Orbigny, 1841); **d** *Atys caribaeus* (d'Orbigny, 1841); **e** *Chelidonura berolina* Er. Marcus & Ev. Marcus, 1970; **f** *Navanax gemmatus* (Mörch, 1863); **g** *Acteocina candei* (d'Orbigny, 1842)

translucent gray with numerous black spots and some opaque white dots. Up to 20 mm long.

Distribution
Florida. Louisiana, Texas, Mexico, Colombia, Venezuela, Bermuda, Puerto Rico, St. Maarten/St. Martin, St. Barthelemy (Valdés *et al*., 2006) and Panama (present study).

Notes
Found on soft bottoms in protected areas near mangrove roots in this study.

Haminoea antillarum (d'Orbigny, 1841)
(Fig. 9c)

Synonyms
Bulla cerina Menke, 1853; *Haminea guadaloupensis* G.B. Sowerby II, 1868.

Description
Shell external, rounded, lacking any marking other than light growth lines. Shell translucent, showing through the viscera with orange and dark brown spotting. Cephalic shield with two extensions visible. Head with two conspicuous eye spots on the dorsal side. Foot broad on the posterior end. Small parapodial flaps cover the anterior portion of the shell. Up to 40 mm long.

Distribution
From Florida to Brazil, including Cuba, Cayman Islands, Jamaica, Puerto Rico, Virgin Islands, Guadeloupe, Bermuda (Valdés *et al*., 2006; García-García *et al*., 2008; Caballer Gutiérrez *et al*., 2015).

Notes
Typically found on red algae in highly turbulent areas. As with other Haminoeidae, this species is herbivorous (Capper & Paul, 2008). It is a common species in the intertidal zone.

Genus *Atys* Leach, 1816
Atys caribaeus (d'Orbigny, 1841)
(Fig. 9d)

Synonymy
Bulla speciosa A. Adams, 1850.

Description
Shell external, elongate, translucent, with conspicuous spiral grooves near the anterior and posterior ends. Body very elongate, with a deeply notched cephalic shield (posteriorly). Parapodia short, covering a small portion of the anterior end of the shell. Background color translucent white with irregular opaque white spots and some black dots, sometimes with a dense covering of brown dots. Shell sometimes with brown patches. Up to 20 mm long.

Distribution
North Carolina, Florida to Brazil, Greater and Lesser Antilles (Valdés *et al*., 2006).

Notes
Found on soft bottoms near mangrove roots in this study.

Family Aglajidae Pilsbry, 1895
Genus *Chelidonura* A. Adams, 1850
Chelidonura berolina Er. Marcus & Ev. Marcus, 1970
(Fig. 9e)

Description
Shell reduced, internal. Body elongated with a cephalic shield slightly longer than the visceral hump. Posterior end of the body with two lobes, the left one being much longer. Background color black with a submarginal yellow band on the parapodial edge, posterior end of the cephalic shield and anterior and posterior ends of the body. Anterior edge of the body translucent. Dorsum covered by white and yellow patches in some specimens, not present in others. Up to 12 mm long.

Distribution
From Mexico to Colombia, Cayman Islands, Cuba, Jamaica, Martinique, Puerto Rico, Bermuda, Bahamas (Valdés *et al*., 2006; Ornelas-Gatdula *et al*., 2011; Malaquias, 2014).

Notes
Common on shallow sandy areas as it buries itself in the sand, can be found crawling among seagrass at daytime (Valdés *et al*., 2006; Malaquias, 2014). A taxonomic revision of *Chelidonura* in the Caribbean was recently published (Ornelas-Gatdula *et al*., 2011).

Genus *Navanax* Pilsbry, 1895
Navanax gemmatus (Mörch, 1863)
(Fig. 9f)

Synonyms
Aglaja hummelincki Er. Marcus & Ev. Marcus, 1970.

Description
Shell reduced, internal. Body elongated with well-formed cephalic shield and parapodia. Posterior end of the body with two lobes, the left one with a thin elongate projection. Background color from opaque yellow to dark brown. Dorsum with white and brown longitudinal lines and

some whitish areas. Edge of the parapodia with a row of bright blue spots. Up to 50 mm long.

Distribution
From Florida to Brazil, Lesser Antilles, Cuba, Jamaica, Bahamas, Bermuda (Valdés *et al*., 2006; Ornelas-Gatdula *et al*., 2012; Camacho-García *et al*., 2014; Caballer Gutiérrez *et al*., 2015).

Notes
Feeds on other sea slugs and inhabits rocky areas (Valdés *et al*., 2006). Ornelas-Gatdula et al. (2012) studied the *Navanax aenigmaticus* (Bergh, 1893) species complex using morphological and molecular data and proposed that the valid species name for the Western Atlantic species was *Navanax gemmatus.*

Family Acteocinidae Dall, 1913
Genus *Acteocina* Gray, 1847
Acteocina candei (d'Orbigny, 1842)
(Fig. 9g)

Description
Shell external, solid, oval to elongate. Spire long, conical, with 2–3 channeled whorls. Umbilicus absent. Columellar margin thickened, slightly oblique, with a small, simple fold. Head with two large posterior lobes, parapodia absent. Background color translucent white. Shell translucent white with the viscera visible as an irregular pattern of white pigment on a slightly reddish background. Up to 5.3 mm long.

Distribution
North Carolina, Texas, Florida to Brazil, Argentina, Bermuda, Bahamas, Cuba, Jamaica, Puerto Rico, Virgin Islands, Guadeloupe, Martinique, Guyana (Valdés *et al*., 2006; Caballer Gutiérrez *et al*., 2015) and Panama (present study).

Notes
Found on soft bottoms near mangrove roots in this study.

Order Anaspidea Fischer, 1883
Suborder Aplysioidea Lamarck, 1809
Family Aplysiidae Lamarck, 1809
Genus *Aplysia* Linnaeus, 1767
Aplysia dactylomela Rang, 1828
(Fig. 10a)

Synonyms
Aplysia protea Rang, 1828; *Aplysia schrammi* Deshayes, 1857; *Aplysia aequorea* Heilprin, 1888; *Aplysia megaptera* Verrill, 1900.

Description
Shell reduced, internal. Body elongated with two tough and leathery parapodia that cover the mantle cavity. Rhinophores rolled, oral tentacles reduced. Background color usually greenish brown with large dark or black rings, which are characteristic of this species. Dark or black reticulate lines also present. Up to 200 mm long.

Distribution
Amphiatlantic. Western Atlantic: from Florida to Brazil, Greater and Lesser Antilles (Valdés *et al*., 2006; Alexander & Valdés, 2013; Caballer Gutiérrez *et al*., 2015).

