UNIVERSITAT DE BARCELONA

Contributions to the knowledge of marine heterobranch sea slugs (Mollusca: Gastropoda): Panama biodiversity and cryptic species

Darío Eliecer Córdoba González

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DARÍO ELIECER CÓRDOBA GONZÁLEZ

Doctoral thesis

2022

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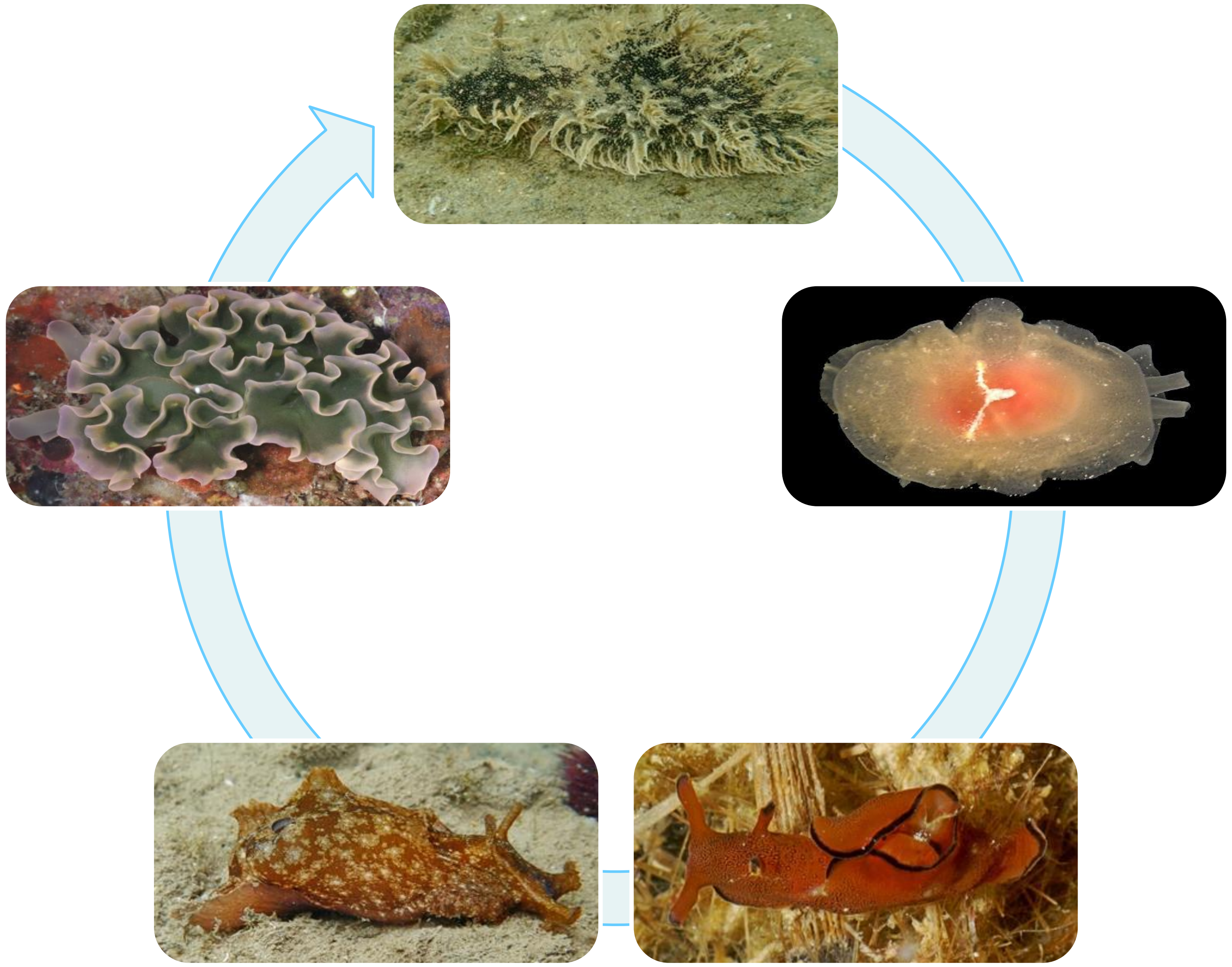

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CONTRIBUTIONS TO THE KNOWLEDGE OF MARINE HETEROBRANCH SEA SLUGS (MOLLUSCA: GASTROPODA): PANAMA BIODIVERSITY AND CRYPTIC SPECIES.

Memory presented by

Darío Eliecer Córdoba González

To opt for the degree of Doctor from the University of Barcelona

Barcelona, May 27, 2022

The doctoral student,

Darío Eliecer Córdoba González

The thesis director,	**Thesis director and tutor**
Dr. Ángel Valdés	**Dr. Manuel Ballesteros**

For you, O Lord Jehovah, are my hope,
My safety from my youth.

Psalm 71:5

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Advisor's Report

As director of the doctoral thesis entitled "CONTRIBUTIONS TO THE KNOWLEDGE OF MARINE HETEROBRANCH SEA SLUGS (MOLLUSCA: GASTROPODA): PANAMA BIODIVERSITY AND CRYPTIC SPECIES", carried out by Darío Eliecer Córdoba González, I present the follow-up report on the contribution of the doctoral student /a in the co-authored publications that make up the thesis:

Chapter I. Córdoba Dario, Valdés Ángel & Ballesteros Manuel (2022). Two oceans: biogeographic and taxonomic review of the marine heterobranch sea slugs (Mollusca: Gastropoda) from Panamanian waters. Zootaxa in evaluation or peer review process.

Contribution of the doctoral student: Participation in the design of the experiments, field work, data collection, analysis of the results and writing of the manuscript.

About the journal: Zootaxa in the 2020 Journal Citation Reports (JRC) has an Impact Index of 1,091. It is found at number 119 of 174 in the area of Zoology (3rd quartile).

Chapter II. Córdoba Dario, Enguidanos Alba, Valdés Ángel, Pontes Miquel & Ballesteros Manuel (2022). Where do I come from? Phylogenetic analysis of *Bursatella leachii* Blainville, 1817 (Mollusca: Gastropoda: Heterobranchia) from the Catalonian coasts. It has not been published.

Contribution of the doctoral student: Participation in the design of the experiments, field work, data collection, analysis of the results and writing of the manuscript.

Chapter III. Córdoba Dario, Enguidanos Alba, Valdés Ángel & Ballesteros Manuel (2022). Molecular analysis and population monitoring of *Berthella stellata* (Risso, 1826) (Mollusca: Gastropoda: Heterobranchia) from the Catalonian coasts (NE Spain). It has not been published.

Contribution of the doctoral student: Participation in the design of the experiments, field work, data collection, analysis of the results and writing of the manuscript.

Chapter IV. Córdoba Dario, Valdés Ángel & Ballesteros Manuel (2022). Changing feeding habits and ontogenetic dimorphism in juvenile and adult *Aplysia punctata* (Cuvier, 1803) (Mollusca, Gastropoda, Heterobranchia) in the Mediterranean. Mediterranean Marine Science in evaluation or peer review process.

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Dr./a Manuel Ballesteros (Thesis Director and Tutor)
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Abstract

The biodiversity of a country is part of its natural wealth and the study of it is fundamental for a scientific researcher, such is the case of the Panamanian marine coasts in which there has not been an exhaustive taxonomic description of the Panamanian species of sea slugs. heterobranch recorded by different authors. Here in the first chapter we try to describe the biodiversity of Panamanian sea slugs by providing descriptions of all sea slugs from the coasts of Panama, based on published references and confirmed photographs of all species collected in Panamanian coastal waters; complementing the available information, with specimens collected by us in different Panamanian coastal areas. In a second chapter we cover what happens when climate change and some human activities intervene that contribute to the dispersal of species considered exotic from tropical waters to semi-temperate waters, such as *Bursatella leachii*. As its introduction into Mediterranean waters has not been well established for this species, we have carried out a molecular analysis study of the populations of this species found on Catalonian coasts to determine the origin of the Mediterranean populations and determine whether the wide Atlantic Ocean is a barrier. natural for this type of species. Furthermore, in a third chapter we compiled the records of *Berthella stellata* on the Catalan coast and did a study over time of a permanent population of *B. stellata* in the town of Es Caials (Costa Brava, NE Spain). For this, we collected and photographed live specimens and studied details of their morphology, their radula and jaws, as well as molecular data to compare them with GenBank data from other specimens from different parts of the world, in order to determine to which regions, the Catalan populations of *B. stellata*. Ending with a fourth chapter where we compare the small red specimens of the *Aplysia* genus previously considered as *Aplysia parvula*, with the larger *Aplysia punctata*. These specimens of *A. punctata* that inhabit the Catalonian coast show two different color patterns, which are believed to represent two different species. As we do not know why the color change, we set ourselves the goal of knowing what this color change is due to. of the *A. punctata*. Obtaining in the first chapter a resulting catalog for the coasts of Panama of 233 species, of which 118 are found on the Caribbean coast, 127 on the Pacific coast, eight on both coasts and eighteen Amphi-Atlantic; results that confirm the high biodiversity of heterobranch sea slugs in the Panamanian coasts. In the second chapter we obtained that the haplotypes of *B. leachii* from the Catalonian coasts are the same as those of the populations of the American Atlantic and Africa, and that the first colonizers of *B. leachii* possibly entered through the Strait of Gibraltar for those from the Atlantic; concluding that the wide Atlantic Ocean is not a natural barrier. In the third chapter we find that the population of *B. stellata* from Es Caials shares both morphological and molecular aspects with specimens from the Northeast Atlantic and the Mediterranean in Europe and we conclude with the results of the fourth chapter in which we confirm that the small red specimens of *A. punctata* feed on red algae, mainly *Sphaerococcus coronopifolius* and *Plocamium cartilagineum*; that they give it a morphological appearance very similar to the adults of *A. parvula* and that the adults of *A. punctata* feed preferentially on the green algae *Ulva lactuca* where it hides and escapes from predators. Which led us to conclude that this change in feeding behavior is probably related to defensive camouflage strategies.

Resumen

La biodiversidad de un país, es parte de su riqueza natural y el estudio de ella es fundamental para un investigador científico, tal es el caso de las costas marinas panameñas en la que no ha habido una descripción taxonómica exhaustiva de las especies panameñas de babosas marinas heterobranquias registradas por diferentes autores. Aquí en el primer capitulo tratamos de conocer la biodiversidad de babosas marinas panameñas proporcionando las descripciones de todas las babosas marinas de las costas de Panamá, basadas en referencias publicadas y fotografías confirmadas de todas las especies recolectadas en las aguas costeras panameñas; complementando la información disponible, con ejemplares recolectados por nosotros en diferentes zonas costeras panameñas. En un segundo capitulo abarcamos lo que sucede cuando intervienen el cambio climático y algunas actividades humanas que contribuyen a la dispersión de especies consideradas exóticas de aguas tropicales a aguas semi-templadas, como la *Bursatella leachii*. Como en esta especie no ha sido bien establecida su introducción en aguas mediterráneas, hemos realizado un estudio de análisis molecular de las poblaciones de esta especie encontradas en costas catalanas para determinar el origen de las poblaciones mediterráneas y determinar si el ancho Océano Atlántico es una barrera natural para este tipo de especies. Además, en un tercer capitulo recopilamos los registros de *Berthella stellata* en la costa catalana e hicimos un estudio a lo largo del tiempo de una población permanente de *B. stellata* en la localidad de Es Caials (Costa Brava, NE de España). Para eso recolectamos y fotografiamos ejemplares vivos y se estudiaron detalles de su morfología, su rádula y mandíbulas, así como datos moleculares para compararlos con los datos del GenBank de otros ejemplares de diferentes partes del mundo, con el fin de determinar a qué regiones pertenecen las poblaciones de *B. stellata* catalanas. Finalizando con un cuarto capitulo en donde comparamos los pequeños ejemplares rojos del género *Aplysia* considerados anteriormente como *Aplysia parvula*, con los de mayor tamaño de *A. punctata*. Estos ejemplares de *A. punctata* que habitan las costas catalanas muestran dos patrones de coloración diferente, que se cree que representan dos especies distintas, como no sabemos porque el cambio de coloración, nos planteamos el objetivo de saber a qué se debe este cambio de color de las *A. punctata*. Obteniendo en el primer capitulo un catálogo resultante para las costas de Panamá de 233 especies, de las cuales 118 se encuentran en la costa del Caribe, 127 en la costa del Pacífico, ocho en ambas costas y dieciocho anfiatlánticas; resultados que confirman la alta biodiversidad de babosas de mar heterobranquios en las costas panameñas. En el segundo capitulo obtuvimos que los haplotipos de *B. leachii* de las costas catalanas son los mismos que los de las poblaciones del Atlántico americano y África, y que los primeros colonizadores de *B. leachii* posiblemente entraron por el Estrecho de Gibraltar para los del Atlántico; concluyendo que el ancho Océano Atlántico no es una barrera natural. En el tercer capitulo encontramos que la población de *B. stellata* de Es Caials comparte aspectos tanto morfológicos como moleculares con ejemplares del Atlántico nororiental y del Mediterráneo en Europa y finalizamos con los resultados del cuarto capitulo en cual confirmamos que los pequeños ejemplares rojos de *A. punctata* se alimentan de algas rojas, principalmente *Sphaerococcus coronopifolius* y *Plocamium cartilagineum*; que le dan apariencia morfológica muy similar a los adultos de *A. parvula* y que los adultos de *A. punctata* se alimentan preferentemente del alga verde *Ulva lactuca* en donde se esconde y se escapa de los depredadores. Lo cual nos llevó a concluir que este cambio en el comportamiento alimentario probablemente esté relacionado con estrategias defensivas de camuflaje.

General introduction

The Heterobranch and the early taxonomic classifications

Since the pre-Cambrian period, the biodiversity of our planet has made its contribution through fossils, with mollusks, through their history, which have left an advantageous resource for the understanding of diversity schemes (Castillo-Rodríguez 2014). According to Zhi-Qiang (2011), there are 117 358 living species of the Phyllum Mollusca in a descriptive evolutionary classification. With this number species, these invertebrates have a greater number of species than vertebrates (64 832), but are below the arthropods that have approximately 1 242 042 described.

Ortea *et al.* (2003) indicate that marine mollusks occupy a wide variety of niches and in particular the most specialized ones; these have been considered as focal elements of marine biodiversity measurements due to the interrelationships with other groups of organisms. His study serves as a basis for biological sciences and collectors, among other specialties, thanks in large part to the different characteristics that contribute to its successful colonization of reef areas, mangrove forests and coastal lagoons; establishing ecological niches, down to depths of 5 000 m, starting with the intertidal zone, continuing along the slopes and ocean depths (Castillo-Rodríguez 2014).

Gastropoda, for Bieler (1992), is a class of mollusks that includes snails, slugs and their relatives, it is hyper diverse with respect to the number of species, morphology and habitat. They are found in marine, freshwater and terrestrial systems, and show a wide disparity of the body plan. According to Appeltans *et al.* (2012) there are described a total of 32 000 – 40 000 living marine species, but it is believed that they represent only between 23 and 32% of the estimated total. In addition, Barker (2001) says that there are large numbers of snails and slugs that have yet to be described, many of which are threatened to an unprecedented degree among other invertebrate groups (Collen *et al.* 2012).

The Gastropods were divided into two subclasses in the late 19th and early 20th centuries: Streptoneura and Euthyneura. The first subclass more or less included the "Prosobranchia" (marine snails), and the second included two very different groups, considered as orders: those with aquatic respiration (Opistohranchia, the marine sea slugs in broad sense) and those with air respiration through a vascularized paleal cavity or lung (Pulmonata, land snails and slugs). Two suborders Tectibranchia and Nudibranchia, due to the possession or not of a shell, respectively, were included within the Opisthobranchia.

The species in the "Opisthobranchia" have a relatively recent history, as they appear to have been unknown to naturalists prior to Linnne, who describes only seven species of the genera *Doris*, *Syllaea*, and

Tethys, in his twelfth edition of "Systema Naturae" in 1767. He classifies them within the Vermes class. Between 1788 and 1806, O.F. Muller in his four volumes of "Zoology Danica", includes 14 species of the nudibranch and sacoglossal groups. In the years 1804 and 1815, another of the first naturalists interested in marine animals, Montagu, published in a series of notes, the description of 12 species of British nudibranchs belonging to the genus *Doris*. Currently none of Montagu's species belong to the genus *Doris*, and are included into the genera *Doto, Trinchesia, Goniodoris, Thecacera, Coryphella, Hermaea* and *Facelina*.

It had to wait until Cuvier for the true descriptions of the groups studied to appear. He separated these mollusks from the truly testaceous ones, in his numerous dissections made for the publication of his famous "Memoirs" which lead him to discover the affinities of the genera *Tritonia*, *Doris*, *Tethys* and *Glaucus* with the testaceous mollusks and to establish for the first time in 1817, the order of Nudibranchia, where he included mollusks without a shell, with radula, with gills projected to the outside, with a concentrated nervous system and with a single or subdivided digestive gland.

After this, there were numerous investigations by authors who were interested in the fauna of these mollusks based on the rules of the French school. In 1841, Sars, was the first to notice the metamorphosis that these mollusks undergo, when presenting a larval stage of a small shell provided with an operculum. In 1842 at the same time, Milne Edwards, Delle Chiaje and Quatrefages, show the existence of a branched structure called the gastrovascular system, which can penetrate the dorsal papillae of nudibranchs and sacoglossans. In 1844, the first to show that this system was the liver and bile canaliculi was Souleyet.

From 1845 to 1855, Alder and Hancok published their monographs on British nudibranchs in seven parts, then published by the Ray Society of London in two volumes, plus a supplementary volume published in 1910, by Eliot.

The division of the nudibranchs into two groups, is due to Bergh in 1870, who based on the structure of the digestive gland, separated them into nudibranchs with the digestive gland in the form of a compact mass (Holohepatic nudibranchs), without branching, with external symmetry and anus in the line mid-dorsal, surrounded by gill leaves; and nudibranchs with the digestive gland divided into lobes and sometimes profusely branched within the dorsal papillae or cerata (Cladohepatic nudibranchs), with the anus generally lateral (to the right) and without no typical branchial plume In the Holohepatic, the Phanerobranchia stood out, with gills with contractile but not totally retractable capacity, and the Cryptobranchia, with gills capable of fully retracting into a permanent cavity under the mantle, the rhinophores being also retractable (Fischer 1883). Finally, Bergh (1892) proposed to separate the

Phanerobranchia into two large tribes: Suctoria and Nonsuctoria, considering the existence or not of an aspirating or ingluvio crop that can present as a dorsal bypass of the pharynx. However, Odhner (1934) introduces the innovations that are followed by most modern researchers until the advent of molecular biology, saying that the digestive gland of nudibranchs could have been differentiated in several lines from more primitive forms, he proposes four different orders of nudibranchs: Doridacea, Aeolidacea, Dendronotacea and Arminacea.

Later, Pruvot-Fol (1954) proposed dividing the Cladohepatic into those characterized by having deciduous spindle-shaped papillae and generally with cnidosac (Cladohepatica sensu stricto), and those with dorsal appendages in a single row on each side of the back, not deciduous and may even be missing (Heterohepatic).

Currently, molecular phylogenetic studies face conflicting phylogenetic signals regarding the markers and methods used for the inference of true results. Producing contradictory phylogenetic hypotheses and contradictory taxonomic classifications, leading to an enormous variety of taxonomic names and concepts. Haszprunar (1985) talk about some of these problems in his work where he redefined the Heterobranchia concept and broadened our vision on Euthyneura. More than 34 years later, has been extensively revised the taxonomic literature on Gastropoda Heterobranch using molecular data to update plausible current systematic concepts that may serve as the basis for future studies on these enigmatic animals. One of the most drastic consequences provided by molecular biology is the paraphyletic consideration of the Opisthobranchia, which lose their taxonomic category and that from here on we will call "opisthobranchs".

The foundations of this new classification are in the taxonomic work of Bouchet & Rocroi (2017) and is currently followed with some minor changes in the World Register of Marine Species (WoRMS) and the Check List of European Marine Mollusca (CLEMAM).

The current taxonomic scheme of gastropods would be as follows:
Class Gastropoda Cuvier, 1795
  Subclass Amphigastropoda Simroth 1906 †
  Subclass Archaeobranchia Parkhaev 2001 †
  Subclass Patellogastropoda Lindberg 1986
  Subclass Neomphalina McLean 1981
  Subclass Cocculiniformia Haszprunar 1987

SubclassVetigastropoda Salvini-Plawen 1980
Subclass Neritimorpha Golikov & Starobogatov 1975
Subclass Caenogastropoda Cox 1960
Subclass Heterobranchia Burmeister 1837

The first six subclasses correspond to groups of gastropods previously included within the Prosobranchia (sea snails). The first two subclasses correspond to fossil mollusks. Within the Heterobranchia subclass (=different gills) all the traditional "opisthobranchs", the pulmonates and some minor groups of ancient prosobranchs are integrated.

The molecular biology and recent taxonomy of the Heterobranchia

Behrens & Hermosillo (2005) indicate that within the Heterobranchia subclass, more than 3000 living species of sea slugs (previously known as "Opisthobranchia") are known in the world, most of them marine, with a variety of very striking shapes and colors.

Jörger *et al.* (2010) have carried out a phylogenetic analysis of the small group of the Acochlidia, small interstitial gastropods traditionally considered "opisthobranchs", to glimpse its origin and its relationships with the other groups of the Heterobranchia. Also, Schrödl *et al.* (2011) have analyzed the phylogeny of Eutineura based on molecular analysis and have obtained results that substantially modify the most recent taxonomic and phylogenetic schemes (Figure 1).

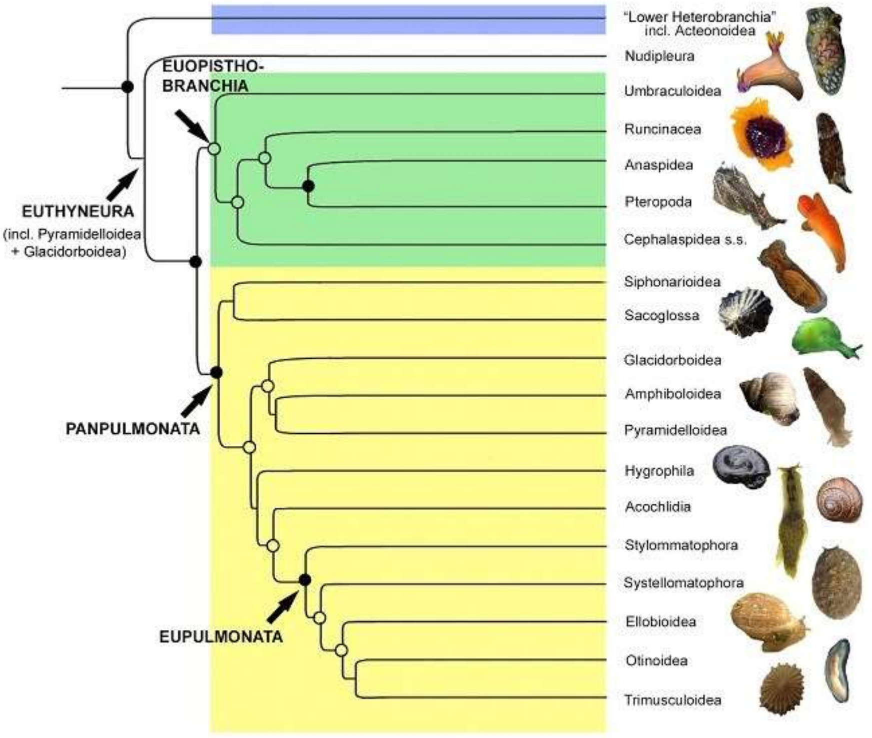

Figure 1. Phylogenetic scheme of the Eutineurans according to Jorger *et al.* (2010).

The results of the work of Jörger *et al.* (2011) indicate three main clades in the Euthyneura, that of the Nudipleura, which includes all the traditional Nudibranchia (sea slugs in the strict sense) and the Pleurobranchida, that of the Euopisthobranchia where all the other traditional groups of "opisthobranchs" except for the Sacoglossa that are included in the third clade, the Panpulmonata, where all terrestrial and freshwater snails and slugs are integrated, as well as other marine groups such as the Pyramidellomorpha and the Acochlidia from the work of Jorger *et al.* (2010).

The controversies that exist in some points of the phylogenetic cladogram mean that more molecular analyzes are carried out to confirm or not the previous affirmations, especially those referring to the composition of the two clades of the Euopisthobranchia and the Panpulmonata. Although the internal relationships between clades remain unresolved, this phylogenetic hypothesis has been repeatedly tested and consensus has now been reached (see review in Wägele *et al.* [2014]). The phylogeny given in Figure 2 shows the relationships between the current heterobranch subclades, leaving the concept of "Opisthobranchia" as a historical and emotional value. The Heterobranchia are divided into some "lower clades" and a group characterized by detorsion of the nervous system called Euthyneura (= euthyneury), the latter characterized by having rhinophores innervated by N3 (rhinophoral nerve). The Euthyneura comprise the Nudipleura (sensu Wägele & Willan 2000), and Tectipleura (sensu Schrödl *et al.* 2011), which are a monaulic taxon Nudipleura consisting of Pleurobranchoidea and Nudibranchia (they are sea slugs in a strict sense). The possession of a blood gland, a dialogical reproductive system and the loss of the osphradium (Wagele & Willan 2000), are characteristics that define Nudipleura. The main synapomorphy of Tectipleura is the possession of a single flow for autosperm, allosperm and ovules; characteristics that divide it into Panpulmonata, including Sacoglossa, Pulmonata and Euopisthobranchia, which present a cuticularized esophagus (Schrödl *et al.* 2011, Wägele *et al.* 2014). The latter group includes the well-known orders of "opisthobranchs'" such as the most primitive and traditional Cephalaspidea, the Aplysiida or sea hares, and the pelagic Pteropoda.

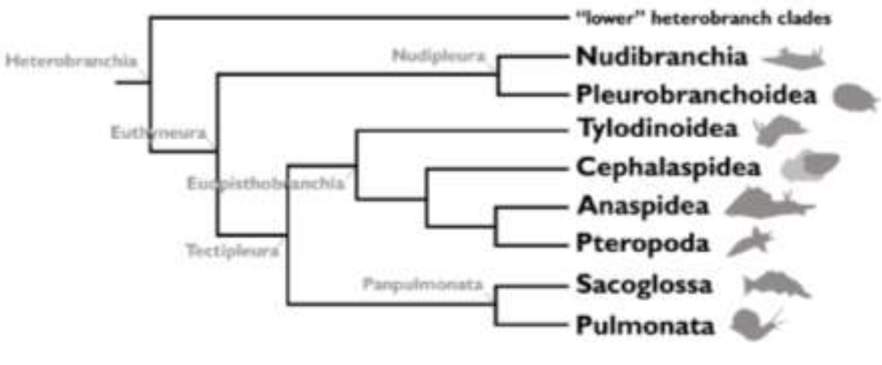

Figure 2. Consensus tree of the phylogenetic relationships of the main groups of Heterobranchia. Source: modification made by Moles 2016 of those made by Wägele *et al.* 2014 and Zapata *et al.* 2014.