Notes
This species produces purple ink when disturbed and animals mate in chains (Valdés *et al*., 2006). Atlantic populations were recently classified as *Aplysia dactylomela* and separated from the Indo-Pacific *Aplysia argus* Rüppell & Leuckart, 1830 (Alexander & Valdés, 2013). *Aplysia dactylomela* has been introduced into the Mediterranean sea (Valdés *et al.,* 2013). Found on algae and an algae covered reef in this study.

Genus *Stylocheilus* Gould, 1852
Stylocheilus striatus (Quoy & Gaimard, 1832)
(Fig. 10b)

Synonyms
Notarchus polyomma Mörch, 1863; *Stylocheilus lineolatus* Gould, 1852.

Description
External shell present in juveniles but lost in adults. Body elongated with numerous branched papillae. Background color translucent with shades of cream, brown, and grey. Body with longitudinal or interrupted dark lines and scattered spots. Adults often have bright pink or blue ocelli that are not found in juveniles. Up to 45 mm long.

Distribution
Circumtropical. Western Atlantic: from Florida to Brazil, Greater Antilles and Lesser Antilles, Bermuda, Bahamas (Valdés *et al*. 2006; Camacho-García *et al*., 2014; Caballer Gutiérrez *et al*., 2015).

Notes
Organism feeds on algae and is common in shallow waters. This species has been often assigned to *Stylocheilus longicaudus* (Quoy & Gaimard, 1825), which is a pelagic species associated with floating algae (Valdés *et al.,* 2006).

Genus *Dolabrifera* Gray, 1847
Dolabrifera dolabrifera (Rang, 1828)
(Fig. 10c)

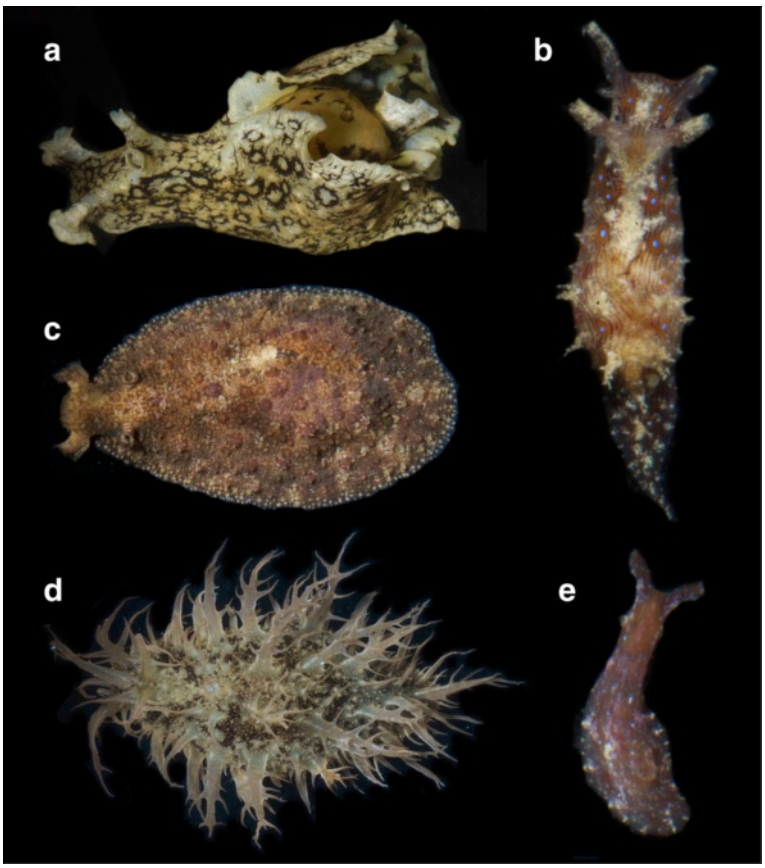

Fig. 10 Euopisthobranchia: Aplysiidae. **a** *Aplysia dactylomela* Rang, 1828; **b** *Stylocheilus striatus* (Quoy & Gaimard, 1832); **c** *Dolabrifera dolabrifera* (Rang, 1828); **d** *Bursatella leachii* Blainville, 1817; **e** *Phyllaplysia engeli* Er. Marcus, 1955

Synonyms

Aplysia ascifera Rang, 1828; *Aplysia oahouensis* Souleyet, 1852; *Dolabrifera cuvieri* H. & A. Adams, 1854; *Dolabrifera maillardi* Deshayes, 1863; *Dolabrifera nicaraguana* Pilsbry, 1896; *Dolabrifera olivacea* Pease, 1860; *Dolabrifera sowerbyi* G. B. Sowerby II, 1868; *Dolabrifera swiftii* Pilsbry, 1896; *Dolabrifera virens* Verrill, 1901.

Description

Body flattened and tapered anteriorly, with the posterior end usually broader and more rounded. Parapodia fused except for a very small region in the posterior mid-line. Dorsum covered with low tubercles. Background color varies from mottled green to brown (light or dark) to even pink. Up to 90 mm long.

Distribution

Circumtropical. Western Atlantic: North and south American mainland, from Florida to Brazil, Greater and Lesser Antilles, Bermuda, Bahamas (Valdés *et al*., 2006; Camacho-García *et al*., 2014).

Notes

Feeds on patches of algae on rocks. This species can be very abundant in intertidal rocky areas and crawls with a leach-like movement (Valdés *et al*., 2006).

Genus *Bursatella* Blainville, 1817
Bursatella leachii Blainville, 1817
(Fig. 10d)

Synonyms

Notarchus laciniatus Rüppell & Leuckart, 1830; *Aplysia bursatella* Rang, 1834; *Aclesia glauca* Cheeseman, 1878; *Notarchus intrapictus* Cockerell, 1893; *Aclesia africana* Engel, 1926; *Aclesia rosea* Engel, 1926; *Bursatella lacinulata* Gould, 1852; *Bursatella leachii lacinulata* Gould, 1852.

Description

Body rounded, wider towards the posterior end. Head with two rhinophores on the dorsal side and two oral tentacles one on either side of the mouth. Dorsum covered with many papillae along, which gives the animal a fuzzy appearance. Body color dark green to dark brown

with some lighter colored spots. The gill is on the dorsal side covered by two parapodial flaps. Up to 120 mm long, but typically 75–100 mm.

Distribution
Circumtropical. Western Atlantic: from North Carolina to Brazil, Virgin Islands, Jamaica, Aruba, Curaçao, Bermuda, Trinidad (Valdés *et al*., 2006; Caballer Gutiérrez *et al*., 2015).

Notes
Found in tide pools, lagoons and estuaries. This species lives in sea grass beds, feeds on algae and lays long, thin, ribbon-like egg masses. It is currently considered to be circumtropical species, but made up of several subspecies. The subspecies found in the Caribbean is *Bursatella leachii pleii* Rang, 1828 (Valdés *et al.,* 2006).