A very recently published article (Krug *et al.* 2022) confirms the monophyly of the Euthyneura, the Nudipleura (Nudibranchia + Pleurobanchida) as a sister group to the Tectipleura, the Euopisthobranchia (Cephalaspidea + Tylodinoidea + Aplysiida + Pteropoda) as a sister clade to the Panpulmonata and within these the Sacoglossa as a sister clade to the new clade they call Pneumopulmonata (Siphonarioidea + Pyramidolloidea + Acochlidiacea + Eupulmonata).

Bouchet & Rocroi (2017) have recently synthesized all the phylogenetic results based on molecular techniques and have proposed the following taxonomic classification of the Heterobranchia:

- Subclass Heterobranchia Burmeister, 1837
  - Grade or Infraclass"Lower Heterobranchia"
  - Infraclass Euthyneura Spengel 1881
    - Cohort Acteonimorpha
    - Cohort Ringipleura
      - Subcohort Ringiculimorpha
        - Order Ringiculida
      - Subcohort Nudipleura Wägele & Willan 2000
        - Order Pleurobranchida J.E. Gray 1827
        - Order Nudibranchia Cuvier 1817
          - Suborder Doridina (Odhner 1934)
            - Infraorder Bathydoridoidei
            - Infraorder Doridoidei
          - Suborder Cladobranchia Pola & Gosliner 2010
    - Cohort Tectipleura Schrödl, Jörger, Klussmann-Kolb & Wilson 2011
      - Subcohort Euopisthobranchia Jörger, Stöger, Kano, Fukuda, Knebelsberger & Schrödl 2010
        - Order Umbraculida Odhner 1939
        - Order Cephalaspidea Mikkelsen 1996
        - Order Runcinida Burn 1963
        - Order Aplysiida [Anaspidea] Pelseneer 1906
        - Order Pteropoda Cuvier 1804
          - Suborder Euthecosomata Meisenheimer 1905
          - Suborder Pseudothecosomata Meisenheimer 1905
          - Suborder Gymnosomata Blainville 1824

Subcohort Panpulmonata Jörger, Stöger, Kano, Fukuda, Knebelsberger & Schrödl 2010
- Superorder Sacoglossa Ihering 1876
- Superorder Siphonarimorpha
- Superorder Pylopulmonata
- Superorder Acochlidimorpha
- Superorder Hygrophila
- Superorder Eupulmonata Haszprunar & Huber 1990
  - Order Ellobiida
  - Order Systellommatophora Pilsbry 1948
  - Order Stylommatophora A. Schmidt 1855
    - Suborder Achatinina
    - Suborder Scolodontina H.B. Baker 1925
    - Suborder Helicina Rafinesque, 1815

The "Opisthobranchia" and the dispersion of the species

Much emphasis has recently been placed on the geographic distribution of sea slug species, their dispersal throughout the oceans, and the complexes of so-called cryptic species. According to Malaquías & Reid (2009) and Claremont *et al.* (2011) to do this we must review the oceanographic, paleontological and developmental data that are often used to explain transatlantic dispersal and amphitic geographic ranges in mollusks (that is, species that inhabit both the eastern and western coasts of the Ocean Atlantic). One of the people who demonstrated that passive dispersal is very important for the distribution of shallow-water mollusk species was Scheltema (1971, 1979 and 1995).

As the larvae of marine gastropods are capable of frequent long-distance dispersal; they can be expected to serve as agents for colonizing new regions and as gene flow vectors between widely separated populations. According to the fossil record, transatlantic expansions seem to have occurred since the late Oligocene (Vermeij 1995; Maestrati & Lozouet 1996; Petuch 1997), increased after the closure of the Isthmus of Panama in the Pliocene, this made the gulf current stronger and the Atlantic circulation intensified (Vermeij & Rosenberg 1993; Briggs 2003; Teske, Cherry & Matthee 2004; Williams & Reid 2004). These species whose geographic distribution area is located on both coasts (eastern and western) of the Atlantic Ocean, are called amphiatlantic and are currently being studied due to the presence of many of these on coasts that supposedly were not, some are a complex of species only resemble morphologically, but others are circumtropical or pantropical found in different areas of the planet. That is why we are conducting this paper to determine if some species of sea slugs have managed to cross the wide Atlantic Sea from some Caribbean coasts such as Panama and Costa Rica to colonize other areas such as the Mediterranean Sea.

It is very common among the "opisthobranchs" the distributions of amphiatlantic species. A recent biogeographic study (Garcia & Bertsch, 2009) recognized 134 species that occur on both sides of the Atlantic Ocean, that is equivalent to 12.6% of the total diversity in this group.

Anthropogenic activities resulting from the aquaculture trade and maritime navigation are becoming important vectors for the introduction of exotic marine species (Streftaris & Zenetos 2006; Zenetos *et al.* 2008 and 2011; Cervera *et al.* 2010), since Some have been documented, such as the presence in Europe of the Asian species of Cephalaspidea *Haminoea japonica* resulting from the North American oyster trade (Gosliner & Behrens 2006), the introduction of the New Zealand species *Philine auriformis* by navigation in the San Francisco Bay, negatively affecting local fauna (Gosliner 1995) and the occurrence of *Melibe fimbriata* from the Indian Ocean in the Mediterranean Sea (Thompson & Crampton 1984).

Although the lack of barriers is evident for gene flow across the Atlantic, it poses a serious challenge to the idea of regular gene flow between populations inhabiting both margins. According to Scheltema (1971), between 60 and 300 days are necessary to achieve the drift across the Atlantic. This is beyond the larval life of "opisthobranchs"' with planktotrophic larvae which is generally 15-42 days (Schaefer 1996), including some known species with the ability to delay their metamorphosis (Thompson 1958 and 1962; Hadfield & Karlson 1969). To understand what is happening, passive adult displacement can be thought of as a possibility that cannot be ruled out, but this has often been posited as a speculative means of long-distance dispersal, direct evidence would be lacking (Fraser, Nikula & Waters 2011) and so far, no cases have been documented in "opisthobranchs"'.

Due to the evolution of molecular biology, population genetics and phylogeographic methods, research on the evolution and patterns of diversity in the marine environment has been greatly stimulated in the last two decades. Molecular analyzes are a very good tool for detecting sister species and have frequently shown that "species" considered to be cosmopolitan or widely distributed consist of a taxonomic complex of multiple species (Knowlton 1993; Meyer 2003; Williams & Reid 2004; Reid *et al.* 2006; Claremont *et al.* 2011). There is still a long way to go in the use of molecular tools, but their application showed the presence of two different allopatric species of *Bulla striata*, previously considered an amphitic species (Malaquías & Reid 2008 and 2009), they have also intervened in the recognition of cryptic species in the *Melanochlamys* genus of the cephalaspidean in New Zealand (Krug *et al.* 2008).

According to Valdés *et al.* (2006) the sacoglosas *Bosellia mimetica* Trinchese 1891, *Elysia timida* (Risso 1818) and *Thuridilla picta* (Verrill 1901) are three species of "opisthobranchs"' considered amphiatlantic. The first two have the Mediterranean as their type locality, respectively Capri (Italy) and Nice (France), while *T. picta* was described from specimens from Bermuda (western Atlantic). These species have a temperate / tropical distribution and thrive in shallow environments in the green algae on which they feed. *Bosellia mimetica* has a planktotrophic larva (Clark & Jensen 1981) and *E. timida* has a direct or lecithotrophic development (Rahat 1976; Bonar 1978; Marin & Ros 1989, 1992 and 1993; Jensen 2001). The development of *T. picta* is unknown, but a similar species *T. hopei* has lecithotrophic larvae and field observations have revealed that the eggs of this last species resemble those of *T. picta* (Jensen 2001).

General anatomy and morphology

The detorsion process is the main characteristic of the anatomical organization of heterobranch sea slugs' mollusks, it lies in a radical change in the organization of the body during the development process. Its digestive system is characterized by the presence of a muscular oral mass that contains the radula and the labial armor. The radula is a strip of chitinous teeth that is used for food in different ways. Its shape varies greatly among "opisthobranches"' and is generally a good distinguishing feature between species.

The buccal mass is usually attached to a pair of salivary glands and the esophagus. The latter in many groups of "opisthobranches"' has a crop with numerous chitinous plaques and connects to the intestine through the stomach, which is a more or less dilated area to which the digestive gland joins; there is a digestive cecum that connects the esophagus and the stomach, in some groups. Its circulatory system is open, as in the rest of the mollusks excep cephalopods, and the circulation of the blood is partially produced by a two-chambered heart and the movement of the body; the nervous system is composed of a ring of ganglia located around the anterior region of the esophagus joined by commissures and connective tissue. Figures 3, 4 and 5 show the external characteristics of different groups of heterobranch sea slugs.

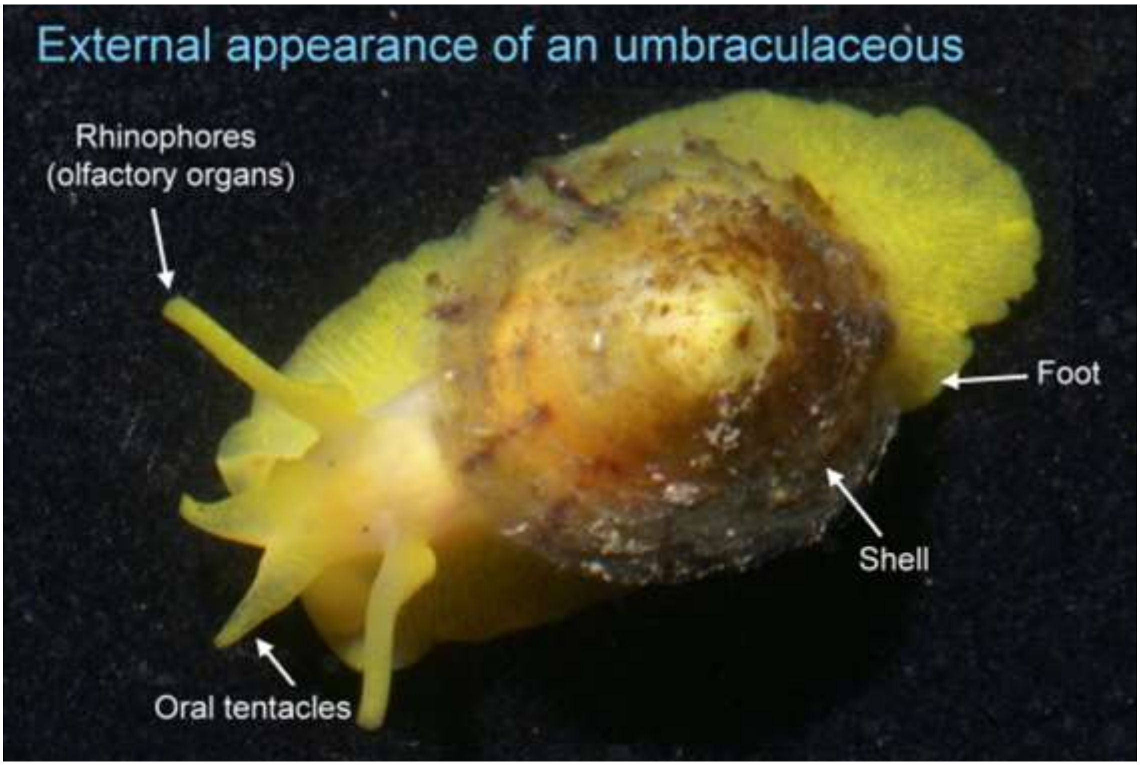

Figure 3. External appearance of a umbraculacean heterobranch sea slug like *Tylodina perversa*

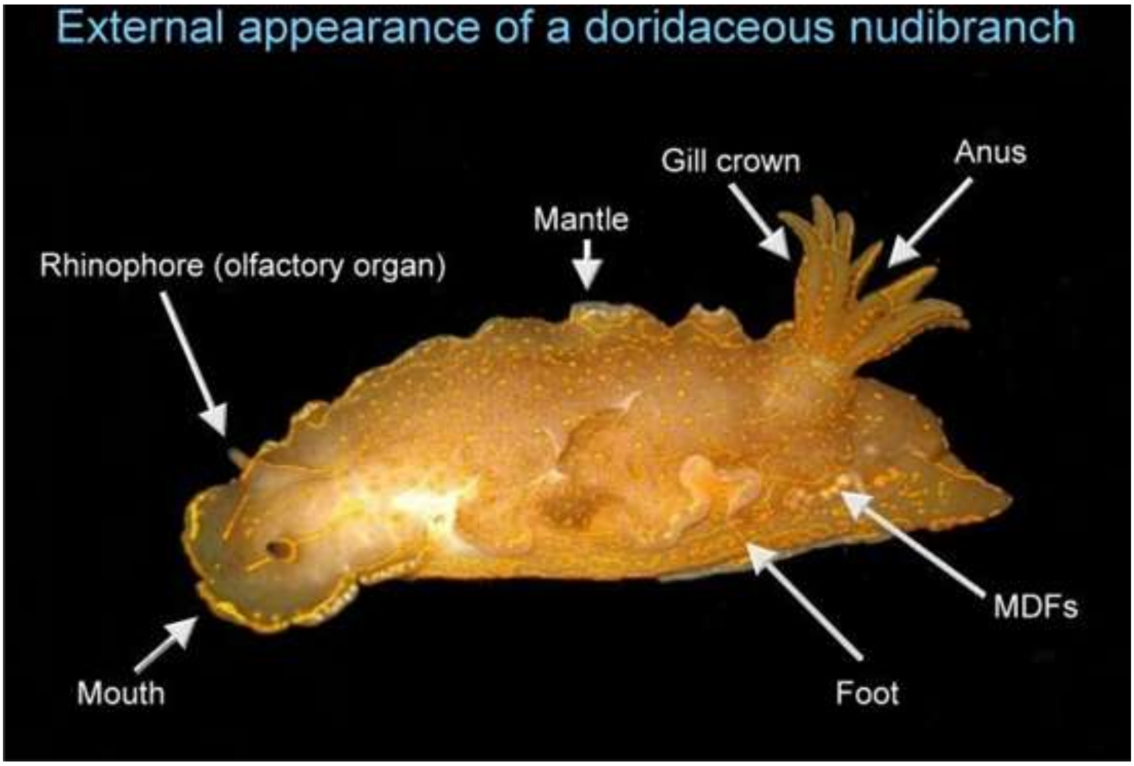

Figure 4. External appearance of a doridacean holohepatic nudibranch like *Felimare picta*.

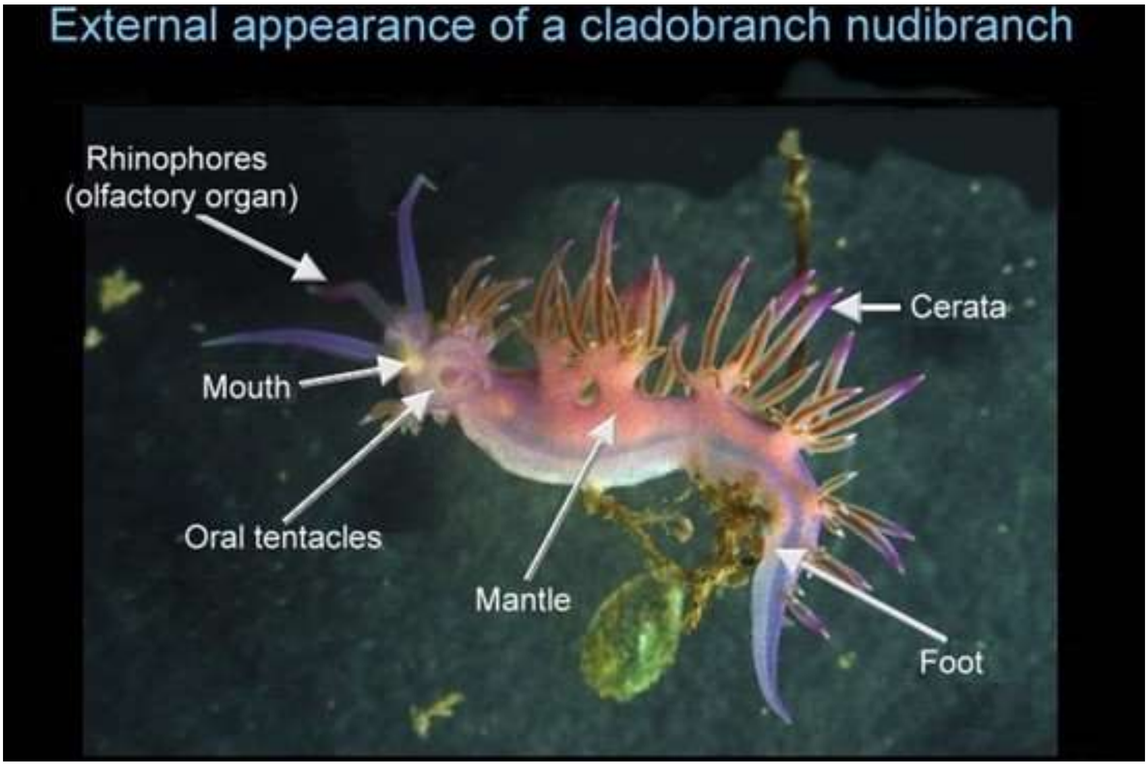

Figure 5. External appearance of a cladobranch nudibranch like *Flabellina affinis*

Defensive strategies of sea slugs

For understanding sympatric predator-driven evolution through the study of chemical defenses and the glandular structures involved, marine heterobranch sea slugs are excellent models since they have a wide range of defensive strategies (Wägele & Klussmann-Kolb 2003; Wägele *et al.* 2006; Wilson *et al.* 2013). Most heterobranch taxa contain unshelled species and bare representatives in addition to nudibranchs. Therefore, current phylogenies suggest that the loss of the shell occurred several times during its evolution (Medina *et al.* 2011; Zapata *et al.* 2014; Wägele *et al.* 2014).

From an evolutionary point of view, the loss of the shell represents an advantageous energy saving, that would otherwise be used for its production and transport, as well as other respiratory and excretory advantages. However, this implies investing in alternative defense strategies to survive against suspected predators. In fact, the loss of the shell in sea slugs led to a variety of defensive strategies, including the use of chemicals (Ávila 1995; Cimino & Ghiselin 2009; Putz *et al.* 2010).

One of the key innovations behind the evolutionary success of sea slugs is the ability to steal functional structures, i.e. cleptoplastia, cleptocnidae (kleptochemistry) from other organisms. Sacoglossa heterobranch, such as *Elysia viridis*, steal chloroplasts from algae for energy and camouflage (Händeler *et* *al.* 2009), while most aeololids nudibranchs steal nematocysts at the tip of their cerata from cnidarians which they feed on to use as protective devices (Putz *et al.* 2010) (Figure 6).

Figure 6. Cnidosacs with nematocysts at the tip of the cerata of the aeolidacean nudibranch *Nemesignis banyulensis* (Portmann & Sandmeier 1960).

Kleptochemistry, on the other hand, is the incorporation of NPs from the diet, which can then be used for its own defense (Ávila 1995; Cimino & Ghiselin 2009). Dietary-derived bioactive metabolites can be transferred and accumulate in exposed and vulnerable areas, such as the mantle, foot, and gills; within secretions of mucus or ink; in specialized glands; and occasionally in eggs, embryos and larval stages (for example, Avila 1995, Wägele *et al.* 2006; Cimino & Ghiselin 2009) (Figure 7). For example, the species of the Mediterranean nudibranch *Felimare* gather furanoterpenoids from their prey sponges of the genus *Dysidea* sp. and locate them along the exposed edge of the mantle to defend themselves from predators such as fish and crustaceans (Ávila *et al.* 1991a; Fontana *et al.* 1994).

Figure 7. Release of secondary metabolites with a defensive mission in doridacean nudibranchs. On the left *Paradoris indecora* and on the right *Felimare picta* releasing longifolina.

Some species are capable of biotransforming the metabolites in their diet to make them less toxic for the slug itself, or more harmful and persuasive for predators (Ávila 1995; Cimino & Ghiselin 2009). This is the case of *Felimare orsinii* (Vérany 1846), who obtains sesterterpenoids from the sponge *Cacospongia mollior.*

Schmidt, 1862 and transforms it into deoxoscalarin by deoxygenation (Cimino *et al.* 1993). Finally, some marine links can biosynthesize simple precursor chemicals in a completely new way (Cimino & Ghiselin, 1999; Cimino *et al.* 2001). For example, the nudibranch *Dendrodoris limbata* (Cuvier 1804) and *D. grandiflora* (Rapp 1827) form sesquiterpenoids and accumulate them in the mantle and egg masses for defense against predators such as fish (Avila *et al.* 1991b). In general, heterobranch mollusks possess a wide range of bioactive compounds that protect them against potential predators and therefore improve their ecological performance.

The diversity of body shapes and colors are possibly the most fascinating peculiarities of heterobranch sea slugs. They range from those that resemble the substratum where they live to try to go unnoticed (crypsis Figure 8), to those that warn of their presence with striking colors (aposematic coloration Figure 9).

Figure 8. Exemple of crypsis on the substrate: The nudibranch *Duvaucelia odhneri* on the white gorgonian *Eunicella singularis* in the Meditrranean Sea.

Figure 9. Exemple of aposematic coloration: the mediterranean nudibranch *Felimida luteorosea*

Cryptic species are animals that morphologically resemble or have a disruptive coloration, or in taxonomy to be externally similar to congeners, but reproductively isolated, they can only be recognized by molecular analysis; some of these species resemble the environment in which they live.

Something that has forced them to use different defense methods is the total or partial loss of the shell, which can change or combine, according to their state of development. Not being detected by predators is the most effective strategy, which is why various heterobranch use mimicry, crypsis or camouflage, imitating the coloration and shape of the substrate, as the first defensive barrier. On the shores of the Mediterranean you can find multiple examples, one of these is the aplysiid *Petalifera petalifera*, which lives in the leaves of *Posidonia oceanica* where it cannot be differentiated thanks to its greenish coloration. It is also in the sacoglossi we have another example, they show a coloration similar to the algae on which they feed and live. Furthermore, it is very difficult to differentiate specimens of *Elysia viridis* on the green background of an alga of the genus *Codium*. This happened too in many doridacean nudibranchs, which resemble the coloration of the sponge that they feed on.

An example of crypsis is that of the dendronotacean *Duvaucelia odhneri*, a small nudibranch that lives coiled in the branches of gorgonians of the genus *Leptogorgia* or *Eunicella*, which it imitates color (the nudibranch's coloration is almost black in red gorgonians), additionally, the dorso-lateral or cerata projections copy the gorgonian polyps (Figure 8).

Very striking colorations usually present the species with aposematic colorations, instead of trying to go unnoticed, they inform their predators of their toxicity or bad taste, etc. However, if the fish were to learn that these brightly colored animals are not good food, the few heterobranch that survived would be seriously damaged. Thanks to this, when a fish bites a heterobranch with chemical defenses, it immediately expels it and the other fish in the same group learn that these small and showy animals are not so good at feeding (Sánchez 2017).

Some species, such as the Swiss vaquita *Peltodoris atromaculata*, have disruptive colors that make their location difficult, with the same purpose of not being detected (Figure 10). When they are located, other mechanical or chemical defensive systems appear (Sánchez 2017). The mechanical ones are pointed structures that deter the predator from biting its prey, while the chemical ones are based on the emission of toxic substances with a bad taste or with very low pH, obtained through food. These substances are usually released by glands located in the dorsal part of the same or the edge of the mantle, such as the dermal formations of the mantle. Contributions to the knowledge of marine heterobranch.

Figure 10. Exemple of disruptive coloration on the doridacean nudibranch *Peltodoris atromaculata*.

The caryophyllid tubercles are a type of physical defense that many doridaceans possess, they consist of small protrusions surrounded by pointed spicules that provide the animal with a scratchy texture that deceive the predator.

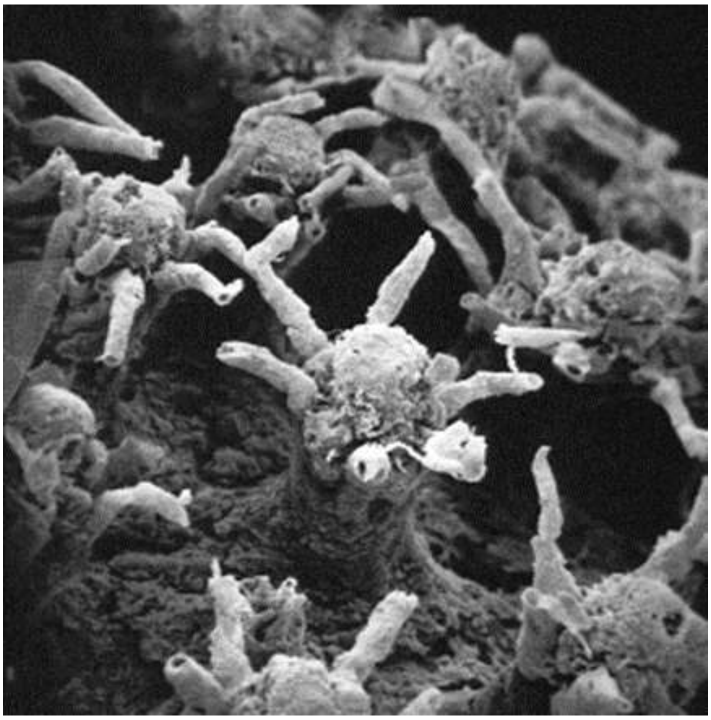

Figure 11. Scanning electron image of the cariophyllid tubercles of the nudibranch of the genera *Acanthodoris*.

The spicules are another case with a deterrent function, they are embedded in the wall of the body, mainly on the edge of the mantle, with the rhinophores and the final part of the foot. Juveniles of some genera of doridaceans generally possess this type of defense (for example, species of the genera *Felimare*, *Felimida* and *Dendrodoris*). However, Sánchez (2017) indicates that the adults of these genera have developed chemical systems, leaving behind the spicules of the mantle and only those of the rhinophores and the final part of the foot remain.

In species of the genus *Felimare*, such as *Felimare bilineata* and *F. villafranca*, the large, pointed spicules of the mantle are replaced by more numerous ones, less than 100 µM in size and with blunt ends. Something similar occurs in *Felimida purpurea*, *F. luteorosea*, *F. krohni* and *F. clenchi*, only that in these species the spicules less than 50 µM in size are spherical and are impregnated in a kind of sheet that are located in the wall. internal body. A viable response to these changes is that when they are juveniles and have not yet developed chemical defenses and aposematic coloration, the most effective form of defense, once they are captured, is to trick their predator by posing as a food with an unpleasant texture and when the chemical defenses and aposematic coloration have already been obtained, maintaining these deceptive structures can lead to a loss of energy.

The Aeolidids have a very elaborate defense system. They generally eat cnidarians, taking advantage of their defense system, making it their own by storing the cnidocytes at the ends of their cerata or dorsolateral projections, which are coupled with the digestive system. When a predator attacks them, they can contract and show the cerata as if they were the tentacles of an anemone, they can also detach from them and then regenerate them (Sánchez 2017).

Food and radulae

The heterobranch sea slugs feed on a great diversity of organisms. The vast majority of them are highly specialized carnivorous or herbivorous predators that selectively prey on one organism and that are often limited to a single genus of animal or plant. Most of the species grouped to each family of Heterobranch sea slugs feed on similar prey.

It has been proven that food specialization is so important for some species, because their metamorphosis from the larval stage to the adult stage is induced by the presence in their habitat of the species on which they feed. Thus, the lifespan of a heterobranch can be related to that of its prey and, therefore, two categories can be established according to the type of food, these are: sea slugs that feed on seasonal prey, such as hydrozoans, show short-lived generations each year and sea slugs that feed on non-seasonal prey, such as sponges, manage to live for a year or more.

The radula of molluscs is a very important element for capturing their food. It is composed of rows of chitinous teeth of different shapes that help to chop the food ingested through the mouth. The structure of the radula and the number of radular teeth are of great taxonomic importance in most species.

Within the species, there are taxonomically different differences, in terms of the number of rows of teeth that make up the radula and also the shape of each tooth (Figures 12 and 13). This particularity, once numbered, becomes the "fingerprint" for each individual species and is manifested through a "radular formula". Unfortunately, the use of this does not culminate in the determination of a species, in terms of genera and even within families, because many differences are found in the number of teeth and their shape. This makes radular analysis a very important taxonomic aid, but it should not be used as the only characteristic to identify species.

The radula can be a species-specific instrument ecologically suitable for the food that the animal prefers. Most heterobranch are browsing carnivores, with the exception of the orders Sacoglossa, Aplysiida, and some Cephalaspidea. In general, the conformation of the radula is ideal for the food preferences of any species, but most heterobranch have a pair of jaws, which are in front of the radula, which helps them to capture food when they eat. A broad radula is found in doridacean cryptobranch nudibranchs, with many teeth, to be able to scrape and swallow pieces of sea sponges that they use for food. This is different from that of the doridacean phanerobranchs that have a narrow radula due to the type of food they eat that is articulated and filamentous. With the exception of some dorids, most do not have strong jaws. Quite the contrary, some dendronotacean and aeolidacean nudibranchs that eat hydrozoans and bryozoans, therefore have narrow radulae, but their jaws are strong. Although it is observed, there are differences in the radulae of these groups, but this is generally linked to the type of food they prefer.

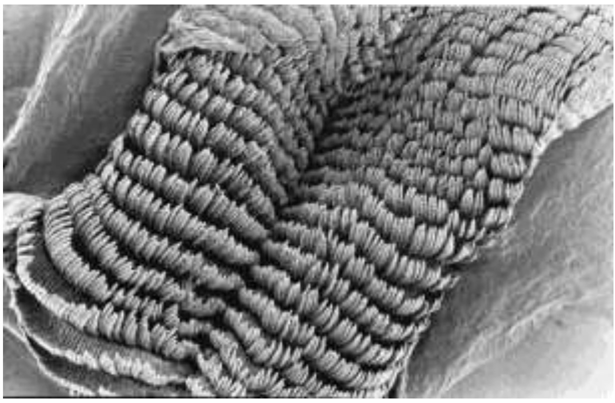

Figure 12. SEM image of the radulae of *Paradoris indecora* (Bergh 1881), a doridacean nudibranch.

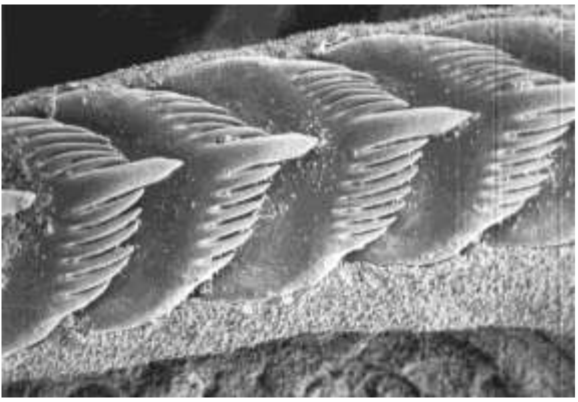

Figure 13. SEM image of the radular teeth of *Cratena peregrina* (Gmelin 1791), a cladobranch aeolidacean nudibranch.

Sea slugs without radula, such as those of the genus *Melibe*, prefer to swallow their food whole, others as those the genera *Doriopsilla*, *Dendrodoris* and *Phyllidiopsis* suck the cell contents using a kind of very specialized "mouth pumps". There are Cephalaspidea species of the Aglajidae family that do not have a radula, but have a very muscular mouth mass that helps them to attack their prey quickly and swallow them whole.

The old and worn teeth are shed and deposited in a sac-like site that is located in the mouth in the superorder Sacoglossa, etymologically giving the name to the group, but the significance of this is unknown. Its radula is a single row of teeth that are positioned to "prick" the cells of algae or the receptacles of the eggs of other heterobranch.

Some Sacoglossa, such as *Elysia timida*, to improve their diet, conserve chloroplasts that they obtain from the algae that serve them as food, making them part of their digestive system, which facilitates the generation of sugars that are absorbed and consumed by them. Also, dendronotaceans and eolidaceans of tropical zones have symbiotic algae in their tissues that emulate the activity of chloroplasts.

Strong jaws, small and fine radula, we find in the Pleurobranchida, with about 200 teeth ready in a single row. Little is known about their preferred prey, but in some species, they are associated with certain tunicates and sponges. A long and wide radula have the Aplysiida have, especially to graze on the algae that serve them as food.

Here are some foods from different genus of heterobranch sea slugs:

- Hydrozoans: *Doto*, *Hancockia*, *Flabellina*, *Facelina*, *Cratena*, *Caloria*, *Eubranchus*, *Cuthona*, *Embletonia*, *Tergipes*
- Anemones: *Aeolidia*, *Aeolidiella*, *Spurilla*
- Sea feathers: *Armina*
- Gorgonians: *Tritonia*
- Calcareous sponges: *Aegires*
- Non-calcareous sponges: *Cadlina*, *Chromodoris*, *Felimare*, *Rostanga*, *Doris*, *Aldisa*, *Discodoris*, *Geitodoris*, *Platydoris*, *Jorunna*, *Thordisa*, *Peltodoris*, *Phyllidia*
- Bryozoans: Okenia, *Onchidoris*, *Polycera*, *Tambja*, *Limacia*, *Crimora*, *Janolus*
- Sea squirts: *Okenia*
- Fish and cephalopod eggs: *Calma*
- Sea slugs' eggs: *Favorinus*
- Other sea slugs: *Roboastra*, *Gymnodoris*, *Facelina*
- Kamptozoans (Entoprocta): *Trapania*

Sensory organs and rhinophores

In the paleal cavity of primitive slugs there are sensory folds called osphradium. This sensory mechanism works in this way: the water currents pass through the osphradium which allows the slug to identify the chemical compounds in its surroundings (substances such as odor).

The most outstanding sensory structures are the so-called rhinophores, they are little horns located on the head; very little is known about them, they are similar to other sections of the animal body, but they lack secretory organs. Most authors agree that foraging for food and identifying other individuals of their own species to reproduce are the main functions of rhinophores. The rhinophores are shaped like rabbit ears and are curled, in a large part of the Sacoglossa, in all the Aplysiida (Figure 14) and Pleurobranchida, the inner part is ciliated favoring the transport of water. The outer tissue (epithelium) is lined with nerve endings as receptors. In Cephalaspidea they are not present, but the function is assumed by the organ of Hancock, or a sensory tube. They are more complicated in nudibranchs, existing lamellae or tubercles, and in cryptobranch doridacean nudibranchs they retract within the body.

Figure 14. Detail of the rhinophores of an Aplysiida, shaped like rabbit ears.

Respiration, cerata and gills

The cerata and the gill feathers or gills are the organs where respiration takes place in sea slugs. Cerata are similar to a finger or stick, they are arranged in uniform groups to one side and on the other to the mantle. They appear in the eolidacean and dendronotacean nudibranchs, also in some arminaceans and sacoglossans. The doridacean nudibranchs have generally a ring of gills near the anus that allows them to breathe. In cephalaspids, aplysiids and pleurobranchids, the gills are more advanced organs, located under the mantle or in a cavity of this.

Reproduction

Heterobranch sea slugs are hermaphrodites and cross copulations are carried out between two individuals, so fertilization is internal. Being hermaphroditic, all mature individuals of any species are suitable for reproduction, which is advantageous because it increases the fertilization of the group.

Copulation between individuals usually occurs at the same time (both animals provide sperm and eggs) (Figure 15). The hermaphroditic gonad or ovotestis produces the two types of germ cells, ovules and sperm, and the rest of the reproductive glands and the genital orifice are located to the right of the body, very close to the head, so the specimens copulate in opposite directions. Many species of sea hares gather to copulate, where several individuals, up to more than 10, can form a chain where the one in first position receives sperm from the second, from this one to the penultimate they give sperm to the one in front and receive from the which is located behind and where the last in the chain only gives sperm to the one in front without receiving from any other

Figure 15. Two especimens of he nudibranch *Polycera quadrilineata* (O.F. Müller 1776) in copulation.

Heterobranch usually lay their eggs in places or organisms where they feed, which is proof that the animal is present at the site. The shape, size and color of the eggs is highly variable between species, which helps in their classification and identification (Figure 16).

In most sea slugs, embryonic development is indirect since there is a free-living larva veliger that lives in the plankton; in these species the eggs are very small in size and the larvae hatch quickly. But there are some species where development is completed by not releasing the larva, this is called direct development (who hatches in the water is a tiny individual very similar to the adult), in these species the eggs are larger because they have a lot of food that serves the embryo in its juvenile stage.

Figure 16. Eggs mass of the nudibranch, *Platydoris argo* (Linnaeus, 1767).

Objectives

- One of the main objectives of this memory has been to know the biodiversity of sea slugs on the coasts of Panama (country of origin of the doctoral student), both on the Caribbean side and on the Pacific coast. Until now, fragmentary data were known from some studies on marine heterobranchs in the Caribbean (Meyer 1977; Collin, 2005; Goodheart *et al.* 2016) and on Coiba Island in the Pacific (Hermosillo 2004; Camacho-García 2006). For this, a complete review of the published literature has been carried out, complemented with data from own collections and an annotated inventory of all the species cited for the Panamanian coasts has been carried out.

- Furthermore, in this study we will try to give an explanation about the appearance of amphiatlantic or cryptic "Opisthobranches" species from both ends of the Atlantic, applying systematics, taxonomy and molecular phylogeny, to test the hypothesis that the width of the Atlantic does not constitute an insurmountable barrier for the dispersal of larvae of species and a molecular phylogenetic study has been carried out to find out the origin of the specimens of the sea hare *Burstella leachii* Blainville 1817 collected in the western Mediterranean and the population of the pleurobranchid *Berthella stellata* (Risso 1826) has been studied on the coast of Catalonia (NE Spain), a species until recently considered to have a very wide geographical distribution it is also intended to definitively clarify, by means of molecular methods, the specific status of the small-sized, red-colored specimens of *Aplysia* specimens from the western Mediterranean, attributed until recently to *Aplysia parvula* Mörch 1863, a species considered to be circumtropical.

Chapter One. The main objective is to describe the biodiversity of Panamanian sea slugs by providing descriptions of all sea slugs from the coasts of Panama, based on published references and confirmed photographs of all species collected in Panamanian coastal waters; complementing the available information, with specimens collected by us in different Panamanian coastal areas.

Chapter Two. Given the doubt about the origin of the *Bursatella leachii* specimens found on the Catalonian coast, it became necessary to carry out a morphological and molecular analysis of *B. leachii* from two Catalan coastal sectors (the Fòrum bathing area, Barcelona and the Ebro Delta, Tarragona), and compare them with other *B. leachii* from different regions of the world to evaluate the origin of the *B. leachii* specimens found in the Western Mediterranean, and to know if the Atlantic Ocean is a natural barrier for the dispersal of this type of species.

Chapter Three. We studied the population of *Berthella stellata* in the municipality of Es Caials (Costa Brava, Catalonia, NE Spain); comparing it with other specimens of the same species from the northeastern Atlantic and Mediterranean regions of Europe, for this we have used morphological aspects, where we analyze the evolution of the population during two decades, the chromatic variability of the specimens and details of their biology; we also combined it with molecular analysis, using two mitochondrial genes (COI and 16S) and one nuclear gene (H3); to compare whether these populations of *B. stellata* are the same, both in the Northeast Atlantic and in the Mediterranean of Europe, with those found by us on the Catalonian coast of Es Caials.

Chapter four. Clarify why *Aplysia punctata* has two colorations in its external morphology throughout its life history, as well as the reasons why the feeding strategy of individuals changes as their size increases. In this article we attempt to address these questions by examining changes in feeding behavior during different life cycle stages of *A. punctata*, as well as reproductive period, mating behavior, egg mass coloration, and other traits based on natural populations and collected individuals for observation in the laboratory. In addition, molecular analyzes were performed to verify the identity of the examined specimens and confirm or refute the results of Golestani *et al.* (2019).

CHAPTER I. Two oceans: biogeographic and taxonomic review of marine heterobranch sea slugs (Mollusca: Gastropoda) from Panama waters.

The Isthmus of Panama is tropical rainy, with well-defined seasons, a dry one that begins in December and ends in April, the rainy one that begins in May and ends in December; the air temperature ranges between 27ºC to 36ºC although there are oscillations in the climate as a result of the relief, the altitude and the conformation of the seas. There are also two coastlines, the Caribbean Sea with a length of 1,287.7 km and with crystal clear, very transparent waters, the water temperature is maintained at 28 ° C while the Pacific coasts have a length of 1,700.6 km., the waters are very cloudy due to the phenomenon of outcropping that allows there to be a lot of biodiversity of different species of marine animals due to the large amount of food available.

Formation of the Isthmus of Panama

The union of South America with Central and North America occurred through the geological formation of the Isthmus of Panama (Figure 1), producing the "great American biological exchange" of terrestrial animals and plants (Stehli & Webb 1985), and cutting simultaneously according to Jackson & Budd (1996) the seaway that had connected the eastern Pacific to the western Atlantic for many millions of years.

Figure 1. Isthmus of Panama. Map taken from the page http://www.orangesmile.com/guia-turistica/panama-pa/mapas-detallados.htm

The American continent that we know today was the result of two interconnected geological processes: such as plate tectonics and volcanism. For Coates & Obando (1996), the movement of the different tectonic plates that form Central and South America moved the igneous base of the Isthmus to its current position, while volcanism, caused by the subduction of the Pacific plates, added material to the insular arc that it is the spine of the Isthmus.

Based on Coates *et al.* (2003) and Coates *et al.* (2004) from 10Ma the geology of the Isthmus suffered a sequence of rapid events. Initially it sank, which once again deepened the Pacific-Caribbean Strait. Later, 5 Ma ago, it began to rise once more, producing the emergence of the mainland around it, although shallow marine connections persisted in the Limón, Canal and Darién basins. According to Collins *et al.*, (1995) the rate of uplift of the Isthmus increased and these connections became progressively narrower and shallower until, finally, the Pacific-Caribbean Strait was closed and sealed.

Having a definite date for the final closure of the Isthmus has turned out to be a complex matter for scientists. Many authors such as Coates & Obando (1996), Kirby & Jackson (2004), Teranes *et al.* (1996) and O'Dea *et al.* (2007) indicate that the marine fossil record shows us that most of the biological and environmental changes that occurred within the marine world in response to closure, had already ended 3.5Ma to 3.1Ma ago, but this does not necessarily mean that the last drop of water from the Pacific will enter the Caribbean at that time. In fact, according to Webb (1985), the terrestrial fossil record suggests that the final coalescence of the earth occurred much later, about 2.5 Ma ago when the mixture of the northern and southern fauna was at its highest level. This enigma can be solved if we consider that the existence of a shallow marine connection between both coasts would have been insufficient to guarantee large-scale mixing between the two oceans, separating the populations of marine animals and introducing the differentiation of the respective marine environments; but, at the same time, they would also constitute an obstacle for the massive migration of terrestrial animals and plants that could not cross bodies of water.

To fully understand the biological effects of such closure, it is first necessary to examine the environmental effects and ecology of the seas on both sides of this site at the present time. Because the Isthmus is a physical barrier to the mixing of Pacific and Caribbean waters, Panama currently has two very different coasts (Jackson & D’Croz 1997).

The Pacific coast experiences the seasonal upwelling of cold, nutrient-rich waters, which stimulates large-scale planktonic productivity, causing benthic communities to be dominated by heterotrophic organisms that, in turn, feed commercially profitable fisheries (D' Croz & Robertson 1997). The high productivity caused by the outcrop is added to the high levels of runoff as a result of the high rainfall, which increases the contribution of nutrients from terrestrial origin. Coral reefs are unable to compete for light and nutrients with the abundant planktonic algae and are therefore scarcer along the Pacific coast.

In contrast, the Caribbean coast does not experience upwelling and consequently many regions have low levels of nutrients and planktonic productivity. Without competition from planktonic algae, coral reefs and seagrasses are able to thrive and dominate the benthic ecology of many of these shores. However, for Best & Kidwell, (2000) some areas such as Almirante Bay in Bocas del Toro also experience high levels of nutrients due to localized runoff, negatively affecting the growth of corals and seagrasses and promoting heterotrophic communities. benthic. Thus, based on O'Dea *et al.* (2007) the Pacific coast is almost completely dominated by heterotrophic benthic communities, while the Caribbean coast contains a much more diverse mosaic of benthic community types ranging from systems dominated by auto- and mixotrophic forms to those dominated by heterotrophs.

Over the millennia when the Isthmus slowly rose, submerged marine deposits rose to the surface. These, and the fossils they contained, provided paleontologists with an opportunity to learn the ecology and biology of animals and plants that were once in the seas near the Isthmus; In addition, they have made it possible to demonstrate how the interruption of the seaway in the American tropics stimulated a profound change in the environment, evolution and ecology of the Caribbean.

According to O' Dea *et al.* (2007) before the closure, the coastal seas of the Caribbean were very similar to those of the Pacific today, with an environment of strong upwelling and benthic communities dominated by heterotrophic organisms. For Schneider & Schmittner (2006) the models of global ocean currents show that most of the surface waters that flowed through an open Central American seaway would do so from the eastern tropical Pacific to the Caribbean, this in O' Dea *et al.* (2007), helps to explain why the Caribbean coast was very similar to that of the Pacific.

At the same time that the seaway was limited, some 4 million years ago, the dominance of the Pacific in the Caribbean was reduced, with the reduction of the strength of the outcrop and the change in the composition of the benthic communities.

Three million years ago the effect of the outcrop had already ceased approximately, suggesting that the seaway was already effectively closed by this time. For O' Dea *et al.* (2007) in response to these surprising environmental changes, the Caribbean marine benthic communities underwent a transformation that included: a dramatic reduction in the proportion of heterotrophic organisms and a concomitant increase in the proportion of autotrophic and mixotrophic organisms. This indicates that the typical environment and general ecological structure that we know today began during the final stages of the closure of the American tropic seaway, around 3.5 Ma ago.

The consequences of the closure on the maritime route of the Isthmus not only focused on the Central American coasts, but were also appreciated beyond that. For example, there is good evidence that due to the formation of the Isthmus the global patterns of ocean water circulation were affected, and these changes possibly started the glaciation of the Northern Hemisphere (Cronin & Dowsett 1996), establishing the situations that have subjected the climate global for the last 2Ma. Even thinking that it has been a key influence in the early evolution of human beings (Stanley 1996).

With the closure of the Isthmus, previously existing populations of marine species in both the eastern Pacific and the Caribbean split in two (Jackson & D' Croz 1997). Many disappeared in the Caribbean or the Pacific, depending on their environmental and ecological adaptations, while others continued to exist on both sides.

The separate populations diverged and followed their own evolutionary paths, because the gene flow between species that survived on both sides was stopped, often giving for example animals that are similar in appearance in both the Caribbean and the eastern Pacific, such as the sea urchins pencil (*Eucidaris*), trambollos (Labrisomidae) and tamaru shrimp (Alpheidae) (Jackson & D 'Croz 1997). These species, descendants of a single ancestor, whose scope was a single ocean when the Isthmus seaway was open, now show differences in behavior and morphology depending on how long they have been separated, allowing it to be deduced at what time both were able to exchange genetic material for the last time.

As a result of the construction of the fourth set of canal locks, other findings were found on the emergence of the Isthmus of Panama, led by STRI researcher and head of the Panama Geological Project, Carlos Jaramillo. This was possible thanks to the analysis of volcanic rock and sediments collected in Panama and Colombia by the geologist Camilo Montes, who designed a new tectonic model which establishes that between 20 and 18 million years there must have been a continuous land mass that separated the sea. Caribbean of the Pacific Ocean and that there are indications that many species of plants and reptiles of South America were already in the isthmus 20 million years ago and that mammals were the last to pass because the findings found date back to 2.3 million years ago , which indicates that both hypotheses (Coates and Jaramillo) would be valid, but for a better understanding of the emergence of the Isthmus of Panama it is necessary to carry out more research.

Isla Colon, Bocas del Toro Province, Panama

The Bocas del Toro Archipelago is located on the Caribbean coast of Panama, near the Costa Rican border. The main islands of the archipelago are Isla Colón (Figure 2), Bastimentos, Solarte, Cristóbal, Popa and Cayo Aqua. The archipelago has a predominantly humid climate. According to Gordon (1982) it receives an average rainfall of 2870 mm per year and a maximum of 7000 mm (Rodríguez *et al.* 1993).

The archipelago's primary marine ecosystems consist of mangroves (dominated by red mangroves), seagrass beds, and coral reef patches (Wysor & Kooistra 2003; Lovelock *et al.* 2004; Collin 2005).

Figure 2. Location of Isla Colón, Bocas del Toro province, Panama. Map taken from https://viajarfull.com/bocas-del-toro-islas-cuantas-son/

Toro Research Station, a well-known marine station of the Smithsonian Tropical Research Institute (STRI), is located on Isla Colón. Numerous researchers from this station, both past and present, have used the waters surrounding the archipelago for various studies. However, this research has often been hampered by a lack of accurate and up-to-date identification / field guidelines. This is particularly problematic for researchers studying heterobranch sea slugs, for which taxonomy and systematics have changed dramatically in recent years. The only field guide available for heterobranch sea slugs in the Caribbean is that of Valdés *et al.* (2006) is outdated and needs revision due to the changes produced by advances in molecular analysis that have been occurring in recent years.

Although the Caribbean Sea is inhabited by hundreds of heterobranch species (Valdés *et al.* 2006), only 19 species had been formally identified and documented in the Archipelago of Bocas del Toro by Collin *et al.* in 2005, representing only a fraction of the total diversity of sea slugs in the Caribbean. But that has been changing nowadays thanks to works such as that of Goodheart *et al.* in 2016 document 86 species in different areas of the archipelago.

Isla Coiba, Veraguas Province, Panama

Created by the Board of Directors of the Extinct National Institute of Renewable Resources (INRENARE), the Coiba National Park (PNC) is located in the Gulf of Chiriquí, in the Southwestern Pacific region of Panama (Figure 3), it is the largest island in the Central American Pacific, whose surface covers 503.14 km2, numerous marine species are concentrated in the PNC (ANAM 2009).

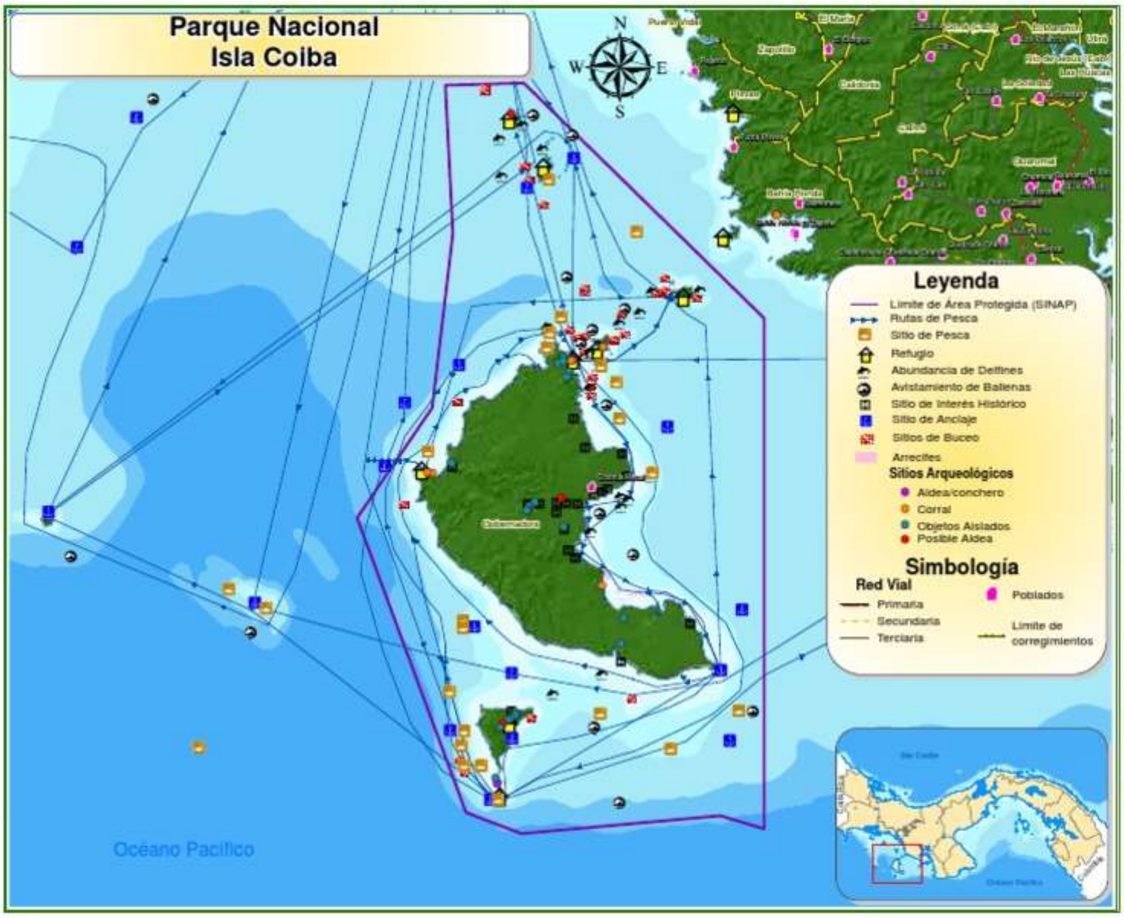

Figure 3. Location of the Isla Coiba National Park, Veraguas province, Panama. Map taken from https://es.scribd.com/document/357137242/Mapa-del-Parque-Nacional-Coiba

Due to its status as a penal island from 1919 to 2004, it lacks permanent human settlements. It has several coastal (neritic) and open water (oceanic) ecosystems rich in species diversity, which makes it important for diving and snorkeling, concentrated on Uvas and Gambute islands; its coral reefs are among the largest in the Eastern Pacific. Within the historical context the first accounts of Coiba, the first settlers were indigenous of Guaymí origin, but, between the 16th and 17th centuries, the population almost did not exist and its mountains were very rich in forests, very little intervened by man. As it is a site declared as a National Park, it is a protected area where many investigations of marine fauna are currently being carried out, including the population of sea slugs.

Two oceans: biogeographic and taxonomic review of the marine heterobranch sea slugs (Mollusca: Gastropoda) from Panamanian waters.

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1.1. Abstract

There has been no exhaustive taxonomic description of the Panamanian species of heterobranch sea slugs (Mollusca: Gastropoda) reported in papers by C.B. Adams (1852), Zetek (1918), Strong & Hertlein (1939), Vega & González (2002), Collin *et al.* (2005), Avilés (2010) and Goodheart *et al.* (2016). The present study aims to describe such descriptions, based on published references and confirmed photographs of all species collected in Panamanian coastal waters. To complement the available information, specimens were collected from different Panamanian coastal areas. The resulting annotated catalog presented herein contains 233 species of heterobranch sea slugs, of which 118 occur on the Caribbean coast, 127 on the Pacific coast, and eight on both coasts. Eighteen species have an amphiatlantic distribution This study confirms the high biodiversity of heterobranch sea slugs that inhabit the Panamanian coasts, but extensive sampling on the Pacific coasts, which have been less studied, is considered necessary.