Genus *Phyllaplysia* P. Fischer, 1872
Phyllaplysia engeli Er. Marcus, 1955
(Fig. 10e)

Description
Body flattened and oval, some specimens with low papillae. Parapodia fused. Background color translucent with varying patches and spots of pink, brown, white and some green. Some specimens have white longitudinal lines. Up to 15 mm long.

Distribution
Florida to Brazil, Curaçao, Bahamas, Puerto Rico, Jamaica, St. Maarten/St. Martin, Barbados (Valdés *et al*., 2006; Caballer Gutiérrez *et al*., 2015).

Notes
Found on sea grasses of the genera *Thalassia* Banks ex König, 1805 and *Halodule* Endlicher, 1841 on which they are extremely cryptic (Valdés *et al*., 2006).

Clade Panpulmonata Jörger, Stöger, Kano, Fukuda, Knebelsberger & Schrödl, 2010
Order Sacoglossa Ihering, 1876
Family Volvatellidae Pilsbry, 1895
Genus *Ascobulla* Ev. Marcus, 1972
Ascobulla ulla (Er. Marcus & Ev. Marcus, 1970)
(Fig. 11a)

Description
External shell slightly calcified with a cylindrical shape and flat apex. Eyes present and positioned in the upper region of the head, covered by the cephalic shield during locomotion and digging, making it difficult to observe in living animals. Cephalic shield has two lobes divided by a deep groove. Translucent shell, mantle and visceral mass define the body color, varying between brown and orange. Head shield has white coloration and opaque white dots on its surface. Up to 6 mm long.

Distribution
Florida, Mexico, Belize, Costa Rica, Venezuela, Bermuda, Bahamas, Turks and Caicos, Cayman Islands, Virgin Islands, Brazil (Valdés *et al*., 2006; Camacho-García *et al*., 2014) and Panama (present study).

Notes
Found on different species of *Caulerpa* Lamouroux, 1809*,* most commonly on rhizoids of *Caulerpa racemosa* Agardh, 1873 or crawling on sand next to algae. May exude a milky substance when disturbed. Fragile shell easily cracked or broken when handled.

Family Oxynoidae Stoliczka, 1868 (1847)
Genus *Oxynoe* Rafinesque, 1814
Oxynoe antillarum Mörch, 1863
(Fig. 11b)

Description
Body elongate with long posterior end of foot resembling a tail. Shell globose and translucent, fragile with a wide opening and partially or fully covered by parapodia in adults. Smaller juvenile parapodia expose much of the shell. Rolled rhinophores prominent. Groove runs horizontally from base of rhinophores through each lateral region of the head. Body color light green with white papillae on parapodial margins and running down midline of tail. White and blue patches on rhinophores, sides of head, and parapodial margins. Juvenile body more elongated and smooth, ground color solid yellow to green with white and blue patches along, or at base of, rhinophores; some blue spots on mantle may be visible through shell. Up to 20 mm long.

Distribution
Florida, Mexico, Belize, Honduras, Costa Rica, Panama, Venezuela, Bahamas, Curaçao, Bermuda, Cayman Islands, Jamaica, Dominican Republic, Puerto Rico, Virgin Islands, Martinique, St. Lucia, Barbados, St. Vincent and the Grenadines, Grenada, Trinidad and Tobago, Brazil (Valdés *et al*., 2006; Camacho-García *et al*., 2014).

Notes
Very common throughout the tropical western Atlantic coast on many species of *Caulerpa,* but primarily on *Caulerpa racemosa*. Specimens sometimes found under rocks or crawling next to algae. Exudes white secretion and may autotomize tail when disturbed. High intraspecific variation and a lack of diagnostic differences in

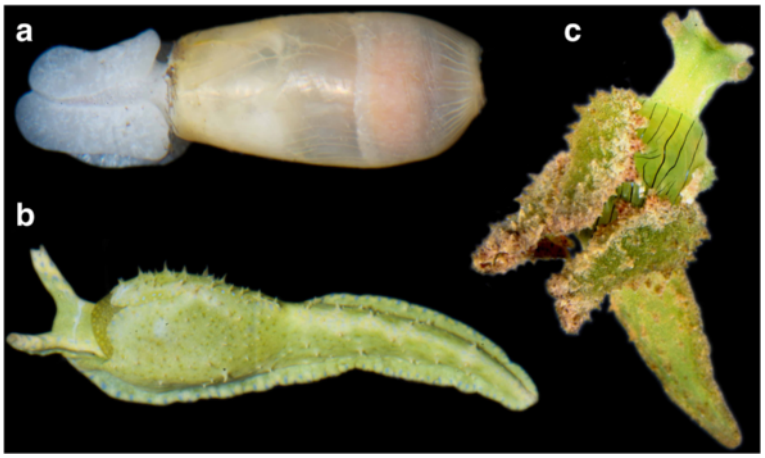

Fig. 11 Panpulmonata: Volvatellidae and Oxynoidae. **a** *Ascobulla ulla* (Er. Marcus & Ev. Marcus, 1970); **b** *Oxynoe antillarum* Mörch, 1863; **c** *Lobiger souverbii* Fischer, 1857

external morphology make it difficult to distinguish from *Oxynoe azuropunctata* Jensen, 1980.

Genus *Lobiger* Krohn, 1847
Lobiger souverbiei P. Fischer, 1857
(Fig. 11c)

Synonyms
Lobiger pilsbryi Schwengel 1941.

Description
Shell extremely fragile with apex directed posteriorly to left side. Some small papillae scattered on rhinophores and lateral sides of the head. Each parapodium expands narrowly in two leaf-like projections upwards from shell, with white papillae on parapodial margins. Rolled rhinophores shorter than head. Foot extends posteriorly to form thick tail and anteriorly to form two lobes. Body coloration light green with yellowish-brown papillae on tail and parapodia. Light green mantle with black longitudinal lines and a few scattered blue dots visible through translucent shell. Up to 30 mm long.

Distribution
Florida, Mexico, Honduras, Costa Rica, Venezuela, Curaçao, Cayman Islands, Jamaica, Puerto Rico, Guadeloupe, Barbados, St. Vincent and the Grenadines, Grenada, Brazil (Valdés *et al*., 2006; Camacho-García *et al*., 2014) and Panama (present study).

Notes
Feeds on *Caulerpa* spp., most commonly found on *Caulerpa racemosa* in high-flow areas. May exude milky secretion and sometimes autotomize parapodial extensions when disturbed.

Family Limapontiidae Gray, 1847
Genus *Ercolania* Trinchese, 1872
Ercolania coerulea Trinchese, 1892
(Fig. 12a)

Synonyms
Stiliger cricetus Er. Marcus & Ev. Marcus 1970.

Description
Cerata short and fusiform arranged in rows on both sides of body. Digestive diverticula irregular inside each ceras. Rhinophores simple, smooth, longer than head. Eyes in dorsolateral position. Pericardial hump short, not covered by cerata. Foot forms thick short tail and large rounded anterior expansion. Opaque translucent body with posterior region colored by yellow digestive gland. Small white dots scattered across entire body, highly concentrated on cerata and rhinophore tips. Some individuals have blue spots clustered at tips of cerata and rhinophores and on top of head. Two longitudinal light green branches of digestive diverticula run anteriorly, branching in cephalic region and inside rhinophores. Body length typically 8–10 mm, up to 16 mm.

Distribution
Florida, Venezuela, Curaçao, Jamaica, Virgin Islands, St. Kitts, St. Lucia, Brazil (Valdés *et al*., 2006) and Panama (present study).

Notes
Found in clumps of the green bubble algae *Dictyosphaeria cavernosa* Børgesen, 1932 and *Valonia* Agardh, 1823. Originally described from Mediterranean Sea, only species of the genus *Ercolania* recorded from the Atlantic and Indo-Pacific (Grzymbowski *et al*., 2007). Recent phylogenetic analysis confirmed placement of *E. coerulea*

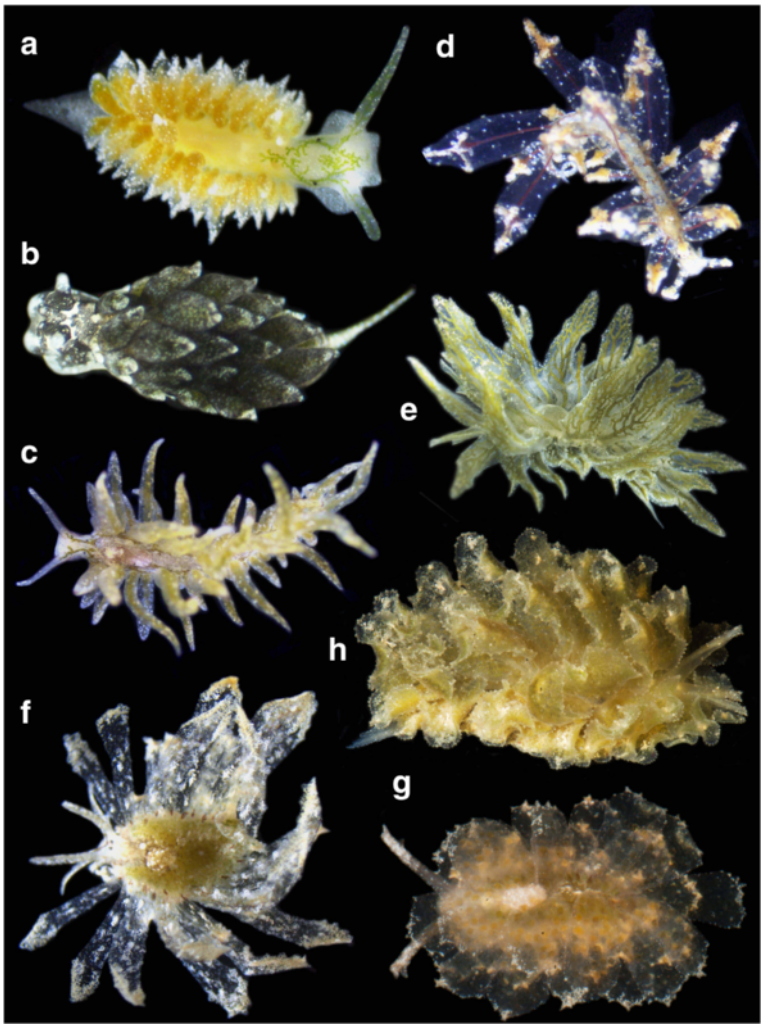

Fig. 12 Panpulmonata: Caliphyllidae, Costasiellidae, Hermaeidae and "Limapontiidae". **a** *Ercolania coerulea* Trinchese, 1892; **b** *Costasiella nonatoi* Ev. Marcus & Er. Marcus, 1960; **c** *Placida kingstoni* Thompson, 1977; **d** *Hermaea cruciata* Gould, 1870; **e** *Caliphylla mediterranea* Costa, 1867; **f** *Cyerce antillensis* Engel, 1927; **g** *Cyerce* cf. *antillensis* Engel, 1927; **h** *Polybranchia viridis* (Deshayes, 1857)

within a larger clade that includes most other species in the genus (Krug *et al*., 2015).

Family Costasiellidae K. B. Clarke, 1984
Genus *Costasiella* Pruvot-Fol, 1951
Costasiella nonatoi Ev. Marcus & Er. Marcus, 1960
(Fig. 12b)

Description

Grooved rhinophores shorter than head. Foot elongated posteriorly in sharp tail longer than half the body length and anteriorly wide and bilobate. Eyes mid-dorsally positioned behind rhinophores. Largest fusiform cerata arranged in dorsal region, while small ones in one row next to foot corner. Overall external color almost entirely black, except for tail, periocular area, border of foot, and tips of rhinophores and cerata, which are transparent or opaque white. Bright whitish or yellowish dots dispersed through foot, rhinophores, cerata, and tail. Up to 4 mm long.

Distribution

North Carolina, Florida, Costa Rica, Venezuela, Cayman Islands, Puerto Rico, Bahamas, Bermuda, Brazil (Valdés *et al*., 2006; Camacho-García *et al*., 2014; Caballer Gutiérrez *et al*., 2015) and Panama (present study).

Notes

Feeds and reproduces on *Avrainvillea* Descaisne, 1842 spp. and crawls among its filaments. Phylogenetic analysis places *C. nonatoi* outside monophyletic group formed by other species of the genus (Krug *et al*., 2015). Characteristics such as grooved rhinophores, eyes positioned behind rhinophores, and absence of photosynthetic ability also

distinguish it from other species of *Costasiella* (Christa *et al.*, 2014; Jensen *et al.*, 2014).

Genus *Placida* Gray, 1847
Placida kingstoni Thompson, 1977
(Fig. 12c)

Description
Opaque translucent body scattered with small white dots, brown dorsal region. Two longitudinal yellow-green digestive system branches run along dorsal region, branching anteriorly next to rhinophores. Elongated fusiform cerata, each containing one unbranched ramification of the digestive diverticula extending almost to tip. Rhinophores enrolled at base, smooth, longer than head. Eyes in a dorsolateral position closer to pericardial hump than to rhinophores. Prominent pericardial hump visible on dorsal region, longer than head. Anal papillae positioned mid-anteriorly on pericardial hump. Foot forms a short tail and small square anterior expansion. Up to 15 mm long.