1.2. Key words: Biodiversity, Heterobranchia, sea slugs, Panamanian coast, Caribbean, Pacific.

1.3. Introduction

The study of heterobranch sea slugs has had an extraordinary boom in recent years, resulting from numerous revisionary studies based on molecular data, which are profoundly modifying our understanding of the taxonomy of some clades and species (i.e., Valdés, 2003; Malaquias *et al.*, 2009; Carmona *et al.*, 2013; Zamora & Malaquias, 2018; Korshunova & Martynov, 2020 among many other works), as well as local, regional or global biodiversity inventories (i.e., Valdés, 2004, 2019; Ardila *et al.*, 2007; Malaquias & Reid, 2008; García & Bertsch, 2009; Martynov & Korshunova, 2012; Caballer *et al*, 2015; Gosliner *et al.*, 2015; Parera *et al.*, 2020; among many others). Citizen science is contributing significantly to this boom, with numerous species records made by divers and amateur naturalists that are reported on web pages readily accessible to researchers and the general public.

The first record of heterobranch sea slugs for the coast of Panama is due to C. B. Adams (1852), who in his catalog of the shells collected in Panama reported *Bulla* (*Tornatina*) *infrequens* (now accepted as *Acteocina infrequens*), *Bulla* (*Cylichna*) *luticola* (now accepted as *Cylichna luticola*), *Bulla punctulata* and another undetermined species of *Bulla*. Zetek (1918) in his list of the mollusks of Panama, in addition to some species of Thecosomata (Pteropoda), also cited the species *Tornatina carinata* [now accepted as *Acteocina inculta* (Gould, 1855)], *Cyichnella atahualpa* [now accepted as *Cylichna atahualpa* (Dall, 1908)], *Cylichna inca* (Dall, 1908), *Cylichna pizarro* (Dall, 1908), *Bulla adamsi* Menke, 1850 [now considered as *nomen dubium*, *B. aspersa* (now accepted as *B. punctulata* A. Adams in Sowerby, 1850)], *B. punctulata*, and unidentified species of the genera *Dolabella*, *Fiona* and *Doriopsis*.

Strong & Hertlein (1939) studied the marine mollusks from the western coast of Panama in an extension of the Allan Hancock Pacific Expedition to the Galapagos Islands conducted in 1931 and 1932; these authors recorded 336 species along the coast of Panama 10 of which were of shelled Cephalaspidea, including three new to science *Cylichna stephensae* (now accepted as *Aliculastrum exaratum* (Carpenter, 1857)), *Cylichna* (*Cylichnella*) *tabogaensis* and *Cylichna veleronis* [now accepted as *Aliculastrum exaratum* (Carpenter, 1857)].

Olsson & McGinty (1958) carried out sampling campaigns on the Caribbean coast of Panama and collect a total of 534 species of marine mollusks, mainly in Bocas del Toro but also in Almirante. Of these species, 15 were heterobranch sea slugs (two Acteonimorpha, 11 Cephalaspidea, 1 Pteropoda and 1 Sacoglossa).

More taxonomically specific lists were also published by Meyer (1977) from Punta Galeta, Colon Province (Figure 1) [with three new species described: *Tambja oliva* (Meyer, 1977, formerly *Martadoris oliva), Doriopsilla nigrolineata* Meyer, 1977 and *Phyllidiella molaensis* (Meyer, 1977, as *Phyllidiopsis molaensis*)], San Martín *et al.* (1997) and Hermosillo (2004) from the Coiba National Park (Pacific coast) and by Collin *et al.* (2005) and Goodheart *et al.* (2016) from the islands of the Bocas del Toro Province. Vega & González (2002), gathered all the information on the marine gastropods of the Pacific coast of the Veraguas Province including Coiba Island, and among them they cited (with specific locations) (Figure 1), a total of 27 species of heterobranch sea slugs (8 Nudibranchia, 1 Sacoglossa, 1 Umbraculida, 3 Pleurobranchida, 4 Aplysiida, 10 Cephalaspidea). Hermosillo (2004) summarized recent records of heterobranch sea slug species for the Pacific coast of Panama (Figure 1); Panamanian species were also cited by Camacho-García *et al.* (2005) in their field guide to the sea slugs of the tropical Eastern Pacific.

The first list of all heterobranch sea slugs from the Panamanian coasts was published by Avilés (2010) who compiled a total of 213 species, based on data by Debelius & Kulter (2007) for both coasts, by Keen (1971) from the Pacific, and by Valdés *et al.* (2006) from the Caribbean.

Since the work of Avilés (2010), numerous articles have been published on the molecular phylogeny of heterobranch sea slugs and related groups, which have profoundly modified the taxonomy of some of these groups and revealed complexes of cryptic species (e.g., Dinapoli & Klussmann-Kolb, 2010, Jörger *et al.*, 2010; Schrödl *et al.*, 2011; Ornelas-Gatdula *et al.*, 2012; Kocot *et al.*, 2013; Krug *et al.*, 2016; Padula *et al.*, 2016; Valdés *et al.*, 2017; Medrano *et al.*, 2018).

In the present paper, an up-to-date catalog of the species of heterobranch sea slugs known from the Panamanian coasts (Pacific and Caribbean) is provided, describing the most important diagnostic characteristics of each species, including unpublished records by various researchers and naturalists, remarks about different species, their geographical ranges, and their records from Panama. This list also includes curated records of species whose photographs appear in different online social networks, after being reviewed and their correct identification verified. Finally, this catalog includes the results of the senior author's field work carried out in March 2019 around Colon Islansd, Bocas del Toro, and adjacent islands such as Bastimentos Island and Solarte Island (Figure 1).

1.4. Material and methods

1.4.1. ***Data gathering***

For the compilation of the species list, all available publications with data on Panamanian heterobranch sea slugs were reviewed. Also, during the month of March 2019 nine sites (Boca del Drago, Punta Caracol, Casa Blanca, Smithsonian Tropical Research Institute, Airport, Punta Hospital, Bahia Delfines, Adriana Cay and Crawl Cay) off the coast of Bocas de Toro (Figure 1) were explored in order to collect heterobranch sea slugs. The samples were collected exclusively during the day by direct observation in the field, mainly snorkeling, but also diving (in an effort of 200 person-hours), or by collecting suitable substrates where heterobranch sea slugs can live (mainly diverse species of algae and hydroids). The collected samples were kept in trays with clean seawater overnight. Most of the specimens were identified in the laboratory using the field guide by Valdés *et al.* (2006).

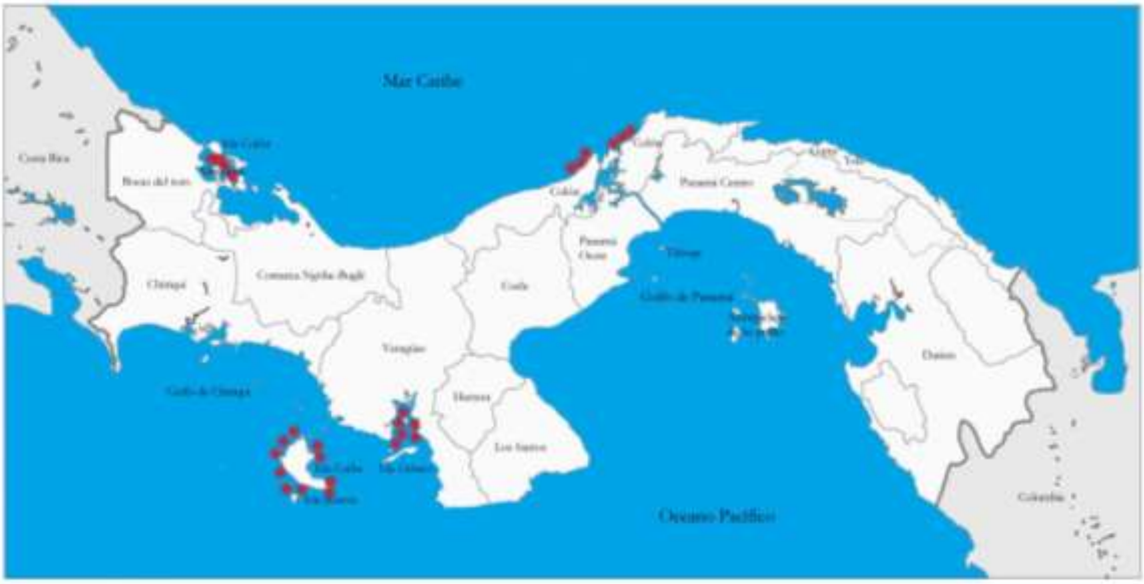

Figure 1. Localities where specimens of sea slugs were collected in Panama (points in red).

1.5. Results

The list presented here includes 233 species of heterobranch sea slugs that have been recorded from Panama, belonging to 108 genera, 46 families and 7 orders, taxonomically arranged as follows: 7 Acteonoidea, 10 Pleurobranchomorpha, 127 Nudibranchia (68 Doridina and 59 Cladobranchia), 2 Umbraculida, 45 Cephalaspidea, 13 Aplysiida, and 29 Sacoglossa. Of all the species, 118 have been recorded for the Caribbean coast, 127 for the Pacific coast, five are found on both Panamanian coasts and 18 have amphiatlantic ranges (nine Nudibranchia, four Sacoglossa, three Cephalaspidea, two Aplysiida).

The taxonomic list of species with bibliographical references for each one is presented in Table 1. The taxonomy and ordering of the taxa were based on Bouchet *et al.* (2017) and the accepted species on the WoRMS (2021) website were reviewed.

1.5.1. *Species descriptions*

Phyllum MOLLUSCA Cuvier 1795
Class GASTROPODA Cuvier 1795
Subclass Heterobranchia Burmeister 1837
Infraclass Euthyneura Spengel 1881
Subterclass Acteonimorpha Dinapoli & Klussmann-Kolb 2010
Superfamily Acteonoidea d'Orbigny 1843
Family Acteonidae d'Orbigny 1843
Genus ***Acteon*** Montfort 1810

1. *Acteon traskii* Stearns 1897 Figure 2a

Diagnosis: shell up to 15 mm in length; shell cream to reddish, with white band on body whorl; shell solid, convex sides; aperture elongated; edge of columella thicker with simple fold; umbilicus absent; sculpture of spiral grooves; protoconch globose.

Distribution: uncommon species reported down to 80 m deep in the Eastern Pacific from Southern California to Colombia (Keen 1971; Camacho-García *et al.* 2005); described based on Holocene material from Southern California (Stearns 1897). Live animals have been reported from Southern California to Panama (Keen 1971; Avilés 2010) and Ev. Marcus (1972) provided descriptions of the radula and penial anatomy.

2. *Acteon panamensis* Dall 1908

Diagnosis: shell up to 7 mm in length; shell white, periostracum pale yellowish; spiral sculpture; narrow aperture, rounded anteriorly with sharp outer lip; umbilicus absent; four whorls visible.

Distribution: deep water species, only known from the Gulf of Panama (Dall 1908; Keen 1971; Avilés 2010).

3. *Acteon candens* Rehder 1939

Diagnosis: shell up to 10 mm in length; body white; shell uniformly white or slightly cream with two white bands on body whorl; fine spiral sculpture; spire large, conical.

Distribution: reported in the Western Atlantic from North Carolina to Brazil (Rosenberg *et al.* 2009), Panama (Avilés 2010), including the Gulf of Mexico (Felder & Camp 2009).

Genus ***Crenilabium*** Cossmann 1889

4. *Crenilabium venustus* (d'Orbigny 1840)

Diagnosis: shell up to 15 mm in length; shell solid, elongate, whitish; body whorl long, slightly channeled suture; aperture narrow, short, about 3/4 of body length; edge of columella with one visible tooth; umbilicus absent; sculpture composed of numerous spiral grooves; elongated protoconch.

Remarks: the material examined by Valdés and Camacho-García (2004) from Costa Rica and Panama coincides with the original description by d'Orbigny (1835–1843) and clearly belongs to the same species. Bouchet (1975) provided anatomical and conchological evidence to accept the fossil genus *Crenilabium* as valid. The type material of *Acteon venustus*, as well as the specimens examined by Valdés and Camacho-García (2004), resemble the conchological characteristics of *Crenilabium*; therefore, these authors provisionally transferred *A. venustus* to *Crenilabium* genus until the study of more specimens is possible.

Distribution: rare, subtidal species recorded down to 65 m deep, reported in the Eastern Pacific, from Costa Rica to Peru, (Keen 1971; Camacho-García *et al.* 2005) including Panama (Valdés & Camacho-García 2004; Avilés 2010).

Genus ***Rictaxis*** Dall 1871

5. *Rictaxis punctocaelatus* (Carpenter 1864)

Diagnosis: shell up to 20 mm in length; body black or dark gray; shell solid, elongated; three white spiral bands at anterior, posterior ends of apex.

Distribution: reported in the Eastern Pacific, from Alaska to Baja California, Mexico (Keen 1971; Skoglund 2002) and San Miguel Island, Panama (Valdés & Camacho-García 2004).

Genus ***Japonactaeon*** Taki 1956

6. *Japonactaeon punctostriatus* (C.B. Adams 1840)

Diagnosis: shell up to 12 mm in length; shell white, solid, elongate, with two brown or pink bands; sculpture composed of numerous punctured spiral grooves.

Remarks: this species has not been seen alive, it has been cited as *Acteon punctostriatus*.

Distribution: Atlantic species reported in the Western Atlantic from Massachusetts to Venezuela and in most of the Caribbean islands (Valdés *et al.* 2006), also in Panama (Olsson & McGinty 1958; Avilés 2010).

Family Aplustridae Gray 1847

Genus ***Micromelo*** Pilsbry 1895

7. *Micromelo undatus* (Bruguière 1792) Figure 2b

Diagnosis: shell up to 30 mm in length; body translucent gray with dull white spots; shell bright white with network of fine dark red zigzagging lines; shell oval, calcified, covering only small portion of body; foot wide.

Biology: inhabits sandy areas, hiding under the rocks during the day, feeds on polychaete worms (Valdés *et al.* 2006).

Remarks: previously considered a circumtropical species, Feliciano *et al.* (2021) determined that it is restricted to the Atlantic Ocean.

Distribution: reported from several localities in the Eastern Atlantic (Valdés 2005; Feliciano *et al.* 2021), and the tropical Western Atlantic, from Florida to Brazil, including some Caribbean Islands and Panama (Valdés *et al.* 2006; Avilés 2010; Miloslavich *et al.* 2010; Feliciano *et al.* 2021).

Subterclass Ringipleura Kano, Brenzinger, Nützel, Wilson & Schrödl 2016

Superorder Nudipleura Wägele & Willan 2000

Order Pleurobranchida Gray 1827

Superfamily Pleurobranchoidea Gray 1827

Family Pleurobranchidae Gray 1827

Genus ***Pleurobranchus*** Cuvier 1804

8. *Pleurobranchus areolatus* Mörch 1863 Figure 2c

Diagnosis: animal up to 150 mm in length; body light brown to dark purple; varying degrees of opaque white pigment on polygonal dorsal tubercles.

Biology: found under rocks and coral debris; it feeds on sea squirts such as *Didemnum* sp. Savigny 1816 from which it extracts rodriguesin A, a precursor for the synthesis of rodriguesic acids, used as defensive metabolites (Pereira *et al.* 2014)

Remarks: the chromatic variability of *Pleurobranchus areolatus* led to the description of 5 different species (*P. crossei* Vayssière 1896; *P. atlanticus* Abbott 1949; *P. reesi* White 1952; *P. evelinae* Thompson 1977; *P. emys* Ev. Marcus 1984) that have recently been synonymized with *P. areolatus* by Goodheart *et al.* (2015) based on molecular and morphological studies.

Distribution: reported in the tropical Western Atlantic from Florida and Bermuda to Brazil and throughout the Caribbean (Thompson 1977; Collin *et al.* 2005; Valdés *et al.* 2006; Rios 2009; Avilés 2010; Miloslavich *et al.* 2010; Yidi & Sarmiento 2011; Caballer *et al.* 2015; Ortigosa *et al.* 2015; Alvin & Pimenta 2016), and in the Bocas del Toro Archipelago, Panama, (Valdés *et al.* 2006; Goodheart *et al.* 2016).

9. *Pleurobranchus digueti* Rochebrune 1895 Figure 2d

Diagnosis: animal up to 106 mm in length; body light brown, opaque white pigment on some tubercles, dorsum completely covered with large, rounded tubercles; foot semi-transparent, yellowish brown with irregular grayish-brown spots; oral veil, rhinophores of same color as mantle, sometimes with opaque white spots.

Remarks: Goodheart *et al.* (2015), based on morphological and molecular studies, confirmed the validity of *P. digueti*, separating it from the Caribbean *P. areolatus*, with which it had been previously synonymized.

Distribution: reported from California to the Galapagos Islands in Ecuador (Behrens & Hermosillo 2005) including records from Panama (Valdés *et al.* 2006).

Genus ***Berthella*** Blainville 1824

10. *Berthella martensi* (Pilsbry 1896) Figure 2e

Diagnosis: animal up to 70 mm in length; body whitish, cream, orange, brown, or almost black, always with dark, light spots depending on background color; frequently with dark band around mantle, foot.

Biology: intertidal and subtidal. Animals often self-autotomize part of the mantle when disturbed (Behrens & Hermosillo 2005). It feeds on sponges and tunicates (Behrens 2005).

Distribution: originally described from Mauritius (Indian Ocean) (Möbius 1880) it has been reported across the Indo-Pacific and the tropical Eastern Pacific (Ortea *et al.* 2014), including the Coiba Island National Park, Panama (Hermosillo 2004; Behrens & Hermosillo 2005).

11. *Berthella californica* (Dall 1900)

Diagnosis: animal up to 30 mm in length; body translucent white to brown, mantle edge with thin white line; small opaque white spots, usually coinciding with small mantle tubercles.

Biology: the egg mass is a wavy and spiral ribbon of white color (Hildering & Miller 2007)

Distribution: reported from Ventura County, southern California to the Coiba Island National Park, Panama (Hermosillo 2004; Behrens & Hermosillo 2005; Ghanimi *et al.* 2020a).

12. *Berthella agassizii* (MacFarland 1909)

Diagnosis: animal up to 25 mm in length; body translucent reddish-brown, with opaque white spots; foot reddish, whitish pedal gland located near posterior end of foot; rhinophores short, coiled.

Distribution: originally described for Brazil, it has also been recorded from the Caribbean Sea (Camacho-García *et al.* 2005) and the Eastern Pacific, from Baja California, Mexico to the Galapagos Islands including Coiba Island National Park, Panama (Hermosillo 2004; Behrens & Hermosillo 2005); it remains to be confirmed if the Eastern Pacific records belong to a different species.

13. *Berthella nebula* Ghanimi, Schrödl, Goddard, Ballesteros, Gosliner, Buske & Valdés 2020

Diagnosis: animal up to 6 mm in length; body translucent, whitish to grayish, opaque white pattern resembling "T" or "Y" near center of mantle; few to numerous opaque white spots near anterior end, lateral margins of oral veil; rhinophores fused for approximately 2/3 of their length, each with an opaque white spot on dorsal tip; gill small, bipinnate, with 10 pinnae on each side.

Remarks: recently described by Ghanimi *et al.* (2020b), previously attributed to *Berthella stellata* (Risso 1826).

Distribution: Caribbean coast of Mexico (Gosliner & Bertsch 1988, as *B. tupala*), Puerto Rico (Er. Marcus & Ev. Marcus 1970, as *B. tupala*), Martinique, Jamaica and the Caribbean coast of Panama (Ghanimi *et al.* 2020b).

14. *Berthella* sp. 1

Diagnosis: animal up to 10 mm in length; specimen morphology not described.

Remarks: Ghanimi *et al* (2020b) after analyzing it molecularly, they could not confirm that it is a different species and concluded that more studies are needed. Specimen collected by Hermosillo (2004, as *B. stellata*) from Canal de Afuera Island in Coiba Island National Park. There are no photos of the live animal nor has it been possible to amplify its COI mitochondrial DNA to be able to compare its sequence with those of other species from Eastern Pacific. Possibly belongs to an undescribed species.

Genus ***Berthellina*** Gardiner 1936

15. *Berthellina quadridens* (Mörch 1863) Figure 2f

Diagnosis: animal up to 25 mm in length; body semi-translucent, yellow to orange or bright red.

Biology: reported to feed on sponges (Willan 1984) or hard corals of the genus *Orbicella* Dana 1846 (Goodheart *et al.* 2016), as well as anemones (Ev. Marcus & Er. Marcus 1967).

Distribution: reported from the Western Atlantic of Mexico, Belize, Colombia, Costa Rica, Panama, Venezuela and the Caribbean Islands (Thompson 1977; Collin *et al.* 2005; Valdés *et al.* 2006; Ríos 2009; Yidi & Sarmiento 2011; Ortea *et al.* 2013; Caballer *et al.* 2015). In Panama it has been collected in Bocas del Toro (Goodheart *et al.* 2016).

16. *Berthellina ilisima* Ev. Marcus & Er. Marcus 1967 Figure 2g

Diagnosis: animal up to 100 mm in length; body uniform apricot orange: rhinophores rolled, short; gill large, on right side of body; foot with whitish pedal gland near posterior end.

Distribution: reported from Southern California to the Galapagos Islands (Camacho-García *et al.*, 2005) and mainland Ecuador (Behrens & Hermosillo 2005), including the Coiba Island National Park, Panama (Hermosillo 2004; Behrens & Hermosillo 2005).

17. *Berthellina grovesi* Hermosillo & Valdés 2008

Diagnosis: animal up to 23 mm in length; body light brown or pink with dorsum covered with large, small rounded tubercles; distinctive brown spot at body center.

Distribution: Pacific species only known from Banderas Bay and Isabel Island, Mexico and the Coiba Island National Park, Panama (Hermosillo 2004; Behrens & Hermosillo 2005; both as *Berthellina* sp. 1).

Order Nudibranchia Cuvier 1817

Suborder Doridina Odhner 1934

Superfamily Doridoidea Rafinesque 1815

Family Undermined

18. Dorid sp. 1

Diagnosis: animal up to 25 mm in length; body light brown to dark, spongy in appearance; rhinophores same color as body.

Remarks: three specimens 4–5 mm in length were collected in Coiba Island National Park among coral debris by Hermosillo (2004); these animals were clearly juveniles and may constitute a new species to be described.

19. Dorid sp. 2

Diagnosis: animal up to 11 mm in length; body pinkish brown, with darker spots, small tubercles on dorsum, unipinnate gill branches.

Remarks: two specimens of 3–11 mm in length were collected by Hermosillo (2004) in Isla Uva, Isla Coiba National Park; they possibly constitute an undescribed species.

20. Dorid sp. 3

Diagnosis: animal up to 12 mm in length; body greyish with dark brown spots, small tubercles on dorsum.

Remarks: only one specimen was collected by Hermosillo (2004) under stone in intertidal zone of Isla Coiba; possibly undescribed.

Family Dorididae Rafinesque 1815

Genus ***Doriopsis*** Pease 1860

21. *Doriopsis granulosa* Pease 1860 Figure 2h

Diagnosis: animal up to 28 mm in length; body pale orange yellow to dark green; dorsal tubercles small rounded; branchial leaves arranged in fan-shaped line, protected by dorsal expansion of mantle.

Biology: feeds on the yellow sponge *Haliclona* (*Reniera*) *phlox* (de Laubenfels 1954) (Young 1967; Behrens & Hermosillo 2005). The egg mass is a spiral low ribbon with 5 whorls and yellow eggs.

Distribution: reported in the Indian and Pacific oceans from Madagascar to the Eastern Pacific of Mexico, Costa Rica, and Panama (Behrens & Hermosillo 2005).

Genus ***Aphelodoris*** Bergh 1879

22. *Aphelodoris antillensis* Bergh 1879 Figure 3a

Diagnosis: animal up to 30 mm in length; body translucent beige cream, with variable pattern of brown, reddish brown, opaque white pigmentation; body elongate; mantle with small rounded conical tubercles slightly visible due to dark pigmentation of trailing edge, may have yellow band interrupted by dark reddish-brown spots.

Biology: lives under rocks and coral debris in living reefs, has the ability to swim by body contractions when disturbed (Valdés *et al.* 2006).

Distribution: one of the most common Caribbean dorids reported from Florida, the Gulf of Mexico and across the entire Caribbean to Venezuela (Collin *et al.* 2005; Valdés *et al.* 2006; Miloslavich *et al.* 2010; Caballer *et al.* 2015; Ortigosa *et al.* 2015). In Panama it has been observed in Punta Galeta, Galeta Island, Colon Province (Meyer 1977).

Genus ***Conualevia*** Collier & Farmer 1964

23. *Conualevia alba* Collier & Farmer 1964 Figure 3b

Diagnosis: animal up to 25 mm in length; body uniform white with opaque white defensive glandular spots around entire mantle margin; tiny conical tubercles all over dorsum; rhinophores smooth, gill white.

Biology: common, lives under stones and feeds on sponges. The egg mass is a flat ribbon tight wrapped in a spiral with up to 7 turns, eggs white, about 89 μm in diameter (Goddard 2007).

Distribution: reported in the Eastern Pacific, from California to the Galapagos Islands, also the Coiba Island National Park, Panama (Keen 1971; Hermosillo 2004; Behrens & Hermosillo 2005).

Family Discodorididae Bergh 1891

Genus ***Atagema*** Gray 1850

24. *Atagema notacristata* Camacho-García & Gosliner 2008

Diagnosis: animal up to 29 mm in length; body brown or reddish brown; dorsum rough, with pronounced tuberculated dorsal crest, tubercles covered caryophyllidia; branchial sheath with three lobes.

Distribution: so far, is only known from the Eastern Pacific, including Banderas Bay (Mexico) (Hermosillo *et al.* 2006), various locations in Costa Rica, and on Coiba Island, Panama (Camacho-García & Gosliner, 2008).

Genus ***Jorunna*** Bergh 1876

25. *Jorunna spazzola* (Er. Marcus 1955) Figure 3c

Diagnosis: animal up to 18 mm in length; body light gray, often with darker, diffuse spots on dorsum; mantle margin usually with white defensive mantle glands; dorsum covered with small caryophyllidia; branchial leaves short.

Biology: lives under rocks, feeds on Haplosclerida sponges of the genera *Callyspongia* Duchassaing & Michelotti 1864 and *Chalinula* Schmidt 1868 (Belmonte *et al.* 2015) on which it is well camouflaged. This species can quickly change color in response to environmental changes (Valdés *et al.* 2006).

Remarks: Camacho-García & Gosliner (2008) compared specimens of *J. spazzola* and *J. evansi* anatomically and concluded that these two species are practically identical and could be synonymous. If so, the name *Jorunna evansi* (Eliot 1906), originally described from Cape Verde would have priority.

Another similar species, *J. luisiae* Ev. Marcus 1976, from the Mediterranean Sea, has been recently synonymied with *J. evansi*. If this is correct, *J. evansi* would have an amphiatlantic distribution including the Mediterranean Sea. On the contrary, Alvim & Pimenta (2013) comparing the anatomy of *J. spazzola* and *J. luisiae* concluded that they are different species. Molecular studies would be necessary to confirm this point, but in this paper, we follow the opinion of Alvim & Pimenta (2013).