Distribution
Florida, Costa Rica, Jamaica, Martinique, Bermuda (Valdés *et al.*, 2006) and Panama (present study).

Notes
Found on green algae in the genus *Bryopsis* Lamouroux, 1809.

Family Hermaeidae Adams & Adams, 1854
Genus *Hermaea* Lovén, 1844
Hermaea cruciata Gould, 1870
(Fig. 12d)

Synonyms
Hermaea coirala Er. Marcus 1955.

Description
Rhinophores bifurcated and slightly longer than the head. Foot forms sharp tail posteriorly and projects anteriorly into small foot corner extensions. Cerata fusiform with a conical tip, variable in size. Largest cerata reaching more than half the body length. A duct of the digestive system run inside each ceras and branches highly only in the apex under the yellow gland. Translucent body with scattered small white dots. Dark red tubules of digestive diverticula, yellow glands at tips of cerata, whitish gonads, and other internal organs visible through translucent body wall. Up to 5 mm long.

Distribution
Massachusetts, New York, Florida, Costa Rica, Trinidad and Tobago, Brazil (Valdés *et al.*, 2006) and Panama (present study).

Notes
Species of *Hermaea* often feed on filamentous red algae (Caballer & Ortea, 2013), as opposed to the green algae that serve as host for most sacoglossans.

Family Caliphyllidae Tiberi, 1881
Genus *Caliphylla* A. Costa, 1867
Caliphylla mediterranea A. Costa, 1867
(Fig. 12e)

Description
Each side of the body has four rows of leaf-shaped cerata. Dorsal midline lacking cerata, starting at the pericardium. Digestive diverticula branch within cerata, bifurcating at margin of each ceras. Oral veil is present. Anus at apex of papilla on right side, at eye level anterior to pericardium. Bifid rhinophores long and grooved. Eyes positioned on median side behind rhinophores. Male genital pore at base of rhinophores, female aperture anus and male pore. Digestive diverticula, varying from dark green to brown, visible through translucent elongated body. Numerous black and white dots scattered throughout body. Up to 35 mm long.

Distribution
Amphiatlantic; Western Atlantic: Florida, Curaçao, Virgin Islands, Trinidad and Tobago, Brazil (Valdés *et al.*, 2006) and Panama (present study).

Notes
Associated with filamentous green algae *Bryopsis plumosa* Agardh, 1823 growing in sheltered areas of rocks, reef corals or mangrove roots. Readily shed cerata and extrude adhesive substance when disturbed. Monotypic genus with type specimen from Mediterranean Sea, but other morphotypes from West Atlantic coast may reveal one or more additional species (Valdés *et al.*, 2006), and at least one cryptic species exists in the Pacific (Krug *et al.*, 2015).

Genus *Cyerce* Bergh, 1870
Cyerce antillensis Engel, 1927
(Fig. 12f)

Synonyms
Cyerce habanensis Ortea & Templado 1989.

Description
Body broad and oval-shaped. Eye spots behind base of rhinophores. Body translucent with light green to yellow-white viscera showing through. Pericardium opaque white. Cerata wide and inflated, almost transparent with scattered white spots that concentrate at the tips and irregular edges. Up to 60 mm long.

Distribution
Florida, Mexico, Belize, Honduras, Costa Rica, Curaçao, Bermuda, Cayman, Islands, Cuba, Bahamas, Jamaica, Puerto Rico, Virgin Islands, Barbados, Tobago (Valdés *et al*., 2006; Camacho-García *et al*., 2014) and Panama (present study).

Notes
Feeds on green algae in the genus *Penicillus* Lamarck, 1813; older reports of other hosts (*Udotea* Lamouroux, 1812, *Halimeda* Lamouroux, 1812) likely reflect unrecognized cryptic species that eat other host genera (Jensen & Clark, 1983; Clark & DeFreese, 1987). May autotomize cerata when disturbed.

Cyerce cf. *antillensis* Engel, 1927
(Fig. 12g)

Description
Body broad and oval-shaped. Eye spots behind base of rhinophores. Body translucent with light green to yellow-white viscera showing through. Pericardium opaque white. Cerata wide and short, almost transparent with orange spots and white at the tips and irregular edges. Up to 30 mm long.

Distribution
Panama (present study).

Notes
Feeds on *Halimeda* green algae. Similar to *Cyerce antillensis* but is genetically distinct (unpublished data), has a white pericardium and broader cerata; it may constitute an undescribed species. Autotomizes the cerata when disturbed.

Genus *Polybranchia* Pease, 1860
Polybranchia viridis (Deshayes, 1857)
(Fig. 12h)

Description
Body oval-shaped. Rhinophores bifid for half of their length or more, cerata and rhinophores covered with small papillae. Body almost transparent with internal viscera giving the animal a light green to pale gold tint. Flattened cerata translucent with opaque white spots and characteristic fold in middle and numerous white glands on edges. Up to 80 mm long.

Distribution
Florida, Costa Rica, Curaçao, Bonaire, Jamaica, Virgin Islands, Guadeloupe, Barbados (Valdés *et al*., 2006) and Panama (present study).

Notes
Feeds on green algae in the genus *Caulerpa*. Found under rocks during the day and active at night.

Family Plakobranchidae Gray, 1840
Genus *Elysia* Risso, 1818
Elysia crispata Mörch, 1863
(Fig. 13a–b)

Synonyms
Elysia schrammi Ørsted & Mörch, 1863; *Tridachia whiteae* Er. Marcus, 1957; *Elysia clarki* Pierce, Curtis, Massey, Bass, Karl & Finney, 2006.

Description
Most conspicuous and one of the largest sacoglossans in the Caribbean. Parapodia highly undulated, resembling lettuce (hence the common name lettuce sea slug). Highly variable in body color, ranging from light to dark green with small or large white spots, to dark green or purple with white spotting (described as *Elysia clarki*), to entirely blue. Parapodial margins also highly variable in color – often white but can also be lined with yellow, red, and/or blue. Foot may be uniformly pale cream, or green with small to large white spots. Dorsal surface between parapodia generally pale green, often with pale cream to white spots. Up to 50 mm long.

Distribution
Florida, Dry Tortugas, Mexico, Belize, Honduras, Costa Rica, Colombia, Venezuela, Aruba, Curaçao, Bonaire, Venezuela, Bermuda, Cayman Islands, Bahamas, Jamaica, Haiti, Puerto Rico, Virgin Islands, St. Maarten/St. Martin, Antigua, St. Lucia, Martinique, Guadeloupe, Turks and Caicos, St. Vincent and the Grenadines, Barbados, Trinidad and Tobago (Valdés *et al*., 2006; Camacho-García *et al*., 2014) and Panama (Collin *et al*., 2005).

Notes
Very common throughout the Caribbean and easily spotted on rocks, coral rubble, or sediment, often crawling or sometimes stationary with parapodia opened giving the appearance of basking in the sun. Uncertainty surrounds feeding ecology, but thought to be highly polyphageous for a sacoglossan. The most recent work using field and lab methods confirmed feeding on one or more species in the genera *Bryopsis*, *Penicillus*, *Halimeda*, *Acetabularia* Lamouroux, 1812, and *Derbesia* Solier, 1846 (Pierce *et al.,* 2003; Curtis *et al.,* 2004, 2006; Middlebrooks *et al.,* 2014). Originally described as *Elysia* (*Tridachia*) *crispata*, now formally recognized as a member of the genus *Elysia*.

Elysia ornata (Swainson, 1840)
(Fig. 13c)

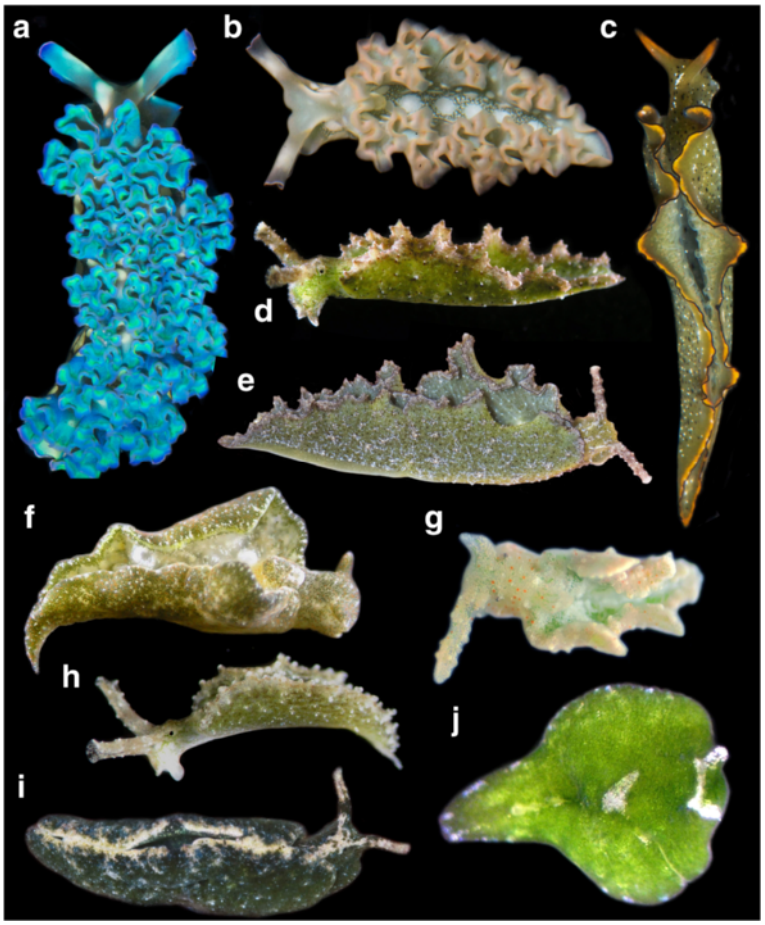

Fig. 13 Panpulmonata: Plakobranchidae. **a**–**b** *Elysia crispata* Mörch, 1863; **c** *Elysia ornata* (Swainson, 1840); **d** *Elysia papillosa* Verrill, 1901; **e** *Elysia subornata* Verrill, 1901; **f** *Elysia canguzua* Er. Marcus, 1955; **g** *Elysia cornigera* Nuttall, 1989; **h** *Elysia zuleicae* Ortea & Espinosa, 2002; **i** *Elysia velutinus* Pruvot-Fol, 1947; **j** *Elysia marcusi* (Ev. Marcus, 1972)

Synonyms

Pterogasteron marginatum Pease 1871.

Description

Parapodia highly arched to form a prominent raised "chimney" halfway along the body, then unite at posterior end of body to a pointed tail. Rhinophores short and taper to a blunt point at rolled tips. Olive green with small black and white spots on dorsal surface and outer parapodia. Sharp black band runs along entire parapodial margin, with more diffuse orange submarginal band on inner and outer parapodia. Rhinophores match orange coloration of parapodia but may lack black edges. Up to 50 mm long.

Distribution

Florida, Belize, Honduras, Costa Rica, Colombia, Venezuela, Bahamas, Curaçao, Bermuda, Jamaica, Puerto Rico, Virgin Islands, Martinique, Turks & Caicos, Barbados, St. Vincent and the Grenadines, Grenada, Trinidad and Tobago, Brazil (Valdés *et al*., 2006; Camacho-García *et al*., 2014) and Panama (present study).

Notes

Commonly found feeding inside clumps of *Bryopsis plumosa* and can be surprisingly cryptic despite relatively large size and bright coloration. This species was thought to have a cosmopolitan distribution, but recent molecular work suggests that the Caribbean population is genetically distinct from several undescribed species in the Indo-Pacific (Krug *et al*., 2013).

Elysia papillosa Verrill, 1901
(Fig. 13d)

Synonymy

*Elysia anneduponta*e Ortea, Espinosa & Caballer, 2005.

Description
Outer parapodial surface covered with rows of white papillae. Parapodial margin tan to dark brown, bears many light tan to brown papillae, with scalloped edge forming several siphonal openings. One large pair of sperm-storage vesicles visible on dorsal surface of large adults, usually near the 6th dorsal vessel. Highly variable external body coloration, generally light green but can range from white/tan to olive green. Sides of head lighter green to white. One or two large white papillae between the eyes on most specimens. Inner parapodial surface and dorsum lightly to heavily speckled with brown or black spots, and with scattered white, rounded papillae. Pericardium round, with brown streaks and spots and low white papillae. Up to 30 mm long.

Distribution
Mexico, Panama, Cuba, Jamaica, Florida, Bahamas, U.S. Virgin Islands, Antigua, Curaçao (Krug *et al*., in press).

Notes
When disturbed, specimens readily swim by undulating their parapodia. Specializes on green algae in the genus *Penicillus*. One of the most abundant sacoglossans in the Caribbean – sometimes visible in the field and often found on collections of *Penicillus* spp. Often confused with *E. zuleicae*, which may be distinguished by its longer rhinophores and extended tail. Also readily confused with *E. patina*, which is externally very similar but can be distinguished by its host alga *Halimeda opuntia* Lamouroux, 1816 and its egg masses – *E. papillosa* produces relatively more numerous, larger eggs (planktotrophic development) with white extra-zygotic yolk, while *E. patina* has larger, fewer eggs (lecithotrophic development) with flat, orange ribbons of extra-zygotic yolk (Krug *et al.*, in press).