Distribution: J. spazzola has been recorded from the coasts of Florida, most of the Caribbean islands, the Yucatán Peninsula (Mexico), Costa Rica and Honduras to Brazil (Valdés *et al.* 2006). In Panama it has been reported from Bocas del Toro (Goodheart *et al.* 2016).

26. ***Jorunna tempisquensis*** Camacho-García & Gosliner 2008

Diagnosis: animal up to 9 mm in length; body light brown to dark violet; dorsum covered with caryophyllidia; dorsum with tiny dark brown spots arranged homogeneously, center of dorsum with large, light brown or black spots of different sizes; rhinophores light brown, speckled with tiny dark brown spots, yellowish-white tips.

Distribution: rare, reported from the Pacific coast of Mexico, Costa Rica (Camacho-García & Gosliner 2008) and Panama (Camacho-García *et al.* 2005).

27. ***Jorunna*** **sp. 1**

Diagnosis: animal up to 25 mm in length; body light brown with slightly darker diffuse spots that give animal spongy appearance; mantle margin with yellow tubercles; rhinophores yellow.

Remarks: possibly a new species.

Distribution: it has been collected from the Pacific coast of Banderas Bay (Mexico), Costa Rica and Panama (Behrens & Hermosillo 2005).

Genus ***Discodoris*** Bergh 1877

28. ***Discodoris branneri*** MacFarland 1909

Diagnosis: animal up to 110 mm in length; body cream to purplish brown, with black, white spots on dorsum; mantle with numerous conical tubercles; hyponotum, foot with brown spots.

Biology: found at 1–5 m depth under the rocks; when disturbed it autotomizes parts of the mantle (Valdés *et al.* 2006). The egg mass is a spiral ribbon of 5–6 whorls, 4–5 cm in diameter and white eggs.

Distribution: previously identified as *Discodoris evelinae* Er. Marcus 1955, but now accepted as *D. branneri* (Dayrat 2010; Alvim & Pimenta 2013), has been reported from the Western Atlantic from Florida to the state of Rio de Janeiro in Brazil and the Caribbean Islands (Valdés *et al.* 2006; Debelius & Kuiter 2007; Alvim & Pimenta 2013; Caballer *et al.* 2015) also in point Galeta, Colon, Panama (Meyer 1977) and in the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

29. *Discodoris ketos* (Ev. Marcus & Er. Marcus 1967) Figure 3d

Diagnosis: animal up to 47 mm in length; body oval, flattened dorso-ventrally, grayish- brown, white when first encoutered in field, darkened when disturbed; dorsal tubercles with dark brown spots; rhinophores brown with light apices; six tripinnate branchial leaves, greyish.

Biology: very common, under stones (Behrens & Hermosillo 2005).

Distribution: in the Eastern Pacific from Baja California, Mexico to the Galapagos (Camacho-García *et al.* 2005; Debelius & Kuiter 2007) also in the Coiba Island National Park, Panama (Hermosillo 2004; Behrens & Hermosillo 2005).

30. *Discodoris* sp. 1

Diagnosis: body yellow, dorsum with dark brown spots; mantle rough, with numerous tubercles, filamentous papillae; rhinophores brown; 6 yellow branchial leaves.

Biology: lives in the subtidal zone, under stones or in underwater cavities (Camacho-García *et al.* 2005).

Distribution: cited from the Pacific coast of Mexico (Banderas Bay, Nayarit) and Panama (Camacho-García *et al.* 2005). Probably is an undescribed species.

Genus ***Platydoris*** Bergh 1877

31. *Platydoris angustipes* (Mörch 1863) Figure 3e

Diagnosis: animal up to 150 mm in length; body uniformly red or orange, sometimes with dorsal white spots; body flattened, leathery; mantle margin wide; dorsum with tiny caryophyllidia; rhinophores red; gill sometimes white.

Biology: one of largest nudibranchs from the tropical Western Atlantic, lives in living reefs and according to Goodheart *et al.* (2016) also under rocks, feeds on red sponges.

Distribution: reported from the Western Atlantic from Florida to Brazil, including Central America, and in almost all the Antilles (Valdés *et al.* 2006; Alvim & Pimenta 2013; Camacho-García *et al.* 2014; Caballer *et al.* 2015). In Panama has been reported from Punta Galeta, Colon Island (Meyer 1977) and the Bocas del Toro Archipelago (Goodheart *et al.* 2016).

Genus ***Thordisa*** Bergh 1877

32. *Thordisa* sp. 1

Diagnosis: animal up to 15 mm in length; body orange to red; mantle with conical papillae with white tips; rhinophores, gill leaves lighter than body.

Biology: lives under stones or on red sponges on which it presumably feeds and it is very cryptic (Camacho-García *et al.* 2005).

Distribution: probably an undescribed species; it has been reported from the Eastern Pacific of Costa Rica and in the Gulf of Chiriqui, Panama (Camacho-García *et al.* 2005).

Genus ***Diaulula*** Bergh 1878

33. *Diaulula aurila* (Ev. Marcus & Er. Marcus 1967)

Diagnosis: animal up to 50 mm in length; body light gray or yellowish; dorsum with diffuse yellowish, white spots, covered by large caryophyllidia of about 190 µm; rhinophores, branchial leaves yellow or light brown.

Distribution: common in the Pacific coast of Costa Rica (Camacho-García & Valdés 2003), also it has been reported in Baja California, Mexico, Mexico (Behrens & Hermosillo 2005; Camacho-García *et al.* 2005) and the Canal Zone of Panama (Ev. Marcus 1976).

34. *Diaulula phoca* (Ev. Marcus & Er. Marcus 1967) Figure 3f

Diagnosis: animal up to 50 mm in length; body uniformly brown to dark brown, with tiny white dots; dorsum covered with caryophilidia; rhinophores, gill same color as body.

Biology: feeds on sponges (Ev. Marcus & Er. Marcus).

Distribution: it has been reported in the Western Atlantic from Florida to Brazil (Ev. Marcus & Er. Marcus 1967; Valdés *et al.* 2006) including the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

35. *Diaulula nayarita* (Orta & Llera 1981)

Diagnosis: animal up to 22 mm in length; body light dirty-yellow to orange; dorsum with abundant brown spots, numerous, small caryophyllidia; branchial, rhinophoral sheaths high; unipinnate gill leaves.

Remarks: *Diaulula nayarita*, was described as *Peltodoris nayarita* by Ortea & Llera (1981) based on specimens collected on Isabel Island, Nayarit, Mexico. *Diaulula greeleyi* was described as *Peltodoris greeleyi* by MacFarland (1909) based on a specimen collected in Alagoas, Brazil. Both species share several coloration and internal anatomy characteristics. After its original description, *D. greeleyi* has been cited in numerous Western Atlantic localities, from South Carolina to Brazil, including some Caribbean islands (Alvim & Pimenta 2013). Camacho-García & Valdés (2003) studied and compared the type specimens of these two species and concluded that they were synonyms. However, Alvim & Pimenta (2013) found significant differences in the length of the caryophyllidia of these two species, which together with their disjuct ranges (Western Atlantic and Eastern Pacific) indicate they are distinct. In this paper we follow Alvim & Pimenta's (2013) opinion and therefore the species reported from Coiba Island National Park by Hermosillo (2004) as *D. greeleyi* is considered to be *D. nayarita*. Molecular studies will be necessary to definitively clarify the taxonomy of these species.

Distribution: so far *D. nayarita* is known from Nayarit (Mexico), Baja California, Mexico (Bertsch *et al.* 2000), the Pacific coast of Costa Rica (Camacho-García & Valdés 2003) and Coiba Island National Park (Hermosillo 2004).

Genus ***Rostanga*** Bergh 1879

36. *Rostanga pulchra* MacFarland 1905 Figure 3g

Diagnosis: animal of up to 30 mm in length; body uniformly reddish or orange with minute black spots; dorsum covered with caryophyllidia, rhinophores with nearly vertically arranged lamellae.

Biology: feeds on red sponges such as *Clathria* (*Microciona*) *pennata* (Lambe 1895) (Camacho-García *et al.* 2005), *Clathria* (*Thalysias*) *originalis* (de Laubenfels 1930) and *Antho* (*Plocamina*) *karykina* (de Laubenfels 1927) (Anderson 1971). The egg mass is a multispiral ribbon with bright red eggs of 80 µm in diameter (Chia & Koss 1977).

Distribution: it has a very wide distribution from Alaska to Chile, also cited in Argentina (Keen 1971; Camacho-García *et al.* 2005; Behrens & Hermosillo 2005).

Genus ***Paradoris*** Bergh 1884

37. *Paradoris mulciber* (Ev. Marcus 1971)

Diagnosis: animal up to 60 mm in length; body uniformly light brown or cream; dorsal tubercles rounded, spaced, of different sizes; rhinophores, gill leaves ochre with white tips.

Biology: according to Collin (2005), is an uncommon subtidal species, found down to 20 m depth.

Remarks: Ortea (1995) questioned the validity of this species and considered it synonymous with the Eastern Atlantic and Mediterranean species *P. indecora.* However, Dayrat (2006) and Camacho-García & Gosliner (2007) concluded that they are two different species based on anatomical differences such as the size of the dorsal tubercles and the disjuct geographical distributions. Camacho-García & Gosliner (2007) published a complete redescription of this species.

Distribution: Western Atlantic, it has been reported from the southern Caribbean to Brazil (Valdés *et al.* 2006); Collin *et al.* (2005) reported it for the first time in Bocas del Toro, Panama.

38. *Paradoris adamsae* Padula & Valdés 2012 Figure 3h

Diagnosis: animal up to 50 mm in length; body dark brown with few small white spots; dorsum covered with conical tubercles of different sizes; rhinophores, branchial leaves lighter, branchial leaf tips cream.

Distribution: only 3 animals known from the coast of Panama, in the Bocas del Toro Province (Valdés *et al.* 2006 as *Paradoris* sp.; Padula & Valdés 2012).

Genus ***Carminodoris*** Bergh 1889

39. *Carminodoris bramale* (Fahey & Gosliner 2003)

Diagnosis: animal up to 25 mm in length; body oval, flattened; dorsum brown with back, covered with large, rounded tubercles, white ring at base of each tubercle.

Biology: uncommon, it feeds on sponges of the genus *Haliclona* (*Reniera*) Grant 1841 (Behrens & Hermosillo 2005).

Distribution: reported from the Eastern Pacific of Banderas Bay, Mexico, Costa Rica and Coiba Island National Park, Panama (Behrens & Hermosillo 2005; Camacho-García *et al.* 2005; Hermosillo 2004). In all cases cited as *Carminodoris bramale* (Fahey & Gosliner 2003)

Genus ***Geitodoris*** Bergh 1891

40. *Geitodoris planata* (Alder & Hancock 1846) Figure 4a

Diagnosis: animal up to 65 mm in length; body flat, gray-brown, with irregular dark brown patches; dorsum with rounded tubercles of different sizes, largest with star-shaped white spots.

Biology: on coral debris in seagrass beds (Goodheart *et al.* 2016).

Remarks: originally described from Europe, where it is relatively frequent in shallow waters under stones in the Mediterranean Sea (Ballesteros, 2007; Ballesteros *et al.* 2016). Valdés *et al.* (2006) considered *G. planata* as an amphiatlantic species. Caribbean populations are morphologically very similar. Alvim & Pimenta (2013) considered that the Brazilian animals studied by García-García *et al.* (2008) are *Geitodoris pusae* (Er. Marcus, 1955). Molecular studies are necessary to clarify the taxonomic status of these two species and similar ones such as *G. immunda* and *Discodoris stellifera* (Vayssière 1903).

Distribution: an amphiatlantic species reported from the Western Atlantic in New Jersey (USA) and Santa Lucia Island (Valdés *et al.* 2006). In Panama it has been recorded from the Bocas del Toro Archipelago (Goodheart *et al.* 2016).

41. *Geitodoris immunda* Bergh 1894 Figure 4b

Diagnosis: animal up to 43 mm in length; body brown with some darker spots, dorsum with scattered white dots; rhinophores, gill same color as body but with white tips; mantle oval, flattened, very wide, with network of slightly elevated ridges, small tubercles at intersections.

Biology: under coral debris (Goodheart *et al.* 2016).

Distribution: it has been reported from the Gulf of Mexico, Costa Rica, Venezuela, Brazil (Valdés *et al.* 2006; Moretzsohn *et al.* 2011) and the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

Genus ***Sclerodoris*** Eliot 1904

42. *Sclerodoris prea* (Ev. Marcus & Er. Marcus 1967) Figure 4c

Diagnosis: animal up to 40 mm in length; body cream or brown; dorsum with numerous caryophyllidia tubercles, larger near center, forming two longitudinal rows from rhinophores to gill, central depression between them.

Distribution: reported from Florida to Venezuela, including some Caribbean islands such as Bahamas, Jamaica, and Barbados (Valdés *et al* 2006; Caballer *et al.* 2015). In Panama it has been recorded from the Bocas del Toro Archipelago (Goodheart *et al.* 2016).

Genus ***Taringa*** Er. Marcus 1955

43. *Taringa aivica* Ev. Marcus & Er. Marcus 1967 Figure 4d

Diagnosis: animal up to 35 mm in length; body variable from cream yellowish to dark brown, with opaque white spots; rhinophores dark gray; branchial leaves yellow or whitish cream; dorsum covered by numerous cariophyilidia, scarcer, conical, more elongate tubercles.

Biology: Behrens & Hermosillo (2005) indicated it feeds on Demospongiae of the genus *Hamacantha* Gray 1867 (*Zygherpe*).

Distribution: reported from California, United States; the Pacific coast of Mexico and Costa Rica, where it is very common (Camacho-García & Valdés 2003; Camacho-García *et al.* 2005). The type locality in Dale Beach, Pacific side of the Canal Zone, Panama (Ev. Marcus & Er. Marcus 1967), it has also been found in the Coiba Island National Park (Hermosillo 2004; Behrens & Hermosillo 2005).

Superfamily Polyceroidea Alder & Hancock 1845

Family Polyceridae Alder & Hancock 1845

Subfamily Polycerinae Alder & Hancock 1845

Genus ***Polycera*** Cuvier 1816

44. *Polycera alabe* Collier & Farmer 1964 Figure 4e

Diagnosis: animal up to 30 mm in length; body black with orange or yellow oval spots; dorsal papillae conical, translucent white; other color variations include black body with yellow lines instead of spots or brown body; oral veil with four appendages; rhinophores, gill black with orange spots, gill with five tripinnate leaves.

Biology: common on bryozoans of the genus *Bugula* Oken 1815 (Camacho-García *et al.* 2005). Santander & Valdés (2013) revealed that *P. alabe* could constitute different species or a complex of several.

Distribution: reported in the Eastern Pacific from Southern California to Chile (Camacho-García *et al.* 2005; Pola *et al.* 2014), also in the Coiba National Park in Panama (Hermosillo 2004; Behrens & Hermosillo 2005).

45. *Polycera hedgpethi* Er. Marcus 1964 Figure 4f

Diagnosis: animal up to 25 mm in length; dark body due to dense black or dark gray spots; light gray middle dorsal ridge; gill leaves, extrabranchial processes with yellow tips.

Biology: it feeds on bryozoans of the genus *Bugula* Oken, 1815 (Behrens & Hermosillo 2005).

Distribution: nearly cosmopolitan species, probably introduced in many regions such as the Mediterranean (Streftaris *et al.* 2005; Keppel *et al.* 2012); originally described from Californian, common from San Francisco Bay to Baja California, Mexico (Keen 1971; McDonald 1983; Behrens & Hermosillo 2005; Hermosillo *et al.* 2006), also reported from the Coiba Island National Park, Panama to the Galapagos Islands (Hermosillo 2004; Behrens & Hermosillo 2005).

46. *Polycera anae* Pola, Sánchez-Benítez & Ramiro 2014 Figure 4g

Diagnosis: animal up to 5 mm in length; body black, mottled with rows of orange lines or dots; oral veil, rhinophores, extrabranchial processes, gill, foot, translucent white.

Remarks: very similar to *P. alabe*, Pola *et al.* (2014) described the differences between these two species. The holotype of *P. anae* was collected on Brincanco Island, Coiba National Park, Panama and the paratypes on Jacarita Island, also in Coiba National Park and on the Pacific coast of Costa Rica (Pola *et al.* 2014).

Distribution: Reported from the Eastern Pacific from Revillagigedos Islands (Mexico), Costa Rica to the Galapagos Islands (Camacho-García *et al.* 2005 as *Polycera* sp.).

47. *Polycera* sp. 1

Diagnosis: animal up to 16 mm in length; body translucent gray, with reddish longitudinal lines; conical papillae yellow with rounded white apex, surrounded by opaque white pigment; velar appendages, lateral papillae, rhinophores, translucent; gill with red pigment.

Distribution: Atlantic species; it is probably an undescribed; it has been reported from the Western Atlantic of Florida, Belize, and Panama (Valdés *et al.* 2006).

Genus ***Polycerella*** A.E. Verrill 1880

48. *Polycerella glandulosa* Behrens & Gosliner 1988 Figure 4h

Diagnosis: animal up to 28 mm in length; body translucent white with whitish yellow, dark brown dots; notum with numerous papillae, two characteristic extrabranchial appendages.

Biology: lives and feeds on bryozoans of the genera *Amathia* Lamouroux, 1812 (= *Zoobotryon* Ehrenberg, 1831) and *Bugula* Oken 1815 (Behrens & Hermosillo 2005; Camacho-García *et al.* 2005).

Remarks: Camps *et al.* (2020) based on stable isotope analysis, shown that *Polycerella emertoni* A.E. Verrill 1880, which also lives on a bryozoan species of the same genus *(A. verticillata,* (Delle Chiaje 1822)), feeds on the periphyton of diatoms that live on the bryozoan colony rather than on the bryozoan.

Distribution: reported in the Eastern Pacific, from San Diego, California, and the Gulf of California to the Coiba National Park in Panama (Turgeon *et al.* 1998; Hermosillo, 2004; Behrens & Hermosillo 2005; Camacho-García *et al.* 2005).

Subfamily Nembrothinae Burn 1967

Genus ***Martadoris*** Willan & Chang 2017

49. *Martadoris oliva* (K.B. Meyer 1977)

Diagnosis: animal up to 20 mm in length; body deep olive to light green; rhinophores very dark; tips of branchial leaves dark purple or dark blue-green.

Distribution: Atlantic species until recently included in the genus *Tambja* Burn 1962; reported from the Caribbean Sea of Costa Rica and also from Point Galeta and Colon Island, in Panama (Meyer 1977; Valdés *et al.* 2006).

Subfamily Triophinae Odhner 1941

Genus ***Limacia*** O.F. Müller 1781

50. *Limacia janssi* (Bertsch & Ferreira 1974) Figure 5a

Diagnosis: animal up to 8 mm in length; body yellowish with numerous orange dots, rhinophores semitransparent, with orange lamellae; three tripinnate gill leaves of same color; edge of notum with three rows of bulbous tubercles.

Biology: feeds on encrusting bryozoans (Behrens & Hermosillo 2005).

Distribution: reported from the Eastern Pacific, from the Gulf of California to the Coiba National Park in Panama (Bertsch & Ferreira 1974; Hermosillo 2004; Behrens & Hermosillo 2005; Camacho-García *et al.* 2005).

Family Chromodorididae Bergh 1891

Genus ***Tyrinna*** Bergh 1898

51. *Tyrinna evelinae* (Er. Marcus 1958) Figure 5b

*Diagnosis***:** animal up to 30 mm in length; body white, semi-transparent, with small rounded orange spots scattered all over; rhinophores, gill leaves same color as body with opaque white tips; some animals with spots larger near mantle margin; mantle margin white with conspicuous opaque white defensive glands.

Biology: lives under stones, in Brazil feeds on dysideid and chalinid sponges (Belmonte *et al.* 2015).

Remarks: animals from the Pacific and the Atlantic coasts are morphologically similar, but molecular data is needed to confirm if they constitute a complex of cryptic species.

Distribution: Currently considered an Eastern Pacific and amphiatlantic species. In the Eastern Pacific it has been recorded from the Gulf of California to Peru (Behrens & Hermosillo 2005). In the western

Atlantic it has been reported from Costa Rica, Jamaica, Puerto Rico and the Dominican Republic to Brazil (Camacho-García *et al.* 2005; Valdés *et al.* 2006; Caballer *et al.* 2015). In Panama it has been recorded both on the Pacific (reference) and the Caribbean coast of Bocas del Toro (Goodheart *et al.* 2016).

Genus ***Felimare*** Ev. Marcus & Er. Marcus 1967

52. *Felimare agassizii* (Bergh 1894) Figure 5c

Diagnosis: animal up to 80 mm in length; body blackish brown, with numerous rounded yellow spots, larger white spots on dorsum, sides of body; mantle margin with three lines, outer yellow, middle dark blue or black, internalmost blue; edge of foot blue; rhinophores black with yellow middorsal line, gill leaves violaceous with white rachises.

Distribution: common; Pacific species, it has been reported in the Eastern Pacific from the Gulf of California, Panama, Colombia, and the Galapagos Islands (Behrens & Hermosillo 2005; Camacho-García *et al.* 2005; Debelius & Kuiter 2007; Johnson & Gosliner 2012).

53. *Felimare bayeri* Ev. Marcus & Er. Marcus 1967 Figure 5d

Diagnosis: animal up to 60 mm in length; body dark blue, dorsum with series of longitudinal yellow lines, wide white submarginal band, series of black circular spots around mantle margin.

Biology: lives in association with sponges of the genus *Dysidea* Johnston 1842 (Rudman 2005).

Distribution: Atlantic species reported in the Western Atlantic from Florida (Valdés *et al.* 2006; Debelius & Kuiter 2007; Ortigosa *et al.* 2015) to point Galeta, Colon, Panama (Meyer 1977; Miloslavich *et al.* 2010).

54. *Felimare kempfi* (Ev. Marcus 1971) Figure 5e

Diagnosis: animal up to 20 mm in length; body whitish, darkened by more or less extensive bluish spots; mantle margin with broad yellow band; central longitidunal white band from rhinophores to gill; rhinophores purple; gill leaves pale blue with darker rachises.

Distribution: Atlantic species, reported in the Western Atlantic from Florida to Brazil (Collin *et al.* 2005; Valdés *et al.* 2006; Debelius & Kuiter 2007; Caballer *et al.* 2015) also Point Galeta, Colon Island, Panama (Meyer 1977) and Bocas del Toro, Panama (Goodheart *et al.* 2016).

55. *Felimare ruthae* (Ev. Marcus & Hughes 1974) Figure 5f

Diagnosis: animal up to 30 mm in length; body very dark blue color with several longitudinal yellow lines running down back, also curved yellow line in front of rhinophores; fine yellow line on edge of mantle, inside this an opaque white band interrupted in center of body; rhinophores, branchial leaves like body but with white lines on back, rachis respectively; tail with yellow lines, white spots.

Distribution: Atlantic species, reported in the Caribbean Sea from Mexico to Venezuela and in numerous Caribbean islands (Debelius & Kuiter 2007; Caballer *et al.* 2015); also recorded in Point Galeta, Colon Is., Panama (Meyer 1977).

56. *Felimare fregona* (Ortea & Caballer 2013)

Diagnosis: animal up to 40 mm in length; body elongated, narrow, white, pale blue to gray at times; three yellow lines on dorsum; mantle with black circular spots, surrounded with white line; rhinophores white, with purple line running from base.

Biology: it feeds on a sponge of the genus *Dysidea* Johnston 1842. The egg mass is a narrow ribbon with 2.5–3 whorls and white eggs (Valdés *et al.* 2006).

Distribution: originally described from Guadeloupe (Ortea *et al.* 2013) but previously known from various parts of the Caribbean such as Venezuela, Puerto Rico, the Virgin Islands, and Curaçao (Valdés *et al.* 2006 as *Hypselodoris* sp. 3). In Panama has been reported in the Bocas del Toro Archipelago (Goodheart *et al.* 2016).

Genus ***Felimida*** Ev. Marcus 1971

57. *Felimida clenchi* (Russell 1935) Figure 5g

Diagnosis: animal up to 30 mm in length; polychromatic species, body reddish, pink, or whitish, with opaque white, bluish spots forming complex patterns; white spots on dorsum bordered by fine yellow lines; mantle edge with red line, wide white submarginal band with rounded extensions towards interior of mantle; rhinophores, gill leaves purplish blue.

Remarks: molecular and chromatic variability studies carried out by Padula *et al.* (2016) have made it possible to clarify the chromatic variability of this species and its separation from the similar species *F. binza*; Padula *et al.* (2016) also found that *F. neona* is a junior synonymous of *F. clenchi.*

Distribution: Atlantic species reported in the Western Atlantic from the Bahamas, Florida, Costa Rica, Colombia, Venezuela, and the Caribbean Islands to Brazil (Valdés *et al.* 2006; Debelius & Kuiter 2007; Caballer *et al.* 2015) In Panama it has been recorded from Point Galeta and Limon Bay, Colon Island (Meyer 1977) and the Bocas del Toro Archipelago (Goodheart *et al.* 2016).

58. *Felimida baumanni* (Bertsch 1970) Figure 5h

Diagnosis: animal up to 65 mm in length; body whitish with numerous red spots, some specimens appearing completely red; mantle edge white; rhinophores with white basal part, red distal part; up to 20 whitish gill leaves with purple apices.

Distribution: Pacific species reported in the Eastern Pacific from the Gulf of California to Ecuador and the Galapagos Islands (Camacho-García *et al.* 2005), also in the Coiba Island National Park, Panama (Hermosillo 2004).

59. *Felimida sphoni* Ev. Marcus 1971 Figure 6a

Diagnosis: animal up to 35 mm in length; body purplish red with small orange spots, white longitudinal bands near mantle margin, interrupted in middle zone; narrow submarginal yellow band; rhinophores, gill leaves pinkish cream with purple streaks.

Distribution: Pacific species reported in the Eastern Pacific from the Gulf of California to the Galapagos Islands (Behrens & Hermosillo 2005; Camacho-García *et al.* 2005; Debelius & Kuiter 2007), also in the Coiba Island National Park, Panama (Hermosillo 2004).

60. *Felimida marislae* (Bertsch 1973)

Diagnosis: animal up to 70 mm in length; body greyish white, with irregular orange rings surrounded by white, mainly on mantle margins; center of mantle usually free of orange; mantle edge white, wavy; rhinophores, gill leaves as body with white rachises.

Distribution: common Pacific species reported in the Eastern Pacific from the Gulf of California to Coiba Island National Park, Panama (Hermosillo 2004; Behrens & Hermosillo 2005; Debelius & Kuiter 2007).

61. *Felimida grahami* (T.E. Thompson 1980)

Diagnosis: animal up to 20 mm in length; body white, dark pink, dorsum with red dots; mantle margin with broad white band, yellow marginal band; rhinophores, gill leaves brown or pink with white apices.

Distribution: Atlantic species reported in the Western Atlantic in Panama (Miloslavich *et al.* 2010), Venezuela, and some Caribbean Islands (Valdés *et al.* 2006; Caballer *et al.* 2015).

Genus ***Chromolaichma*** Bertsch 1977

62. *Chromolaichma dalli* (Bergh 1879) Figure 6b

Diagnosis: animal up to 65 mm in length; body gray, green, or bluish brown, with small greenish, yellow, white, green or bluish spots on entire dorsum; small rounded dorsal tubercles, edge of mantle with pink or orange line; rhinophores, gill leaves with red or pink color with white apices.