Elysia subornata Verrill, 1901
(Fig. 13e)

Description
Coloration ranges from yellow to olive to dark green. Sides of parapodia dusted with white to varying degrees, with white pigment often arranged in star-shaped clusters around base of white papillae. Tiny black or brown dots scattered all over head and body. Some specimens have few papillae, others are densely covered in elongated white papillae. Rhinophores short relative to body length, with tan to lavender to dark brown coloration and white tips. Distinctive fine black line along the edge of parapodia, with tan to dark brown margin, sometimes with white speckling. Inner parapodia green with white speckling. Mostly symmetrical, simple vessels extending from center of dorsal surface. Up to 50 mm long.

Distribution
Florida, Mexico, Belize, Costa Rica, Bermuda, Bahamas, Aruba, Cayman Islands, Jamaica, Puerto Rico, Virgin Islands, Martinique, Grenada, Trinidad and Tobago, Brazil (Valdés *et al*., 2006; Camacho-García *et al*., 2014; Padula *et al*., 2012; Galvão Filho *et al.*, 2015) and Panama (present study).

Notes
Egg masses have continuous string of bright orange extra-zygotic yolk, larvae metamorphose inside egg capsules (Krug *et al.*, in press). Slugs are usually found in association with *Caulerpa* and are known to feed on at least eight different species in the genus. Adults do not swim when disturbed.

Elysia canguzua Er. Marcus, 1955
(Fig. 13f)

Synonyms
Elysia eugeniae Ortea & Espinosa 2002.

Description
Rhinophores short, blunt-tipped, same color and texture as head but with white patch at tip. Three siphonal openings in parapodial folds at head, middle, and posterior end. Dark to olive green on head and outer parapodia, mostly smooth with low sparse papillae. Body densely covered with distinctive red/orange spots, and smaller iridescent blue specks. Uneven rows of white spots on head and across sides of parapodia. Up to 12 mm long.

Distribution
Costa Rica, Brazil (Valdés *et al*., 2006; Camacho-García *et al*., 2014) and Panama (present study).

Notes
Found feeding on *Bryopsis* sp. growing on loose sediment 1–2 m depth. Preferred hosts reported to be both *Bryopsis plumosa* and *Codium* Stackhouse, 1797 (Jensen & Clark, 1983). Parapodia typically held open when resting, adults do not swim when disturbed.

Elysia cornigera Nuttall, 1989
(Fig. 13g)

Description
Rhinophores long and curled, white to light green with red dots and many white papillae. White to grey on parapodia and head with numerous warty papillae. Red granules dotting head and rhinophores, smaller red dots scattered on parapodia. Densely enervated green digestive diverticula inside of parapodia. Up to 8 mm long.

Distribution
Florida, Cuba, Cayman Islands, Bahamas (Valdés *et al*., 2006) and Panama (present study).

Notes
One small specimen found on coral rubble near *Caulerpa racemosa*, but only confirmed host is *Acetabularia crenulata* Lamouroux, 1816. Formerly synonymized with *Elysia timida* Risso, 1818, subsequently resurrected based on genetic, morphological, and developmental characteristics, and differences in photosynthetic ability (Krug *et al.,* 2011, 2013). Upper surface of egg mass has flat ribbon of white to translucent ribbon of extra-zygotic yolk with granular appearance (Krug *et al.,* in press).

Elysia zuleicae Ortea & Espinosa, 2002
(Fig. 13h)

Description
External morphology quite variable. Rhinophores long and rolled. Narrow tail often extends a few millimeters beyond posterior end of parapodia, but some specimens have no tail. Parapodia are thin, sometimes with slight undulation but no siphonal openings. Body coloration typically olive to dark green. Head light to dark green, sometimes with rust-colored patches. Rhinophores colored white to brown-purple with scattered white papillae and white patches of pigment concentrated at tips. Outer surface of parapodia are green with scattered white specks and low white papillae. White papillae run along parapodial margin, sometimes forming crown-like clusters that appear to rise and fall along the margin. Some specimens, particularly juveniles, have a thin black line along parapodial margins surrounded by thicker white submarginal bands.

Distribution
Cuba, Costa Rica, Jamaica, Venezuela (Valdés *et al*., 2006; Caballer Gutiérrez *et al*., 2015) and Panama (present study).

Notes
Specializes on the green alga *Udotea flabellum* Howe, 1904. Juveniles hold parapodia flat against algal blade are distinctly darker green than adults. Adults swim readily by undulating parapodia when disturbed. Egg masses have a thin, white ribbon of extra-zygotic yolk.

Elysia velutinus Pruvot-Fol, 1947
(Fig. 13i)

Description
Parapodia form one small siphonal opening about halfway down the body. Body coloration varies from light to dark green, with spots or large patches of white or tan pigment. Head has large Y-shaped white to tan patch of pigment, starting anterior of pericardium and running up to the base of each rhinophore. Rhinophores are green at the base but distally become white or tan, sometimes with small papillae. Panamanian specimens tend to have less white pigmentation/fewer papillae on external surface of parapodia compared with those found in the Bahamas. Up to 15 mm long.

Distribution
Florida, Mexico, Honduras, Costa Rica, Panama, Colombia, Venezuela, Bermuda, Bahamas, Curaçao, Cayman Islands, Jamaica, Puerto Rico, Virgin Islands, St. Maarten/St. Martin, St. Lucia, Barbados, St. Vincent and the Grenadines, Grenada, Brazil (Valdés *et al*., 2006; Malaquias, 2014; Caballer Gutiérrez *et al*., 2015).

Notes
Typically associated with *Halimeda* spp., most commonly the upright branching species *H. incrassata* J.V. Lamouroux, 1816 and *H. monile* J.V. Lamouroux, 1816. Parapodia held together when resting, slugs do not swim when disturbed. Egg masses have continuous ribbon of bright yellow extra-zygotic yolk. This species was previously known as *Elysia tuca* Ev. Marcus & Er. Marcus, 1967 but Krug *et al*. (in press) found that *Elysia velutinus* is a senior synonym.

Elysia marcusi Ev. Marcus, 1972
(Fig. 13j)

Description
Small bodied. Parapodia fused to body with fusion line visible running dorsally down the body. Uniformly light to dark green, sometimes with white patches. Rhinophores solid white, simple, flat (not rolled), and fully retractable into head. Up to 5 mm long.

Distribution
Florida, Costa Rica, Bahamas, Jamaica (Valdés *et al*., 2006) and Panama (present study).