Distribution: Pacific species reported in the Eastern Pacific from Baja California, Mexico to the Galapagos Islands and mainland Ecuador (Camacho-García *et al.* 2005), also in the Coiba Island National Park, Panama (Hermosillo 2004).

63. *Chromolaichma sedna* (Ev. Marcus & Er. Marcus 1967) Figure 6c

Diagnosis: animal up to 65 mm in length; body uniformly white, elongate, slightly wavy edge of mantle; narrow yellow marginal stripe, reddish submarginal line; edge of foot with yellow stripe as mantle; rhinophores, gill leaves white at base, reddish lamellae.

Remarks: Matsuda & Gosliner (2018) summarized the nomenclatural history of this species, initially described as *Casella sedna* Ev. Marcus & Er. Marcus 1967 for the Gulf of California, later transferred to *Glossodoris* and more recently to *Dorisprismatica* (Johnson & Gosliner 2012). Matsuda & Gosliner (2018) suggested including this species in the genus *Chromolaichma*, as Bertsch (1977) had already indicated several decades ago.

Distribution: records of this species in the Eastern Pacific range from California, Mexico, Central America to the Galapagos (Bertsch 1988), also in the Coiba Island National Park, Panama (Hermosillo 2004).

64. *Chromolaichma cf. sedna* (Ev. Marcus & Er. Marcus 1967)

Diagnosis: animal up to 65 mm in length; body oval, white with yellow marginal band on mantle, foot; submarginal red band; rhinophores, gill leaves white at base, reddish lamellae.

Remarks: Goodheart *et al.* (2016) suggested that records of this species in the Caribbean could be the result of a recent introduction but Matsuda & Gosliner (2018) analyzed sequence data of specimens from the Eastern Pacific and the Florida Keys and found substantial genetic distances between them (p-distance > 11). Matsuda & Gosliner (2018) concluded the existence of two cryptic species, one in the Pacific and another in the Western Atlantic.

Distribution: Western Atlantic from Florida to Panama (Valdés *et al.* 2006), where it has been cited in Bocas del Toro (Goodheart *et al.* 2016).

65. *Chromolaichma edmundsi* (Cervera, García-Gómez & Ortea 1989)

Diagnosis: animal up to 35 mm in length; body gray-blue; dorsum with many small tubercles, scattered, abundant black spots, small orange circular spots surrounded by smaller yellow ones; greyish-blue rhinophores with three visible orange lines converging at apex; rhinophoral, gill pockets surrounded by orange rings; rhinophores perfoliate with 17–19 lamellae; up to 30 branchial leaves, greyish, semi-translucent near apex, orange pigmentation on internal, outer edges of rachis; anal papilla grayish blue.

Remarks: this species has been cited by San Martín (1997) from Isla Coiba; however, Hermosillo (2004) believes that this record corresponds to an identification error with *Felimida dalli* (Bergh 1879) as *Glossodoris dalli* that is regularly found in the Coiba National Park, it may also be *Felimida punctilucens* (Bergh, 1890) as *Chromolaichma punctilucens*. The presence of *C. edmundsi* in the Pacific of Panama must be confirmed with new records.

Distribution: Atlantic species, reported in the Eastern Atlantic of the Canary Islands (Cervera *et al.* 1989) and in Sao Tomé & Principe (Matsuda & Gosliner 2018), also in the Coiba Island National Park, Panama (Hermosillo 2004).

Genus ***Mexichromis*** Bertsch 1977

66. *Mexichromis tura* (Ev. Marcus & Er. Marcus 1967) Figure 6d

Diagnosis: animal up to 10 mm in length; body purplish-black with yellow or orange dorsal spots; edge of mantle with external yellow line, followed by black submarginal, bluish submarginal lines; inside these lines usually yellow or white band, sometimes interrupted, almost surrounding entire mantle; purplish black rhinophores; whitish gill leaves with dark purple tips.

Distribution: rare Pacific species reported in the Eastern Pacific from the Gulf of California to the Panama Canal Zone (Behrens & Hermosillo, 2005; Camacho-García *et al.* 2005; Debelius & Kuiter 2007; Avilés 2010).

67. *Mexichromis antonii* (Bertsch 1976) Figure 6e

Diagnosis: animal up to 12 mm in length; body pale blue with dashed white or yellow line down center of dorsum; mantle edge with external yellow line, intermediate black line, internal broad opaque white band, usually divided into two; rhinophores, gill leaves pink with black tips.

Distribution: common Pacific species, reported in the Eastern Pacific from the Gulf of California to Coiba Island National Park, Panama (Hermosillo 2004; Behrens & Hermosillo 2005; Camacho-García *et al.* 2005; Debelius & Kuiter 2007; Avilés 2010).

Family Hexabranchidae Bergh 1891

Genus ***Hexabranchus*** Ehrenberg 1828

68. *Hexabranchus morsomus* Ev. Marcus & Er. Marcus 1962 Figure 6f

Diagnosis: animal up to 100 mm in length; body reddish to creamy white with red, orange spots; mantle margin narrow, wavy, sometimes with opaque white band; rhinophores semitransparent at base, reddish lamellae; gill leaves red or yellowish with red tips.

Biology: is found under rocks or coral debris, mainly on live reefs (Collin *et al.* 2005). when disturbed, it swims by undulating movements of the mantle margin and flexing the body.

Distribution: Atlantic species reported in the Western Atlantic from Honduras, Costa Rica to Venezuela and the Caribbean Islands (Valdés 2002; Collin *et al.* 2005, Valdés *et al.* 2006; Avilés 2010; Caballer *et al.* 2015). In Panama it has been recorded from Point Galeta, Colon Island (Meyer 1977) and in the Bocas del Toro Archipelago (Collin *et al.* 2005; Goodheart *et al.* 2016), also collected by us in Crawl Cay, Bocas del Toro Province (present paper).

Family Cadlinidae Bergh 1891

Genus ***Aldisa*** Bergh 1878

69. *Aldisa* sp. 1

Diagnosis: animal up to 22 mm in length; body red with characteristic transverse, incomplete creamy white band just behind rhinophores, yellow spots scattered on dorsum; two darker circular areas on dorsum, one behind rhinophores, another just anterior to gill; rhinophores, branchial leaves red.

Remarks: it is probably an undescribed species and very similar to *Aldisa sanguinea* (J.G. Cooper 1863) which is found in California and Oregon in United States, and in Mexico.

Distribution: Valdés *et al.* (2006) reported this species in the Caribbean Sea (St. Vincent and the Grenadines, Puerto Rico and St. Lucia), also reported in the Pacific in Uva Is. of Coiba National Park, Panama (Hermosillo & Camacho-García 2006).

Genus ***Cadlina*** Bergh 1879

70. *Cadlina sparsa* (Odhner 1921) Figure 6g

Diagnosis: animal up to 35 mm in length; body uniform white, cream, to light yellow; body oval, flat; dorsum with small rounded tubercles, some yellow, forming somewhat irregular ring around notum; rhinophores, branchial leaves white, light yellow, or brown.

Biology: feeds on sponges of the genus *Aplysilla* Schulze 1878 (Behrens & Hermosillo 2005).

Distribution: Pacific species with a wide range along the Eastern Pacific, reported from Alaska to Juan Fernández Island in Chile (Camacho-García *et al.* 2005; Debelius & Kuiter 2007) and Argentina (Schrödl 2000). In Panama has been reported in the Coiba Island National Park (Hermosillo 2004; Behrens & Hermosillo 2005).

71. *Cadlina rumia* Er. Marcus 1955 Figure 6h

Diagnosis: animal up to 15 mm in length; translucent white or slightly yellowish; body elongated, flat; dorsum covered with numerous small tubercles, larger yellow forming ring around notum; rhinophores, gill leaves white or yellowish.

Biology: lives under rocks in the intertidal zone and feeds on several sponges of different genera such as *Dysidea* Johnston 1842*, Haliclona* Grant 1841*, Callyspongia* Duchassaing & Michelotti 1864 or *Scopalina* Schmidt 1862 (Belmonte *et al.* 2015).

Distribution: Atlantic species recorded in the tropical Western Atlantic from Florida to Brazil and various Caribbean islands (Edmunds 1981; Valdés *et al.* 2006; Debelius & Kuiter 2007; García-García *et al.* 2008; Caballer *et al.* 2015) and Ghana (Edmuds 1981). In Panama it has been recorded from the Bocas del Toro Archipelago (Collin *et al.* 2005; Goodheart *et al.* 2016). Goodheart *et al.* (2016) indicate that it is an amphiatlantic species but do not indicate the places where it has been cited in the Eastern Atlantic.

72. *Cadlina luarna* (Er. Marcus & Ev. Marcus 1967) Figure 7a

Diagnosis: animal up to 60 mm in length; body light brown with small dark brown spots on dorsum; numerous well-spaced, rounded tubercles of various sizes; rhinophores, gill leaves brown.

Distribution: Pacific species, common in Baja California, Mexico, reported in the Eastern Pacific from the Gulf of California to Coiba Island National Park, Panama (Hermosillo 2004; Behrens & Hermosillo 2005; Camacho-García *et al.* 2005).

73. *Cadlina* sp. 1

Diagnosis: animal up to 10 mm in length; body white, dorsum covered with small, rounded tubercles, some of them yellow; rhinophores white with basal brown band; white bipinnate gill leaves.

Remarks: it is probably an undescribed species; very similar to *C. sparsa*.

Distribution: Pacific species reported from Baja California, Mexico to Costa Rica (Camacho-García *et al.* 2005), also on Uva Island in the Coiba Island National Park, Panama (Hermosillo & Camacho-García 2006).

Superfamily Onchidoridoidea Gray 1827

Family Aegiridae P. Fischer 1883

Genus ***Aegires*** Lovén 1844

74. *Aegires sublaevis* Odhner 1932 Figure 7b

Diagnosis: animal up to 12 mm in length; body whitish, light yellow, to lemon yellow with brown spots of different sizes; dorsum with rounded tubercles; rhinophores, gill leaves same color as body; bilobed oral veil.

Biology: feeds in Bermuda Island on sponges of the genus *Clathrina* Gray 1867 (Thompson 1981).

Distribution: amphiatlantic species, reported in the Western Atlantic from Florida to Venezuela, including some Caribbean islands (Templado *et al.* 1987; Valdés *et al.* 2006; Caballer *et al.* 2015). In Panama it has been recorded in Point Galeta Colon Island (Meyer, 1977). In the Eastern Atlantic it has been recorded in the Azores, the Canary Islands and the Mediterranean Sea (Odhner 1932; Schmekel & Portmann 1982; Cervera *et al.* 2004; Malaquias *et al.* 2009; Ballesteros *et al.* 2019).

75. *Aegires ortizi* Templado, Luque & Ortea 1987 Figure 7c

Diagnosis: animal up to 8 mm in length; body cream or pale brown, with conical tubercles on dorsum, tail; each tubercle with dark brown spot at apex; three gill leaves, same color as body, protected by three thick anterior tubercles; rhinophores smooth, rhinophoral sheath with three large tubercles on upper edge.

Distribution: after its original description from Cuba (Templado *et al.* 1987) it has only been recorded in the Cayman Islands, the Bahamas, Venezuela, and Panama (Valdés *et al.* 2005; Caballer *et al.* 2015). In Panama it has been collected in Bocas del Toro Archipelago (Goodheart *et al.* 2016).

Family Goniodorididae H. Adams & A. Adams 1854

Genus ***Okenia*** Menke 1830

76. *Okenia evelinae* Er. Marcus 1957

Diagnosis: animal up to 9 mm in length; body whitish, with small purple spots, larger spot between rhinophores, sometimes with lemon-yellow spots; oral veil with two elongated papillae; six elongated papillae on each dorsal side, four mid-dorsal papillae between gill, rhinophores; very long rhinophores, purple at base, lamellae on posterior side; five white gill leaves.

Biology: feeds on bryozoans such as *Amathia convoluta* (Lamarck 1816) and *A. vidovici* (Heller 1867) (Ortea *et al.* 2009).

Distribution: amphiatlantic species reported from the Canary Islands in the Eastern Atlantic (Ortea *et al.* (2009) and in the Western Atlantic from Florida to Brazil, also in Barbados and Cuba (Caballer *et al.* 2015); in Panama it has been recorded from Point Galeta, Colon Island (Meyer 1977).

Genus ***Trapania*** Pruvot-Fol 1931

77. *Trapania inbiotica* Camacho-García & Ortea 2000

Diagnosis: animal up to 10 mm in length; body cream or white with numerous reddish-brown spots darkening body; posterior end of tail yellow; extrarhinophoral, extrabranchial papillae with yellow tips; rhinophores, gill leaves whitish, also with yellow tips.

Distribution: Pacific species only recorded so far in Costa Rica and Panama (Camacho-García & Ortea 2000; Camacho-García *et al.* 2005).

78. *Trapania* sp. 1

Diagnosis: animal up to 10 mm in length; body whitish with small opaque brown, white spots; oral tentacles with brown band approximately midway.

Remarks: Valdés *et al.* (2005) suggested this is an undescribed species.

Distribution: only known from the Caribbean coast of Panama (Valdés *et al.* 2006).

Superfamily Phyllidioidea Rafinesque 1814

Family Phyllidiidae Rafinesque 1814

Genus ***Phyllidiella*** Bergh 1869

79. *Phyllidiella molaensis* (Meyer 1977)

Diagnosis: animal up to 45 mm in length; body black with characteristic opaque white, black concentric rings; dorsum with numerous conical tubercles; rhinophores black with white tips; gill lamellae located between hyponotum, foot, from head to posterior end of body.

Distribution: Atlantic species originally described from Galeta Point and Portobelo, on the Caribbean coast of Panama (Meyer, 1977) and subsequently recorded from Costa Rica (Valdés *et al.* 2006).

Family Dendrodorididae O'Donoghue 1924 (1864)

Genus ***Dendrodoris*** Ehrenberg 1831

80. ***Dendrodoris fumata*** (Rüppell & Leuckart 1830) Figure 7d

Diagnosis: animal up to 95 mm in length; body highly variable, grey, greyish-green, pink, red or black; mantle margin wide, wavy; dorsum smooth; rhinophores, gill leaves same color as body with white tips.

Remarks: the black form can be confused with *Dendrodoris nigra* (Stimpson 1855); the orange/red color forms of *D. fumata* have been frequently cited as *D. rubra*, which is considered synonymous of the former.

Distribution: Indo-Pacific species recorded in numerous locations from the Red Sea and Tanzania (Eastern Africa), Japan, the Philippines, Australia, and Hawaii to the Eastern Pacific (Mexico, Costa Rica and Colombia) (Behrens & Hermosillo 2005; Ballesteros *et al.* 2012-2020). In Panama it has been recorded from the Coiba National Park (Hermosillo, 2004). It is considered a non-indigenous species (NIS) in the Mediterranean Sea where it has arrived from the Red Sea through Lessepsian migration (Streftaris *et al.* 2005; Cem *et al.* 2012).

81. ***Dendrodoris krebsii*** (Mörch 1863) Figure 7e

Diagnosis: animal up to 150 mm in length; body variable across entire color spectrum; dorsum uniformly colored or with irregular brown, gray or reddish spots; mantle margin broad, wavy, with transverse striations; rhinophores, gill leaves same color as body with whitish tips.

Biology: under dead coral or rocks, one of the most common species of nudibranchs in the Caribbean (Goodheart *et al.* 2016). Belmonte *et al.* (2015) recorded active feeding of *Dendrodoris krebsii* on a haplosclerid sponge.

Remarks: Valdés *et al.* (2005) provided photographs of live animals covering almost the entire color variability. Brodie (2000) suggested that *D. krebsii* could be a complex of species rather than a single species with broad chromatic variation. Molecular analysis is needed to clarify this issue.

Distribution: Atlantic species, reported in the Western Atlantic from Georgia, USA to Brazil and most of the Caribbean islands (Collin *et al.* 2005; Camacho-García *et al.* 2005; Valdés *et al.* 2006; Ríos 2009; Caballer *et al.* 2015; Ortigosa *et al.* 2015). In Panama it has been recorded in Galeta Point, Colon (Meyer

1977) and in the Bocas del Toro Archipelago (Goodheart *et al.* 2016); also collected by us in Crawl Cay, Bocas del Toro Province (present paper).

82. *Dendrodoris albobrunnea* Allan 1933 Figure 7f

Diagnosis: animal up to 80 mm in length; body variable from whitish or pale gray to brown, with irregular patches of different colors, often with star-shaped white spots; mantle with conical tubercles, wide margin.

Distribution: Pacific species reported in the Eastern Pacific from the Coiba National Park, Panama (Hermosillo 2004) to Colombia (Camacho-García *et al.* 2005).

Genus ***Doriopsilla*** Bergh 1880

83. *Doriopsilla janaina* Er. Marcus & Ev. Marcus 1967 Figure 7g

Diagnosis: animal up to 25 mm in length; body brown or reddish, with black dots, pair of darker longitudinal bands; dorsum with numerous, wide, rounded tubercles; gill leaves yellowish.

Distribution: common Pacific species reported from Baja California, Mexico to Panama and the Galapagos Islands (Camacho-García *et al.* 2005). In Panama it has been recorded from the Canal Zone (Ev. Marcus & Er. Marcus 1967), the Gulf of Montijo (Vega & González 2002) and Coiba Island (Behrens & Hermosillo 2005; Hermosillo & Camacho-García 2006).

84. *Doriopsilla nigrolineata* Meyer 1977

Diagnosis: animal up to 30 mm in length; body cream or orange dark lines; dorsum with rounded tubercles; rhinophores, gill leaves yellow.

R*emarks*: very similar to the Eastern Atlantic species *D. areolata* Bergh 1880, of which it was considered a subspecies by Valdés and Ortea (1997), but later Valdés and Hamann (2008) confirmed that it is a different species.

Distribution: reported in the Western Atlantic of Honduras (Meyer 1977; Valdés *et al.* 2006) and Panama (Miloslavich *et al.* 2010), including the Bocas del Toro Archipelago (Goodheart *et al.* 2016).

85. *Doriopsilla rowena* Er. Marcus & Ev. Marcus 1967 Figure 7h

Diagnosis: animal up to 12 mm in length; body off-white to pale yellow, pink or orange, with reddish-brown specks scattered over dorsum, large round opaque white spots arranged longitudinally; small spiculated dorsal tubercles.

R*emarks*: The taxonomic status of this species has been recently reviewed by Goddard & Valdés (2015).

Distribution: reported in the northern Gulf of California to Panama, (Ev. Marcus & Er. Marcus 1967; Keen 1971; Poorman & Poorman 1978; Bertsch & Kerstitch 1984; Camacho-Garcıia *et al.* 2005;

Goddard & Hermosillo 2008; Angulo-Campillo 2005), the Galapagos Islands, Ecuador and La Jolla, California to El Campo, near Punta Eugenia, Baja California Sur, Mexico (Behrens & Hermosillo 2005).

Suborder Cladobranchia Willan & Morton 1984

Family Bornellidae Bergh 1874

Genus ***Bornella*** Gray 1850

86. ***Bornella sarape*** Bertsch 1980 Figure 8a

Diagnosis: animal up to 40 mm in length; body elongate, brown with lighter spots; mid-dorsal ridge extending along length of animal; 4–5 pairs of dorsolateral cerata; rhinophores very long, with tentaculiform processes.

Biology: able to swim by lateral undulating contractions of the body (Bertsch 1980).

Distribution: Pacific species reported from the Gulf of California to Banderas Bay in Mexico (Bertsch, 1980; Bertsch & Kerstitch, 1984; Hermosillo *et al.* 2006). Records from Panama are from Coiba Island (Hermosillo & Camacho-García 2006).

Superfamily Arminoidea Iredale & O'Donoghue 1923 (1841)

Family Arminidae Iredale & O'Donoghue 1923 (1841)

Genus ***Armina*** Rafinesque 1814

87*.* ***Armina californica*** (J.G. Cooper 1863)

Diagnosis: animal up to 70 mm in length; body light pink or brown with ~25 whitish prominent longitudinal ridges, secondary between them; rhinophores small, close together, with longitudinal lamellae; numerous gill leaves between hyponotum, foot.

Biology: capable of burying itself in sediment, it is quite common on sandy or muddy bottoms where it feeds on pennatulaceans of the genera *Virgularia* Lamarck 1816 and *Renilla* Lamarck 1816 (Camacho-García *et al.* 2005).

Distribution: Pacific species reported from Alaska to Peru (Baez *et al.* 2011), in Pacific coast Panama in the Coiba Island National Park (Hermosillo 2004; Behrens & Hermosillo 2005) and Ladrones Island (Báez *et al.* 2011).

88. ***Armina*** sp. 1

Diagnosis: animal up to 33 mm in length; body white-yellow-orange, ridges all along dorsum.

Remarks: animals caught by trawling at depths between 65 and 95 m deep; probably an undescribed species; reported from the Coiba Island National Park (Hermosillo 2004).

Genus ***Histiomena*** Mörch 1860

89. *Histiomena marginata* (Mörch 1859)

Diagnosis: animal up to 75 mm in length; body wide, flattened, brown or reddish with numerous white markings all over dorsum; mantle margin with orange band, external white line; rhinophores with longitudinal lamellae; gill lamellae forming two groups, one anterior, one posterior, between foot, hyponotum.

Biology: like other Arminidae species, they can burrow in the sand during the day and come out at night to search for food., mainly pennatulaceans of the genus *Ptilosarcus* Verrill 1865 (Camacho-García *et al.* 2005)

Distribution: Pacific species reported from the Gulf of California to Panama (Behrens & Hermosillo 2005).

Superfamily Tritonioidea Lamarck 1809

Family Tritoniidae Lamarck 1809

Genus ***Tritonia*** Cuvier 1798

90. *Tritonia exsulans* Bergh 1894

Diagnosis: animal up to 200 mm in length; body whitish, yellow, pink or reddish; foot very wide, with white border as well as lateral margins of head; rhinophoral sheath raised with white upper border; bilobed frontal veil with numerous short fingerlike extensions; edge of dorsum wavy with up to 20 short branched gills.

Remarks: this species has been cited on the Eastern Pacific as *Tritonia diomedea* Bergh 1894 and as *Tochuina tetraquetra* (Pallas 1788). Currently *T. tetraquetra* is included within the genus *Tritonia* and *T. diomedea* is considered synonymous with *T. tetraquetra*. The type locality for the latter species is the Northern Kuril Islands. *T. exsulans*, whose type locality is the Californian coast, was also considered synonymous with *T. diomedea* in several articles. Korshunova & Martynov (2020) have recently conducted a morphological and molecular analysis of the Tritoniidae species from the North Pacific and conclude that *T. tetraquetra* and *T. exsulans* are different species. In this work we consider that the citations attributed to *T. diomedea* or *T. tetraquetra* on the Pacific coasts of Central America should be attributed to *T. exsulans*. Korshunova & Martynov (2020) also dismantle the idea accepted until now that large specimens of Tritoniidae (*Tochuina gigantea* or *Tritonia diomedea*) were consumed raw or cooked by the Ainu natives of the Kuril Islands when in fact the seafood they consumed was the sea squirt *Halocynthia aurantium* (Pallas 1788).

Distibution: its geographical area of distribution ranges from British Columbia to Panama (Behrens & Hermosillo 2005; Korshunova & Martynov 2020).

Genus ***Tritonicula*** Korshunova & Martynov 2020

91. *Tritonicula bayeri* (Ev. Marcus & Er. Marcus 1967) Figure 8b

Diagnosis: animal up to 11 mm in length; body translucent gray, with numerous white lines forming complex lattice; oral veil with 4 short finger-like extensions; rhinophores with raised sheaths having lateral fingerlike extensions like in oral veil; about 15 branching cerata on each side of notum, alternating in size, large ones directed upwards, small ones laterally.

Biology: found on gorgonians and coral debris, in reefs down to 77 m depth, feeds on the octocorals *Briareum asbestinum* (Pallas, 1766), *Leptogorgia virgulata* (Lamarck 1815), and *Pseudopterogorgia* sp. (Ev. Marcus & Er. Marcus 1967; McDonald & Nybakken 1999).

Remarks: This species was included in the genus *Tritonia* until the recent work by Korshunova & Martynov (2020) in which it was assigned to the new genus *Tritonicula*, differing morphologically from *Tritonia* by having a non-bilobed frontal veil with few finger-like processes and few lateral teeth in the radula (Korshunova & Martynov 2020).

Distribution: Atlantic species reported from Georgia, USA to Panama, and some Caribbean islands such as the Cayman Islands, the Virgin Islands, Guadeloupe and Barbados. In Panama has been recorded at the Bocas del Toro Archipelago (Goodheart *et al.*, 2016).

92. *Tritonicula pickensi* (Marcus & Marcus 1967) Figure 8c

Diagnosis: animal up to 25 mm in length; body translucent, with continuous opaque white band from rhinophores to tail, with extensions into base of arborescent cerata; viscera visible, whitish or pinkish; oral veil rounded; rhinophores with raised sheaths laterally with finger-like appendage.

Biology: uncommon, feeds on several species of gorgonians, including *Leptogorgia chilensis* Verrill, 1868 (Camacho-García *et al.* 2005). In the original description, Ev. Marcus & Er. Marcus (1967) indicated that in the type locality (Puerto Peñasco, Mexico) in each gorgonian there were at least 4 specimens of this species.

Remarks: Recently transferred to the genus *Tritonicula*, see the remarks of *T. bayeri*.

Distribution: Pacific species reported from the Channel Islands, California to Panama, where has been recorded from the Coiba Island National Park (Hermosillo 2004; Behrens & Hermosillo 2005; Camacho-García *et al.* 2005).

93. *Tritonicula myrakeenae* (Bertsch & Mozqueira 1986)

Diagnosis: animal up to 18 mm in length; body pale brown, semitransparent, with some white spots on dorsum; oral veil with 4–7 short, finger-like processes; lateral margins of dorsum with 8–9 branching cerata directed upward, laterally.

Biology: uncommon, lives in the intertidal and sublittoral zones feeding on octocorals, possibly of the genus *Clavularia* Blainville, 1830 (Camacho-García *et al.* 2005).

Remarks: recently transferred to the genus *Tritonicula*, see the remarks of *T. bayeri.*

Distribution: Pacific species reported from Southern California to Panama (Camacho-García *et al.* 2005).

94. *Tritonicula hamnerorum* (Gosliner & Ghiselin 1987) Figure 8d

Diagnosis: animal up to 15 mm in length; body greyish or pink with about 20 longitudinal white lines from head to tail; semicircular oral veil with 4–6 short papillae; rhinophoral sheath with upper edge lobed, outermost most developed; up to 9 cerata with short branches on each side of notum.

Biology: feeds on gorgonians such as *Gorgonia ventalina* Linnaeus 1758 and *Gorgonia flabellum* Linnaeus 1758 (Gosliner & Ghiselin 1987), from which it obtains secondary metabolites and stores them for its own defense (Cronin *et al.* 1995); Cronin *et al.* (1995) found up to 1,700 specimens of *T. hamnerorum* in a single colony of *G. ventalina* in the Florida Keys, USA.

Remarks: recently transferred to the genus *Tritonicula*, see the remarks of *T. bayeri*.

Distribution: Caribbean species reported from Florida to Panama, the Bahamas and the Cayman Islands (Valdés *et al.* 2006). In Panama it has been recorded at the Bocas del Toro Archipelago (Goodheart *et al.* 2016).

Genus ***Marionia*** Vayssière 1877

95. *Marionia kinoi* Angulo & Bertsch 2013

Diagnosis: animal up to 40 mm in length; body semitransparent, with orange viscera, whitish spots mainly distributed on dorsal margins; oral veil with about 10 tentaculiform extensions; rhinophoral sheaths with upper edge with rounded tubercles; up to 12 pairs of branched cerata.

Biology: feeds on octocorals of the genus *Carijoa* Müller 1867 (Camacho-García *et al.* 2005).

Distribution: Pacific species reported from the Gulf of California to Panama and the Galapagos Islands (Camacho-García *et al.* 2005; Angulo & Bertsch 2013).

Superfamily Dendronotoidea Allman 1845

Family Dotidae Gray 1853

Genus ***Doto*** Oken 1815

96. *Doto caramella* Er. Marcus 1957

Diagnosis: animal up to 8 mm in length; body dark orange with opaque white spots on dorsum; 5–8 cerata on each side of body with rounded tubercles; rhinophores long, smooth.

Remarks: Atlantic species reported in the Western Atlantic from the southern Caribbean to Brazil including the Bocas del Toro Archipelago, Panama (Collin *et al.* 2005, as cf.).

97. *Doto chica* Ev. Marcus & Er. Marcus 1960 Figure 8e

Diagnosis: animal up to 10 mm in length; body semitransparent, greyish with brown, white spots on dorsum; 5–6 large cerata on each side of notum, with elongated tubercles, cream or brown digestive gland; rhinophores same color as body.

Biology: Ortea (2001) cites this species living on hydroids of the genus *Dentitheca* Stechow 1920; on mangrove roots in Cayo Diego Pérez, Southern Cuba and on hydroids of the species *Eudendrium carneum* Clarke 1882 in Puerto Morelos, Quintana Roo, Mexico and the north coast of Cuba.

Distribution: Caribbean species reported from Florida to Brazil, also in Puerto Rico, Curaçao, and Cuba (Ortea 2001). In Panama has been recorded from the Bocas del Toro Archipelago (Goodheart *et al.* 2016).

98. *Doto lancei* Ev. Marcus & Er. Marcus 1967 Figure 8f

Diagnosis: animal up to 9 mm in length; body white or cream with brown pigment on veil, notum, rhinophoral sheaths, cerata; 7–8 cerata on each side of notum, with rounded tubercles, upper 3 rows with black subapical ring, most with apical black spot.

Biology: lives on hydroids of the genus *Aglaophenia* Lamouroux 1812 (Camacho-García *et al.* 2005).

Distribution: Eastern Pacific species reported from Monterey Bay, California to Panama (Behrens & Hermosillo 2005).

99. *Doto wildei* Er. Marcus & Ev. Marcus 1970

Diagnosis: animal up to 4 mm in length; body with some opaque white spots on dorsum; 6–7 pairs of tall cerata, orange due to digestive gland; 5–6 rows of rounded tubercles on each cerata, grayish or cream.

Biology: found in hydrozoans (Goodheart *et al.* 2016).

Distribution: Atlantic species that has been reported from Florida to Brazil, also in some Caribbean islands as Puerto Rico, Curaçao and Cuba. In Panama it has been cited from the Bocas del Toro Archipelago (Goodheart *et al.* 2016).

100. *Doto escatllari* Ortea, Moro & Espinosa 1998 Figure 8g

Diagnosis: animal up to 5 mm in length; body translucent with cream or yellowish viscera; numerous black spots scattered throughout body; 4–5 pairs of cerata with rounded blue tubercles arranged in 3 rings; each cerata with black spot at base, pseudobranch formed by three branches; rhinophores smooth, rhinophoral sheath with anterior border protruding forward.

Biology: lives on colonies of Sertulariidae hydrozoans (Ortea 2001).

Distribution: Atlantic species that has been recorded from Costa Rica and Barbados (Valdés *et al.* 2006) as well as from the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016). Also found in the Canary Islands, Cape Verde, and Morocco (Ortea 2001; Ortea & Moro 2017).

101. *Doto* sp. 1

Diagnosis: animal up to 14 mm in length; body pink, darker towards dorsum; cerata with round tubercles, variable color, forming clusters.

Biology: lives on hydrozoans of the genus *Macrorhynchia* Kirchenpauer 1872 (formerly *Lytocarpus* Allman 1883) (Behrens & Hermosillo 2005)

Remarks: probably an undescribed species.

Distribution: Eastern Pacific species reported from Banderas Bay, Guerrero, Mexico (Behrens & Hermosillo 2005, as *Doto* sp. 3). Hermosillo (2004) reports its presence on Coiba Island, Panama (as *Doto* sp. 1).

102. *Doto* sp. 2

Diagnosis: animal up to 9 mm in length; body yellowish with brown pigment, white spots; 6–7 cerata on each side of notum with rounded tubercles, each with purple spot; yellowish digestive gland; rhinophores with dark pigment.

Remarks: probably an undescribed species.

Distribution: Caribbean species reported from the coast of Panama (Valdés *et al.* 2006, as *Doto* sp. 2).

Family Scyllaeidae Alder & Hancock 1855

Genus ***Crosslandia*** Eliot 1902

103. *Crosslandia daedali* Poorman & Mulliner 1981

Diagnosis: animal up to 25 mm in length; body greenish-brown with white spots, some rounded blue spots on sides of body; parapodia divided into two lobes, most anterior largest, both with irregular sharp extensions on edges; some conical tubercles on each side of body.

Biology: rare, feeds on epiphytic hydrozoans on *Halimeda* Lamouroux 1812 *and Padina* Adanson 1763 (Behrens 2004).

Distribution: Eastern Pacific species reported from Baja California, Mexico to Panama (Camacho-García *et al.* 2005; Debelius & Kuiter 2007).

Genus ***Notobryon*** Odhner 1936

104. *Notobryon panamicum* Pola, Camacho-García & Gosliner 2012

Diagnosis: animal up to 20 mm in length; body brown, semi-transparent, revealing yellowish internal organs; numerous irregular olive-green, white, yellowish spots all over body; two rounded lobes on each side of body, each with 4 secondary gills.

Biology: rare (Camacho-García *et al.* 2005), when disturbed it swims by lateral movements of the body; it feeds on hydrozoans of the genus *Macrorhynchia* Kirchenpauer 1872 (formerly *Lytocarpus* Allman 1883) (Behrens & Hermosillo 2005).

Remarks: In the Eastern Pacific this species has been recorded under the name of *N. wardi* Odhner 1936*,* a tropical Indo-Pacific species. Pola *et al.* (2012) listed the anatomical and molecular differences between *N. wardi* and *N. panamicum* as well as the very similar South African species *N. thompsoni* Pola, Camacho-García & Gosliner 2012.

Distribution: Eastern Pacific species known only from the Panamic Province including the southern coast of Mexico, Costa Rica, and Panama (Camacho-García *et al.* 2005, as *Notobryon* sp.; Behrens & Hermosillo 2005, as *N. wardi*; Pola *et al.* 2012).

Family Lomanotidae Bergh 1890

Genus ***Lomanotus*** Vérany 1844

105. ***Lomanotus vermiformis*** Eliot 1908 Figure 8h

Diagnosis: animal up to 40 mm in length; body very elongated, narrow, brown with network of white lines; cerata very numerous, giving appearance of polychaete.

Biology: cryptic on the hydrozoan *Macrorhynchia philippina* Kirchenpauer 1872 on which it feeds (McDonald & Nybakken 1999); swims with lateral flexions of the body when disturbed (Valdés *et al.* 2006).

Distribution: it seems to be a circumtropical species that has been recorded in different localities of the Indo-Pacific (Rudman 1999a) and the Western Atlantic, including Florida, the Bahamas, the Bocas del Toro Archipelago, Panama (Collin *et al.* 2005; Goodheart *et al.* 2016), and the Coiba Island National Park, Panama (Hermosillo 2004; Behrens & Hermosillo 2005).

Superfamily Flabellinoidea Bergh 1889

Family Flabellinidae Bergh 1889

Genus ***Flabellina*** Gray 1833

106. ***Flabellina engeli*** Ev. Marcus & Er. Marcus 1968 Figure 9a

Diagnosis: animal up to 25 mm in length; body semitranslucent, with greyish or pinkish hue; dorsum with opaque pigment on each side, between groups of cerata; cerata of each group emerge from well-spaced common bases, with orange band approximately in middle zone; rhinophores with lamellae.

Distribution: Atlantic species reported in the Western Atlantic from Florida to Brazil and some Caribbean islands such as Barbados, Cuba, Puerto Rico, Curaçao, St. Lucia, Martinique, and Grenada (Valdés *et al.* 2006; Debelius & Kuiter 2007). In Panama it has been recorded from the Bocas del Toro Archipelago (Goodheart *et al.* 2016).

107*. Flabellina bertschi* Gosliner & Kuzirian 1990 Figure 9b

Diagnosis: animal up to 30 mm in length; body white, foot translucent; cerata orange or red, with white tips.

Biology: uncommon, feeds on hydrozoans of the genus *Eudendrium* Ehrenberg 1834 (Camacho-García *et al.* 2005).

Distribution: Pacific species reported from the Eastern Pacific from Baja California, Mexico to Ecuador (Hermosillo 2003; Behrens & Hermosillo 2005; Camacho-García *et al.* 2005). In Panama it has been recorded from the Coiba Island National Park (Hermosillo 2004).

Genus ***Coryphellina*** O'Donoghue 1929

108. *Coryphellina marcusorum* (Gosliner & Kuzirian 1990) Figure 9c

Diagnosis: animal up to 30 mm in length; body whitish to light purple; oral tentacles, cerata, rhinophores with purplish band; intense white cerata apices; rhinophores with small papillae on posterior end.

Biology: common, feeds on hydrozoans of the genus *Eudendrium* Ehrenberg 1834 (Camacho-García *et al.* 2005).

Remarks: this species was described in the genus *Flabellina* and has been recently transferred to the new genus *Coryphellina* by Korshunova *et al.* (2017).

Distribution: a species native to Baja California, Mexico that has been cited as far south as Panama and the Galapagos Islands (Behrens & Hermosillo 2005; Camacho-García *et al.* 2005), in Panama it has been found in the Coiba Island National Park (Hermosillo 2004). It has also been cited in the Western Atlantic from Costa Rica to Brazil (Valdés *et al.* 2006) but it probably constitutes a distinct species, which needs to be confirmed with molecular analyses.

Genus ***Edmundsella*** Korshunova, Martynov, Bakken, Evertsen, Fletcher, Mudianta, Saito, Lundin, Schrödl & Picton 2017

109. *Edmundsella vansyoci* (Gosliner 1994)

Diagnosis: animal up to 30 mm in length; body uniform reddish or intense pink; some white spots on cerata, cnidosacs whitish; rhinophores laminated.

Biology: uncommon, it probably feeds on hydrozoans of the genus *Eudendrium* Ehrenberg 1834 (Camacho-García *et al.* 2005).

Remarks: this species was described in the genus *Flabellina* but has been recently transferred to the new genus *Edmundsella* by Korshunova *et al.* (2017).

Distribution: Pacific species reported in the Eastern Pacific from Baja California, Mexico to Panama (Behrens & Hermosillo 2005; Camacho-García *et al.* 2005) where has been recorded in the Coiba Island National Park (Hermosillo 2004).

Family unassigned

Genus ***Kynaria*** Korshunova, Martynov, Bakken, Evertsen, Fletcher, Mudianta, Saito, Lundin, Schrödl & Picton 2017

110*. Kynaria cynara* (Ev. Marcus & Er. Marcus 1967)

Diagnosis: animal up to 60 mm in length; body translucent with pink or reddish tones; edge of foot with bluish line; cerata, rhinophores with sub-apical purple band, white cnidosac at tip of each cerata.

Biology: the animals can swim by moving the cerata rhythmically back and forth, thus managing to escape possible predators; feeds on hydrozoans (Camacho-García *et al.* 2005).

Remarks: this species was described in the genus *Flabellina* and has been recently transferred to the new genus *Kynaria* by Korshunova *et al.* (2017).

Distribution: Pacific species reported in the Eastern Pacific from Baja California, Mexico to costa Rica and the Coiba Island National Park, Panama (Hermosillo 2004; Behrens & Hermosillo 2005; Camacho-García *et al.* 2005).

Superfamily Fionoidea Gray 1857

Family Fionidae Gray 1857

Genus ***Tenellia*** A. Costa 1866

111. *Tenellia lugubris* (Bergh 1870)

Diagnosis: animal up to 40 mm in length; body yellowish with white spots; numerous cerata with brown digestive gland branches, opaque white apices.

Remarks: the similar species *P. panamica* is probably a synonym (Fritts-Penniman *et al.* 2020). The record of *P. melanobranchia* from the Eastern Pacific (Behrens & Hermosillo 2005) needs confirmation.

Distribution: Pacific species reported throughout the Indo-Pacific (Camacho-García *et al.* 2005), in the Eastern Pacific from Baja California, Mexico Sur to Colombia and the Galapagos Islands, also in Panama (Behrens & Hermosillo 2005).

112*. Tenellia tina* (Er. Marcus 1957)

Diagnosis: animal up to 4.5 mm in length; body grayish with opaque white pigment all over; cerata same color as body with digestive gland branches brown; oral tentacles, rhinophores with brown area underneath.

Distribution: Atlantic species recorded in the Western Atlantic from North Carolina to Brazil, included Panama (Valdés *et al.* 2006).

113. *Tenellia lizae* Angulo-Campillo & Valdés 2003

Diagnosis: animal up to 6 mm in length; body reddish or pink with an opaque white patch on pericardium and behind; cerata pinkish brown with white punctuations, cream cnidosac; oral tentacles, rhinophores ruby-red at base, cream or yellowish apically.

Distribution: Pacific species reported in Baja California, Mexico (Angulo-Campillo & Valdés 2003), Isabel Island, Nayarit and Banderas Bay, Mexico (Behrens & Hermosillo 2005) and the Coiba Island National Park, Panama (Hermosillo & Camacho-García 2006)

114. *Tenellia behrensi* Hermosillo & Valdés 2007

Diagnosis: animal up to 5 mm in length; body whitish; cerata whitish with some orange spots below yellowish apices; end of cerata rounded, lacking apparent cnidosac; rhinophores, oral tentacles basally white, yellowish in upper two thirds.

Distribution: only known by the type locality, Los Frailes, Peninsula de Azuero, Gulf of Chiriqui, Panama (Hermosillo & Valdés 2007).

115. *Tenellia destinyae* Hermosillo & Valdés 2007

Diagnosis: animal up to 6 mm in length; body translucent white with dark spots mixed with intense olive green to black spots following midline of notum; body sides with dark brown markings; cerata covered with dark specks; brown spots on sides of oral tentacles, some scattered white spots.

Distribution: reported in the Pacific of Zihuatanejo Mexico (Behrens & Hermosillo 2005; Hermosillo & Valdés 2007) to Costa Rica and the Galapagos (Camacho-García *et al.* 2005), also in the National Park, Coiba Island Panama (Behrens & Hermosillo 2005).

116. *Tenellia luciae* Valdés, Medrano & Bhave 2016

Diagnosis: animal up to 12 mm in length; body grayish or whitish with blue spot on head; numerous cerata covering almost entire dorsum; rhinophores whitish with light-yellow band followed by subapical blue band, yellow apices; oral tentacles yellow at base, orange at distal end.

Remarks: possibly related to the complex of the European *T. caerulea* (see Korshunova *et al.* 2019)

Distribution: Atlantic species recorded from Florida to Brazil (Thompson & Brown 1984; Valdés *et al.* 2006). In Panama it has been reported in the Bocas del Toro (Goodheart *et al.* 2016; Valdés *et al.* 2016b).

117. ***Tenellia*** **sp. 1**

Diagnosis: animal up to 4 mm in length; body pale translucent-brown with yellowish white dots; cerata with yellow, dark turquoise, yellow, light turquoise rings, pale-yellow tips.

Remarks: probably it is an undescribed species; recently, Korshunova *et al.* (2019) carried out a morphological and molecular analysis of the European species attributed to *Trinchesia caerulea* and verified it is a complex of cryptic species with very little morphological variation but with notable genetic distances, describing three new species. *Trinchesia* sp. appears to fit within this complex of species.

Distribution: Pacific species found in the Eastern Pacific of Costa Rica and the Coiba Island National Park, Panama (Hermosillo, 2004; Camacho-García *et al.* 2005), both as *Cuthona* sp. 1.

Family Eubranchidae Odhner 1934

Genus ***Eubranchus*** Forbes 1838

118*.* ***Eubranchus conicla*** (Er. Marcus 1958)

Diagnosis: animal up to 4 mm in length; body semitransparent, greyish, with white spots all over, often dark brown or green spots on tail, sides of body white cerata with rings of tubercles.

Biology: the animals found in Panama were living on *Sargassum* C. Agardh 1820.

Distribution: Atlantic species recorded from Florida to Brazil and some Caribbean islands (Goodheart *et al.* 2016).

119. ***Eubranchus cucullus*** Behrens 1985

Diagnosis: animal up to 10 mm in length; body whitish with some small light brown spots on dorsal margins; opaque white line among bases of cerata; cerata globose, same color as body.

Biology: it is found on plumularid hydrozoan colonies.

Distribution: Pacific species reported at the Eastern Pacific from the Gulf of California to Coiba Island National Park, Panama (Hermosillo 2004; Behrens & Hermosillo 2005).

120. ***Eubranchus*** **sp. 1**

Diagnosis: animal size unknown; body yellow; cerata also yellow; rhinophores with central red ring.

Remarks: species only known from a photograph.

Distribution: probably an undescribed species only reported from the Coiba Island National Park, Pacific coast of Panama (Hermosillo 2004).

121. *Eubranchus* sp. 2

Diagnosis: animal up to 15 mm in length; body translucent with faint reddish or brownish tint, silver spot on head; cerata with rings of tubercles, dark brown digestive gland; viscera cream.

Distribution: it is probably an undescribed species. Reported from the Eastern Pacific of the Gulf of California, Panama and the Galapagos Islands (Camacho-García *et al.* 2005).

Family Unidentiidae Millen & Hermosillo 2012

Genus ***Unidentia*** Millen & Hermosillo 2012

122. *Unidentia angelvaldesi* Millen & Hermosillo 2012

Diagnosis: animal up to 20 mm in length; body reddish or semi-transparent, almost colorless; three longitudinal purple lines, one mid-dorsal, two runing along sides of dorsum between groups of cerata; cerata of each group emerge from same basal stalk; basal half of oral tentacles purple.

Distribution: Pacific species recorded in the Eastern Pacific from Isla Isabel, Nayarit, Mexico to Cohiba Island, Panama (Millen & Hermosillo 2012).

Superfamily Aeolidioidea Gray 1827

Family Aeolidiidae Gray 1827

Genus ***Spurilla*** Bergh 1864

123. *Spurilla braziliana* MacFarland 1909 Figure 9d

Diagnosis: animal up to 75 mm in length; body pale cream, orange, or reddish, with white spots all over; numerous cerata arranged in up to 9 groups on each side of body, with 5 to > 20 cerata in each group; cerata curved towards center of body; rhinophores with up to 14 lamellae, whitish apices.

Remarks: until recently, the Mediterranean species *Spurilla neapolitana* (Delle Chiaje 1841) was considered to have a circumtropical range and was cited in places as distant as the Caribbean, the Hawaiian Islands, Japan, Peru and Australia (Valdés *et al.* 2005; Kay 1979; Hamatani 2000; Uribe & Pacheco 2012; Willan 2006, respectively). Carmona *et al.* (2014a) studied the anatomy and molecular data from numerous specimens attributed to *S. neapolitana* collected in different localities and concluded that this is a complex of species. According to Carmona *et al.* (2014a), the species of *Spurilla* present in the Americas is *S. braziliana* MacFarland 1909, which was considered a geographic variation of *S. neapolitana* and with which it has a COI genetic distance of 14.1%.

Distribution: this species has been found in the tropical Eastern Pacific Ocean and Western Atlantic (Carmona *et al.* 2014a). Reported in Panama from the Coiba Island National Park (Hermosillo 2004) as *Spurilla neapolitana*.

Genus ***Berghia*** Trinchese 1877

124. *Berghia creutzbergi* Er. Marcus & Ev. Marcus 1970 Figure 9e

Diagnosis: animal up to 30 mm in length; body translucent gray or brown with numerous opaque white spots covering most of dorsum, cerata, with different coverage among specimens; cerata brown with white spots, curved towards center of body; oral tentacles long; rhinophores brown with large tubercle.

Biology: when the animal is in motion, it moves the cerata from one side of the body to the other (Valdés *et al.* 2006).

Remarks: Carmona *et al.* (2014b) compared the morphology of the species *Millereolidia ritmica* Ortea Caballer & Espinosa 2004 found on the Caribbean coast of Costa Rica and considered it synonymous with *B. creutzbergi*.

Distribution: Atlantic species reported in the tropical Western Atlantic from Florida, to Brazil (Valdés *et al.* 2006), including the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

125. *Berghia rissodominguezi* Muniain & Ortea 1999 Figure 9f

Diagnosis: animal up to 52 mm in length; body whitish; cerata brown giving body darker appearance; base of each group of cerata with orange band, also on side of head in front of each rhinophore; cerata with greenish-brown digestive gland branches, white or yellowish apices; oral tentacles, rhinophores light brown with white tips; rhinophores tuberculated.

Biology: lives in the intertidal zone feeding on anemones, can autotomize the cerata when disturbed (Goodheart *et al.* 2016).

Distribution: Atlantic species reported in the Western Atlantic from Florida, to Argentina, also found in the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

Genus ***Baeolidia*** Bergh 1888

126. *Baeolidia moebii* Bergh 1888

Diagnosis: animal up to 40 mm in length; body greenish brown, greyish, or reddish, whitish spots on dorsum; cerata flattened, same color as body, each often with subapical yellow band; usually whitish ring on head in front of rhinophores; rhinophores papillated.

Biology: feeds on cnidarians (Behrens & Hermosillo 2005)

Remarks: This species was originally described from Mauritius, Indian Ocean, as *Baeolidia moebii* by Bergh (1888). Eliot (1903) independently described the same species as *Berghia major* from Zanzibar, Indian Ocean, which was subsequently transferred to the genus *Spurilla* and cited from the Eastern Pacific. Carmona *et al.* (2014c) clarified the taxonomic status of this species and concluded that the correct name is *Baeolidia moebii*.

Distribution: recorded in numerous locations in the Indian and Pacific oceans. In the Eastern Pacific it has been cited from the Gulf of California to Panama, in most cases as *B. major*. It has recently been reported in Turkey and Cyprus in the Mediterranean Sea, possibly as the result of Lessepsian migration through the Suez Canal (Turk & Furlan 2011; Paz-Sedano *et al.* 2019). In Panama it has been recorded in the Coiba Island National Park (Hermosillo 2004; Behrens & Hermosillo 2005) as *B. major*.

Genus ***Limenandra*** Haefelfinger & Stamm 1958

127. *Limenandra nodosa* Haefelfinger & Stamm 1958.

Diagnosis: animal up to 25 mm in length; body white with opaque olive-green spots scattered over notum; dorsum with several white, yellow circles from head to tail, with shades of red, white in center, absent in some specimens; dull green rhinophores with numerous small white spots; oral tentacles longer than rhinophores with same coloration as body; cerata flattened dorsoventrally.

Remarks: the type species of the genus, *L. nodosa* is considered amphiatlantic, with numerous citations of it in the Mediterranean and on both coasts of the Atlantic (Haefelfinger & Stamm 1958; Er. Marcus & Ev. Marcus 1970; Ortea *et al.* 2001; Cervera *et al.* 2004; Valdés *et al.* 2006; Carmona *et al.* 2014d; Ballesteros *et al.* 2021a). It was also considered until recently as a circumtropical distribution, with some records in the Pacific (Gosliner 1980; Camacho-García *et al.* 2005). Carmona *et al.* (2014d) have carried out a complete morphological and molecular study of the species of the genus *Limenandra*, reinstating the genus as valid (the two species known so far had been included within the genus *Baeolidia*), also describing three new species for the Indo-Pacific. Carmona *et al.* (2014d) indicate that some citations attributed to *L. nodosa* in the Pacific correspond rather to one of these new species, *L. confusa*.

Distribution: amphiatlantic, Mediterranean (Haefelfinger & Stamm 1958), Atlantic coast of France and Madeira Island, Portugal (Carmona *et al.* 2014d), Canary Island, España (Cervera *et al.* 2004), Bahamas (Redfern, 2001), Caribbean (Valdés *et al.* 2006), Atlantic coast Costa Rica (Carmona *et al.* 2014d) and Curacao (Er. Marcus & Ev. Marcus 1970).

128. *Limenandra confusa* Carmona, Pola, Gosliner & Cervera 2014

Diagnosis: animal up to 11 mm in length; body very narrow, elongated, opaque olive-green with small white or cream spots; circular spots on dorsum composed of concentric circles yellow, red, white from outside to inside; up to 11 groups of cerata; cerata flattened, with small tubercles of different sizes; rhinophores with elongated papillae on posterior side.

Remarks: if it is not for the seminal receptacle and salivary glands, the morphology of *L. confusa* and *L. nodosa* cannot be differentiated, but to control this, more experimental work is required (Carmona *et al.* 2014d).

Distribution: Pacific species. Philippines as Midway Islands, eastern Pacific (Carmona *et al.* 2014d), Hawaii (Kay 1979; Gosliner 1980; Pittman & Fiene 2012), Mexico (Gosliner *et al.* 2008), Gulf of California (Bertsch 1972) and Costa Rica (Camacho-García *et al.* 2005); we think the record of *L. nodosa* of

Hermosillo & Camacho-García (2006) from Bahia Damas at the Coiba Is., Panama could correspond to *L. confusa*.

Genus ***Anteaeolidiella*** M.C. Miller 2001

129. *Anteaeolidiella chromosoma* (Cockerell & Eliot 1905) Figure 9g

Diagnosis: animal up to 24 mm in length; body generally orange, sometimes white, with whitish spots all over; cerata, oral tentacles long, same color as body; cerata cylindrical with rounded apices, white cnidosacs; rhinophores lamellate, with white apices.

Remarks: originally described in the genus *Spurilla*, later transferred to the genus *Aeolidiella*, and more recently to genus *Anteaeolidiella* (Carmona *et al.* 2014e).

Distribution: Pacific species known from California to Panama (Er. Marcus 1961; Camacho-García *et al.* 2005) and in Japan (Nakano 2004). In Panama it has been recorded in the Coiba Island National Park (Hermosillo 2004).

130. *Anteaeolidiella lurana* (Ev. Marcus & Er. Marcus 1967) Figure 9h

Diagnosis: animal up to 10 mm in length; body whitish with two zigzagging orange lines on dorsum; two orange lines in front of rhinophores; cerata semitransparent with smooth orange digestive gland branches, white cnidosacs; rhinophores lamellate, orange basally; oral tentacles relatively short, semitransparent.

Remarks: this species has been erroneously cited from other Caribbean localities as *Aeolidiella indica* or *Aeolidiella stephaniae* (see Carmona *et al.* 2014e).