Notes
Found on mixed collection of *Caulerpa racemosa* and *Halimeda* sp., but preferred host is *Halimeda opuntia* (Krug *et al.,* in press). Resting slugs flatten into perfectly round circles, superficially resembling *Bosellia mimetica* Trinchese, 1891. Crawling slugs elongate into form more typical of *Elysia* spp.

Discussion
Few studies of heterobranch sea slugs have reported collecting effort. In the Eastern Pacific, Nybakken (1978)

searched for sea slugs for 120 h and found 31 species in a California intertidal assemblage. Hermosillo (2006) searched for 750 h and found 140 species in Bahía de Banderas, Pacific coast of Mexico, while Bertsch (2008) in Bahía de Los Ángeles, Pacific coast of Mexico found 81 species in 229.3 h of searching. For the Caribbean, Thompson (1976) reported a total of 61 species for a searching time of approximately 298 h, mostly in Jamaica. A recent study conducted in a Mexican Caribbean coral reef reported 32 species observed in a total of 74.4 h of search (Sanvicente-Añorve *et al*., 2012), however in this case indirect methods were also included. The preceding studies also found that the highest number of species belonged to the clade Nudibranchia, which is consistent with the greater overall diversity in this group (Gosliner *et al.* 2015).

Based on the information provided in these prior studies, the collecting effort of our study (307.5 h) represents one of the highest recorded for sea slugs not only in the Caribbean but also in tropical regions. Despite this large collecting effort, relatively few species were found compared to the total known diversity in the Caribbean. Only 82 out of the 308 species reported by Valdés *et al.* (2006) or the 329 species reported by García & Bertsch (2009) were found; this represents about 25 % of known Caribbean species diversity. All the species reported here were included in Valdés *et al*. (2006) except for those that could not be identified at the species level. From the 19 species recorded by Collin *et al*. (2005) five were not observed during the newly conducted field work in Panama: *Atys macandrewii* E. A. Smith, 1872, *Elysia flava* Verrill, 1901, *Aphelodoris antillensis* Bergh, 1879, *Paradoris adamsae* Padula & Valdés, 2012 [as *Paradoris mulciber* (Ev. Marcus, 1971)] (see Padula & Valdés, 2012) and *Doto* cf. *caramella* Er. Marcus, 1957.

The total diversity of sea slugs documented in this study, as well as the total diversity in the Caribbean region is much lower than in the Indo-Pacific region, which is the center of tropical diversity. For example, Gosliner *et al.* (2015) reported 815 sea slug species just in the region of Anilao, located in the Philippine Islands. The total diversity in other Indo-Pacific regions increases dramatically from peripheral areas such as Tanzania (258 spp.), Guam (474 spp.) or French Polynesia (504 spp.) to the Coral Triangle where according to Gosliner *et al*. (2015) diversity reaches unprecedented levels (Philippines 1006 spp., Papua New Guinea 646 spp.). Unfortunately, there are no sea slug diversity studies in the Indo-Pacific region documenting collecting effort and therefore comparisons with the present study are not possible.

For heterobranch sea slugs the experience of the observers in finding species while conducting surveys/inventories is critical, as these animals are difficult to find. Many sea slugs are very small and well-camouflaged, making them nearly invisible to the untrained eye. Even experienced observers often have difficulties finding species in the Caribbean because the abundances of sea slugs in this region are typically lower than in other tropical regions of the world (Valdés *et al.,* 2006). Our results are consistent with this observation, as the total number of specimens found was relatively low and many species were only represented by one specimen.

Most of the sacoglossan species were found by indirect methods. Individuals of these species are very small and remarkably cryptic on their host algae. In spite of this, a few species were found by direct observations (e.g. *Elysia crispata* and *Polybranchia viridis*), primarily due to their more conspicuous size and tendency to periodically leave their algal food sources. *Elysia crispata* is particularly common in the area and throughout the Caribbean (Collin *et al.,* 2005; Valdés *et al.,* 2006). In contrast, most species belonging to other clades (Table 1) were found by direct methods due to their (mostly) larger size and more observer experience finding these groups, especially nudibranchs.

This paper represents a substantial increase in the knowledge of heterobranch sea slug diversity in Bocas del Toro, Panama as compared to the single previous publication from Collin et al. (2005). This increase in known diversity strongly suggests that the distribution of species within the Caribbean is still poorly known (at least in regards to some localities), and thus species ranges may need to be modified as more surveys are conducted.

Abbreviation

STRI, Smithsonian Tropical Research Institute

Acknowledgements

The course "Taxonomy and Biology of Sea slugs" was funded by awards from the US National Science Foundation DEB-1355190 to PJK and DEB-1355177 to AV, and organized by Rachel Collin of the Smithsonian Tropical Research Institute in Bocas del Toro. The two NSF grants also supported the travel of several students (JM, SM, JD, JA and postdoc RE). Other funding agencies made travel possible for other student participants: JAG (Conchologists of America and the University of Maryland Biological Sciences Department Genie Clark Research Award), JD and JA (CSULA Culminating project fund), XGV and KG (STRI fellowships), HG (Fundação de Amparo à Pesquisa do Estado de São Paulo, FAPESP 2014/06979–1), LJ (International Affairs Office of the Universidad de Antioquia) and VB (British Ecological Society, travel grant 5585-6629, and Bombay Natural History Society).

Several staff members of the Smithsonian Tropical Research Institute in Bocas del Toro were extremely helpful supporting the fieldwork and course activities, these are: Plinio Gondola, Urania Gonzalez, Tanyusha Grenald, Arcadio Castillo, Deyvis Gonzalez and Nerea Nieto.

Collecting of some specimens was possible with permits ARAP 27 (2015) and ANAM SE/A-64-15 issued by the Panamanian Government.

Sources of funding

US National Science Foundation, Conchologists of America, University of Maryland, California State University Los Angeles, Smithsonian Tropical Research Institute, Fundação de Amparo à Pesquisa do Estado de São Paulo, International Affairs Office of the Universidad de Antioquia, British Ecological Society, Bombay Natural History Society.

Funding bodies did not participate in the design of the study, data collection, analysis, and interpretation or in writing the manuscript.

Authors' contributions
JAG, RAE, XGV, HCGF, JBM, SMM, VJB, KGM, LMJ, GL, CAH, JDA, JMD, WG, PJK, AV conceived the study, conducted the surveys, identified the specimens, wrote the manuscript. PJK, AV photographed the specimens. SMM, JDA, JMD, RAE, PJK described the egg masses. All authors read and approved the final manuscript.

Competing interests
The authors declare that they have no competing interests.

Data reproduction
All data relevant to this study is reproduced within the paper.

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Received: 11 May 2016 Accepted: 3 June 2016
Published online: 15 July 2016

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