Distribution: amphiatlantic, widespread species found in the Caribbean, Eastern Australia and also in the Eastern and Western Mediterranean (Carmona *et al.* 2014e). In Panama it has been collected in the Caribbean of the Bocas del Toro Archipelago (Goodheart *et al.* 2016).

131. *Anteaeolidiella ireneae* Carmona, Bhave, Salunkhe, Pola, Gosliner & Cervera 2014

Diagnosis: animal up to 24 mm in length; translucent white body, some scattered orange on the notum and head varying from dull to bright orange; rhinophores short, thick at the base and smooth, also bright or matte orange but with a white apex; oral tentacles longer than rhinophores, robust, translucent orange with white tips; Cerata vary in size.

Remarks: originally described in the genus *Spurilla*, later transferred to the genus *Aeolidiella*, and more recently to genus *Anteaeolidiella* (Carmona *et al.* 2014e).

Distribution: Clipperton Island, Eastern Pacific Ocean; Canal de Afuera, Panama; San Marte Bay and Socorro Island, Mexico (Carmona *et al.* 2014e), Pacific coast, Costa Rica as *Aeolidiella indica* (Camacho-García *et al.* 2005).

Genus ***Bulbaeolidia*** Carmona, Pola, Gosliner & Cervera 2013

132. *Bulbaeolidia alba* (Risbec 1928) Figure 10a

Diagnosis: animal up to 15 mm in length; body white with reddish lines surrounding bases of rhinophores; cerata white, numerous, curved towards center of body; rhinophores yellowish with two swellings.

Biology: uncommon, it feeds on small white anemones.

Remarks: the recently created genus *Bulbaeolidia* Carmona, Pola, Gosliner & Cervera 2013 includes two species that were previously included in the genus *Aeolidiella*: *B. alba* and *Bulbaeolidia japonica* (Eliot 1913).

Distribution: Pacific species reported in the Eastern Pacific from Mexico to Panama (Behrens & Hermosillo 2005; Camacho-García *et al.* 2005; both as *Aeolidiella alba*). In Panama it has been recorded in the Coiba Island National Park (Hermosillo 2004) as *Aeolidiella alba*.

Family Facelinidae Bergh 1889

Genus ***Favorinus*** Gray 1850

133. *Favorinus elenalexiae* García & Troncoso 2001 Figure 10b

Diagnosis: animal up to 15 mm in length; body translucent white, with dull white spots on dorsal side of head; up to 7 groups of cerata on each side of dorsum, first two groups with cerata arranged in horseshoe shape, others in oblique lines; cerata with irregular white spots on surface forming ring near apex, pink digestive gland branches; rhinophores dark brown, with three raised cup-shaped rings.

Biology: like other species of the same genus it feeds on the egg masses of other sea slugs (Behrens & Hermosillo 2005).

Remarks: the type locality of this species is Coibita Island, Panama.

Distribution: Pacific species reported in the Eastern Pacific from Baja California, Mexico to the Coiba Island National Park, Panama (Hermosillo 2004; Behrens & Hermosillo 2005) and the Galapagos Islands (Camacho-García *et al.* 2005). In Panama it has been found between 3–19 m deep, on Coiba Island and other islands on the Pacific coast (Ladrones, Montuosa, Jicarita, Contreras, Secas) (García & Troncoso 2001).

Genus ***Phidiana*** Gray 1850

134. *Phidiana lynceus* Bergh 1867 Figure 10c

Diagnosis: animal up to 45 mm in length; body translucent gray or light pink, with mid-dorsal white line dividing into two on head, continuing along dorsal part of oral tentacles, line absent in some animals; numerous elongate, narrow cerata, same color as body, with whitish or yellowish apices; rhinophores with yellowish lamellae.

Biology: found under the rocks, known to feed on hydrozoans (McDonald & Nybakken 1997).

Remarks: Valdés *et al.* (2006) suggested that *Phidiana adiuncta* Ortea, Caballer & Moro 2004 described from the Caribbean of Costa Rica could be synonymous with *P. lynceus* since the color variation of the head and rhinophores would fall within the intraspecific variability.

Distribution: Atlantic species with an amphiatlantic distribution. Reported in the Western Atlantic including many localities from Florida to Brazil, while in the Eastern Atlantic it is known from Ghana and the Canary Islands (García-García *et al.* 2008; García & Bertsch 2009). In Panama it has been recorded from the Bocas del Toro Archipelago (Goodheart *et al.* 2016).

135. *Phidiana lascrucensis* Bertsch & Ferreira 1974 Figure 10d

Diagnosis: animal up to 30 mm in length; body translucent orange, with faint opaque white lines; cerata short with grayish or brown digestive gland branches, white apices; rhinophores bulbous, perfoliate.

Biology: common, feeds on hydroids of the genus *Eudendrium* Ehrenberg 1834 (Camacho-García *et al.* 2005).

Remarks: Eastern Pacific *P. lascrucensis*. Camacho-García *et al.* (2005) suggested that *P. lascrucensis* is synonymous with *P. mariadelmarae*. A molecular study of species of this genus and closely related taxa would allow to definitively clarify the systematics of this group.

Distribution: Pacific species, it has been reported in the Eastern Pacific from Baja California, Mexico to Panama, specifically in the Coiba National Park (Hermosillo 2004; Behrens & Hermosillo 2005; Camacho-García *et al.* 2005).

Genus ***Noumeaella*** Risbec 1937

136. *Noumeaella isa* Ev. Marcus & Er. Marcus 1970

Diagnosis: animal up to 18 mm in length; body long, narrow, semitransparent, white, with opaque white net on dorsum, rhinophores, oral tentacles; cerata curved inward, grouped in 8–9 well-spaced clusters; rhinophores with papillae on posterior side, pointed foot corners, approximately as long as oral tentacles.

Distribution: Indopacific species with widely distribution, reported in Panama in Granito de Oro Island of Coiba Island National Park (Hermosillo & Camacho-García 2006).

137. *Noumeaella rubrofasciata* Gosliner 1991 Figure 10e

Diagnosis: animal up to 10 mm in length; body white, slightly translucent, red-orange spot on head; rhinophores bulbous with papillae; 3–4 well separated groups of cerata, few cerata in each group, cerata white at base, reddish distally due to digestive gland branches; oral tentacles well-developed, elongated.

Distribution: Pacific species reported in the Eastern Pacific from Santa Catalina Island, California to the Coiba Island National Park, Panama (Hermosillo 2004; Behrens & Hermosillo 2005; Camacho-García *et al.* 2005).

Genus ***Herviella*** Baba 1949

138. ***Herviella*** **sp. 1**

Diagnosis: animal up to 23 mm in length; body very narrow, elongate, brown with dorsal zig-zaging silver line branching into cerata groups, divided into two anterior to pericardium; up to 23 groups of cerata on each side of dorsum in 23 mm long specimen, each group with 1–2 short cerata, somewhat curved upward, with brown digestive gland branches, white apices; rhinophores smooth.

Biology: found on floating buoys with abundant hydroids (Hermosillo & Valdés 2007).

Remarks: it is probably an undescribed species. Hermosillo & Valdés (2007) provisionally placed it in the genus *Herviella* according to characteristics such as body shape, smooth rhinophores, uniseriate radula and few cerata in each group.

Distribution: Pacific species that is known from Coiba Island, Panama (Camacho-García *et al.* 2005; Hermosillo & Valdés 2007).

Genus ***Nanuca*** Marcus 1957

139. ***Nanuca sebastiani*** Er. Marcus 1957 Figure 10f

Diagnosis: animal up to 12 mm in length; body narrow, semitransparent, with various tones matching substrate, greenish, bluish or whitish, with orange spots surrounded by opaque white patches, white spots scattered throughout body; four groups of cerata on each side of dorsum, first three well separated from each other, fourth very close to third; cerata with brown digestive gland branches, cream longitudinal lines on surface; oral tentacles long, rhinophores with 3–4 broad lamellae.

Remarks: Furfaro & Mariottini (2021a) regarded *Nanuca* as a junior synonym of *Dondice*, but *Nanuca* has priority (Furfaro & Mariottini 2021b). However, in Furfaro & Mariottini's (2021a) phylogenetic tree, *N. sebastiani* is sister to other species of *Dondice*, thus it is equally valid and more taxonomically stable to maintain *Nanuca* as a distinct genus.

Biology: Goodheart *et al.* (2016) found this species on *Sargassum* C. Agardh 1820 with sertularid hydrozoans.

Distribution: Atlantic species reported in the Western Atlantic from Florida to Brazil including and the Caribbean islands (Valdés *et al.* 2006; Caballer *et al.* 2015). In Panama it has been found at the Bocas del Toro Archipelago (Goodheart *et al.* 2016).

Genus ***Dondice*** Marcus 1958

140. ***Dondice occidentalis*** Engel 1925 Figure 10g

Diagnosis: animal up to 50 mm in length; budy translucent grayish with white or bluish line in center of dorsum from rhinophores to tail; yellow or orange line in center of head, on sides of body; oral tentacles long; rhinophores long, annulate; 4–5 groups of cerata well separated from each other; cerata narrow, with white, bluish stripes along their length, subapical yellow band.

Biology: possibly a complex of cryptic species (press publication)

Remarks: D. parguerensis is very similar in coloration to *D. occidentalis* and these two species have been considered synonyms by some authors. This led González *et al.* (2013) to carry out a molecular study of specimens of both species;

Distribution: Atlantic species recorded from North Carolina to Brazil and the Caribbean islands (Er. Marcus & Ev. Marcus 1970; Valdés *et al.* 2006; Miloslavich *et al.* 2010; Caballer Gutiérrez *et al.* 2015) including the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

141. ***Dondice parguerensis*** Brandon & Cutress 1985 Figure 10h

Diagnosis: animal up to 48 mm in length; body translucent brown with white midline, from front of head to end of body; 6–7 groups of cerata, cerata with brown digestive gland branches, white apices; oral tentacles, rhinophores opaque with white distal half.

Biology: this species lives and feeds exclusively on the tentacles of up-side-down jellies of the genus *Cassiopeia* Péron & Lesueur, 1809 (Valdés *et al.* 2006)

Remarks: D. parguerensis is very similar in coloration to *D. occidentalis* and these two species have been considered synonyms by some authors. This led González *et al.* (2013) to carry out a molecular study of specimens of both species; this study was not conclusive to delimit the two species since there were no differences in the H3 gene but there were some differences in the 16S gene that would indicate that they are different species. Although there are no significant differences in the radular structure of both species, some differences have been found in the coloration, number of groups of cerata and the larval development, planktotrophic in *D. parguerensis* and lecithotrophic in *D. occidentalis*. All this led González *et al.* (2013) to consider these species as a possible example of incipient sympatric speciation promoted mainly by food specialization.

Distribution: Atlantic species reported from the Western Atlantic of Puerto Rico, Venezuela, Guadeloupe (Collin *et al.* 2005; Valdés *et al.* 2006; Mariño *et al.* 2011; Ortea *et al.* 2013; Caballer *et al.* 2015) and the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

Genus ***Palisa*** Edmunds 1964

142. ***Palisa papillata*** Edmunds 1964 Figure 11a

Diagnosis: animal up to 15 mm in length; body translucent gray with numerous opaque white patches on dorsal sides; cerata arranged in 8–9 groups, with pale blue digestive gland branches, black or dark brown spots on base; oral tentacles long, rhinophores tuberculate.

Biology: found among algae.

Distribution: Atlantic species only reported from the Western Atlantic in Florida, Jamaica, and the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

Genus ***Bajaeolis*** Gosliner & Behrens 1986

143*. Bajaeolis bertschi* Gosliner & Behrens 1986 Figure 11b

Diagnosis: animal up to 40 mm in length; body long, narrow, white to reddish with numerous small opaque white spots on head; cerata narrow, cylindrical, with red digestive gland branches; oral tentacles short, rhinophores perfoliated.

Biology: it feeds on athecate hydrozoans of the genus *Eudendrium* Ehrenberg 1834 (Camacho-García *et al.*, 2005).

Distribution: Pacific species that has been reported from the Eastern Pacific in Los Angeles Bay, Baja California, Mexico, Mexico and in Coiba Island National Park, Panama (Hermosillo 2004; Camacho-García *et al.* 2005).

Genus ***Hermosita*** Gosliner & Behrens 1986

144. *Hermosita hakunamatata* (Ortea, Caballer & Espinosa, 2003)

Diagnosis: animal up to 12 mm in length; body dark brown, almost black with small bluish-white spots on margins of dorsum, base of cerata; 5–6 groups of cerata, each cerata with dark colored digestive gland, reddish, white subapical band; oral tentacles with bluish-white dots at base, rest purple with reddish subapical band, white apices; rhinophores with about 12 lamellae, similar in color to oral tentacles.

Biology: uncommon species, living on dark purple hydrozoans of the genus *Solanderia* Duchassaing & Michelin 1846 (Camacho-García *et al.* 2005), where the specimens of *H. hakunamatata* are very cryptic.

R*emarks*: species described based on a single specimen initially included in the genus *Phestilla*. Millen & Hermosillo (2012), studying a collection of specimens collected in Banderas Bay, Mexico and based on anatomical characteristics such as the position of the anus and radular structure, concluded that it should be included in the genus *Hermosita*.

Distribution: Pacific species reported from the Eastern Pacific of Costa Rica and the Coiba Island National Park, Panama (Ortea *et al.* 2003; Hermosillo 2004; Behrens & Hermosillo 2005; Camacho-García *et al.* 2005).

Subcohort Euopisthobranchia

Order Umbraculida Odhner 1939

Superfamily Umbraculoidea Dall 1889 (1827)

Family Tylodinidae Gray 1847

Genus ***Tylodina*** Rafinesque 1814

145. *Tylodina fungina* Gabb 1865 Figure 11c

Diagnosis: animal up to 38 mm in length; body uniform golden yellow; rhinophores well-developed, same color as body; gill on right side of body, with bipinnate or tripinnate leaves; shell patelliform, external, not covering entire animal, periostracum laminar, with some discontinuous purple radial streaks.

Remarks: it feeds on the sponge *Aiolochoia thiona* (Laubenfels 1930) (order Verongida) from which it can possibly extract the yellow body pigment (Camacho-García *et al.* 2005)

Distribution: Pacific species reported from Central California to Costa Rica and the Galapagos Islands (Keen 1971; Collin, 2008; Göbbeler & Klussmann-Kolb 2011). In Panama it has been recorded at the Coiba Island National Park (Hermosillo 2004).

Family Umbraculidae Dall 1889 (1827)

Genus ***Umbraculum*** Schumacher 1817

146. *Umbraculum ovale* (Carpenter 1856)

Diagnosis: animal up to 120 mm in length; body orange or reddish-brown, with numerous tubercles; anterior region of body with deep incision; rhinophores short, dorsal; shell limpet-like, external, not covering entire body; membrane-like periostracum covered with encrusting organisms.

Remarks: often considered a synonym of the circumtropical species *Umbraculum umbraculum* ([Lightfoot] 1786) (see Behrens & Hermosillo 2005) which according to Rudman (1999b) is the only species of the genus. A molecular analysis of Mediterranean, Atlantic and Indo-Pacific *Umbraculum* specimens is needed to clarify the taxonomic status of these species.

Distribution: Eastern Pacific species reported from the Gulf of California to Panama (Keen 1971) where has been found in the Gulf of Montijo and the Coiba Island National Park (Vega & González 2002; Hermosillo 2004; both as *U. umbraculum*).

Order Cephalaspidea Fischer 1883

Superfamily Bulloidea Gray 1827

Family Bullidae Gray 1827

Genus ***Bulla*** Linnaeus 1758

147. *Bulla solida* Gmelin 1791

Diagnosis: shell up to 65 mm in length; shell pink-brown with uneven brown spots, shell thick, globose; aperture, columella white; live animal unknown.

Biology: very little is known about this species, Díaz & Puyama (1994) indicate that it is common in Santa Marta (Caribbean of Colombia).

Remarks: this species has sometimes been confused with *B. mabillei*.

Distribution: Atlantic species, reported in numerous Caribbean locations from Florida to Venezuela, and Panama, where (Malaquias & Reid 2008) indicate the presence of the species without providing a specific locality.

148. ***Bulla occidentalis*** A. Adams 1850 Figure 11d

Diagnosis: animal up to 50 mm in length; numerous opaque whites, brown, grey patches on head, parapodia; shell thick, variable in shape according to geographical location of specimens, from pyriform to globular or oval-quadrangular; shell color variable from whitish to yellowish or brown, with brown spots, sometimes with 3 dark spiral bands; shell with 5–6 whorls turns; white, columella wide.

Biology: this species lives in tidal pools and on shallow sandy bottoms with seagrass down to 3 m depth; Valdés *et al.* (2006) indicated that it has nocturnal activity and buries in the sand during the day, while Malaquias & Reid (2008) pointed out that in Florida the animals are active during the day.

Remarks: this species has often been mistakenly identified as *Bulla striata* Bruguière 1792; see comments of this species. Bruguière's (1792) original description of *B. striata* was based on specimens from the Mediterranean and both sides of the Atlantic Ocean. Since the middle of the last century, there has been controversy regarding the taxonomy of *B. striata* and similar species in the "*B. striata* group", with some authors considering the existence of a single species with an amphiatlantic distribution (Er. Marcus, 1957; Vermeij & Rosenberg 1993) while others admitted the existence of different species on each side of the Atlantic (Poppe & Gotto 1991; Macedo *et al.* 1999; Redfern 2001). Malaquias & Reid (2008) concluded that there are two species of the so-called *B. striata* group in the Atlantic, *B. occidentalis* on the western side and *B. striata* on the eastern side.

Distribution: Western Atlantic species reported in numerous locations from Florida, the Gulf of Mexico, and the Caribbean, to Brazil and Uruguay (Malaquias & Reid 2008). In Panama has been recorded in Almirante, Bocas del Toro Province (Olsson & McGinty 1958; Malaquias & Reid 2008).

149. ***Bulla punctulata*** A. Adams in Sowerby 1850 Figure 11e

Diagnosis: animal up to 70 mm in length; body pale brown or pink, with small white or yellowish spots; shell solid, reddish brown or cream, with brown blotches, black, white irregular dots, sometimes two darker bands columella white.

Distribution: Pacific species common in the Eastern Pacific from Baja California, Mexico to northern Peru (Camacho-García *et al.* 2005; Malaquias & Reid 2008), also in Panama (Strong & Hertlein 1939; Malaquias & Reid 2008) in the Gulf of Montijo (Vega & González 2002) and the Coiba National Park (Hermosillo 2004).

Family Retusidae Thiele 1925

Genus ***Retusa*** T. Brown 1827

150. *Retusa sulcata* (d'Orbigny 1841) Figure 11f

Diagnosis: shell up to 3 mm in length; shell white, elongated, with anterior part somewhat wider, apex umbilicate, aperture as long as shell, outer lip rounded anteriorly, posteriorly; growth lines intertwined with spiral striae; live animal unknown.

Distribution: Atlantic species reported in the Western Atlantic from North Carolina to Venezuela and the Caribbean Islands (Princz 1982; Valdés *et al.* 2006; Rosenberg *et al.* 2009; Miloslavich *et al.* 2010; Yidi & Sarmiento 2011; Caballer *et al.* 2015). In Panama has been recorded in the Bocas del Toro Province (Olsson & McGinty 1958).

Family Rhizoridae Dell 1952

Genus ***Volvulella*** Newton 1891

151. *Volvulella cylindrica* (Carpenter 1864) Figure 11g

Diagnosis: shell up to 6 mm in length; shell white; thin elongated, apical end narrows into well-pronounced spike in some specimens; weak spiral striae present, with thinternal lines in central part.

Distribution: Pacific species common in the Eastern Pacific from Vancouver Island, Canada to Panama and the Galapagos Islands (Keen 1971; Valdés & Camacho-García 2004; Behrens & Hermosillo 2005; Camacho-García *et al.* 2005;), very abundant in Costa Rica (Valdés & Camacho-García 2004). In Panama has been recorded in the Gulf of Montijo, Veraguas Province (Vega & González 2002).

152. *Volvulella persimilis* (Mörch 1875)

Diagnosis: shell up to 6 mm in length; shell translucent white, surface shiny; shell fragile, apical region pointed, sculpture with very fine spiral lines; outer lip thin; umbilicus small.

Distribution: Atlantic species with a wide geographic range from Canada to Argentina and Uruguay (Ev. Marcus & Er. Marcus 1960; Princz 1982; Ríos 1985; Massemin *et al.* 2009; Ríos 2009; Rosenberg 2009; Yidi & Sarmiento 2011). In Panama it has been cited by Miloslavich *et al.* (2010) and the Bocas del Toro and Colon provinces in Panama (Olsson & McGinty 1958).

153. *Volvulella minuta* (Bush 1885)

Diagnosis: shell up to 4.6 mm in length; shell uniformly white, shiny; shell oblong, thin, pointed posteriorly, rounded anteriorly; sculpture absent except 3–4 spiral lines on anterior, posterior areas; aperture very narrow posteriorly, wider, oval anteriorly.

Remarks: sometimes identified as *Volvulella acuta* (d'Orbigny 1841).

Distribution: Atlantic species reported in the Western Atlantic from Florida and the Gulf of Mexico to Venezuela and the Caribbean Islands (Princz 1982; Valdés *et al.* 2006; Rosenberg *et al.* 2009; Caballer *et al.* 2015). In Panama has been recorded by Miloslavich *et al.* (2010).

154. *Volvulella catharia* Dall 1919 Figure 11h

Diagnosis: shell up to 4 mm in length; shell uniformly brownish; shell oval, fragile, anterior, posterior ends rounded; some spiral lines on anterior part; columella thickened, umbilicus absent; live animal unknown.

Remarks: the type locality of this species is the Bay of Panama.

Distribution: Pacific species common in the Eastern Pacific from Southern California to Panama (Valdés 2019).

155. *Volvulella panamica* Dall 1919 Figure 12a

Diagnosis: shell up to 5.5 mm in length; shell whitish, fragile, cylindrical, posterior end slightly pointed, anterior rounded; aperture small anteriorly; columellar margin thick; umbilicus absent; numerous spiral grooves crossed by growth lines; live animal unknown.

Remarks: the type locality of this species is the Bay of Panama.

Distribution: Pacific species common in the Eastern Pacific from Southern California to Panama (Keen 1970; Valdés & Camacho-García 2004; Camacho-García *et al.* 2005).

Family Tornatinidae P. Fischer 1883

Genus ***Acteocina*** Gray 1847

156. *Acteocina candei* (d'Orbigny 1841) Figure 12b

Diagnosis: shell up to 5.3 mm in length; shell translucent white, oval, elongate; spire long, conical; animal can measure up to 3.28 mm with translucent white body that shows the viscera; brown-orange viscera with irregular white spots visible through shell; head with two larges posterior lobes; with 3 well-defined, ribbed spiral whorls; body whorl occupies more than 2/3 of shell; columellar margin thickened; umbilicus absent.

Biology: in Bocas del Toro is found on soft bottoms near the roots of mangroves (Goodheart *et al.* 2016).

Distribution: Atlantic species with a widespread range in the Western Atlantic from North Carolina to Argentina and the Caribbean Islands (Valdés *et al.* 2006; Massemin *et al.* 2009; Rosenberg *et al.* 2009;

Caballer *et al.* 2015). In Panama it has been recorded in the Colon Province (Olsson & McGinty 1958) and the Bocas del Toro Archipelago (Miloslavich *et al.* 2010, Goodheart *et al.* 2016).

157. ***Acteocina recta*** (d'Orbigny 1841)

Diagnosis: shell up to 3.3 mm in length; shell cylindrical with almost straight sides, 3-4 spiral whorls, body whorl occupies almost entire shell length; aperture very narrow over much of its length; sculpture with numerous spiral striations; protoconch rounded, protruding; live animal unknown.

Distribution: Atlantic species reported from the Western Atlantic of Cuba, Dominican Republic, Belize, Panama, Colombia, and the Lesser Antilles (Miloslavich *et al.* 2010).

158. ***Acteocina infrequens*** (C.B. Adams 1852) Figure 12c

Diagnosis: shell up to 9 mm in length; shell elongated whitish, slightly curved edges with 3 spiral whorls; body whorl occupies almost entire shell length; sculpture with numerous spiral lines crossed by growth lines; aperture widens from posterior to anterior area; columella with elongated callus; protoconch rounded, protruding at apex, live animal unknown.

Remarks: the type locality of this species is in Panama.

Distribution: Pacific species distributed in the Eastern Pacific from Southern California to the Galapagos (Valdés, 2019), very common in Costa Rica (Valdés & Camacho-García 2004). In Panama it has been recorded from Taboga Island, Panama Bay, Bahía Honda and the Gulf of Montijo (Strong & Hertlein 1939; Vega & González 2002).

159. ***Acteocina inculta*** (Gould 1855)

Diagnosis: shell up to 4.5 mm in length; whitish, semitransparent, solid, elongate, headshield wider anteriorly; animal white; with a posterior division on cephalic shield, two short parapodia covering shell anteriolaterally; shell with 3 posteriorly carinate whorls; body whorl occupies almost entire length of shell; columella with callus; umbilicus absent.

Remarks: this species is very common on the Pacific coast of Costa Rica where Valdés & Camacho-García (2004) have studied numerous empty shells collected in sediments between 2 and 64 m depth.

Distribution: Pacific species reported in the Eastern Pacific from Southern California to Panama (Behrens & Hermosillo 2005).

160. ***Acteocina inconspicua*** Olsson & McGinty 1958

Diagnosis: shell up to 2 mm in length; shell white or translucent, cylindrical, with smooth surface, slightly curved lateral margins; aperture wide along entire length; parietal callus thin; live animal unknown.

Remarks: the type locality of this species is Bocas del Toro, Panama.

Distribution: Atlantic species reported from the Western Atlantic of Costa Rica, the Gulf of Mexico, the Caribbean Sea, and the Bocas del Toro Archipelago, Panama (Olsson & McGinty 1958; Felder *et al.* 2009; Miloslavich *et al.* 2010).

Superfamily Cylichnoidea H. Adams & A. Adams 1854

Family Cylichnidae H. Adams & A. Adams 1854

Genus ***Cylichna*** Lovén, 1846

161. ***Cylichna atahualpa*** (Dall 1908) Figure 12d

Diagnosis: shell up to 12 mm in length; shell whitish, narrow, elongated, with single visible whorl; aperture as long as shell; sculpture with fine spiral striations; columella thickened, whitish; periostracum yellowish; only shells, preserved specimens known.

Remarks: Valdés & Camacho-García (2004) describe the radula of this species based on specimens collected in the Pacific of Costa Rica.

Distribution: Eastern Pacific species, relatively frequent off Costa Rica (Valdés & Camacho-García 2004). The type locality is the Gulf of Panama, where it was collected at a depth of 590 m; there are no more citations of its presence on the Pacific coast of Panama.

162. ***Cylichna inca*** (Dall 1908)

Diagnosis: shell up to 6 mm in length; shell white, with yellowish periostracum; surface smooth except for growth lines; aperture as long as shell almost quadrangular.

Remarks: only empty shells of this species are known. The taxonomic placement of this species is uncertain, it is maintained here in the genus *Cylichna* until additional material becomes available for study.

Distribution: Eastern Pacific species only known from its original description based on specimens collected in deep waters (2,300 m) off the Gulf of Panama (Keen 1971).

163. ***Cylichna pizarro*** (Dall 1908)

Diagnosis: shell up to 9.75 mm in length; shell slightly oval, white, with thin periostracum, revealing spiral micro-punctate striae, grouped in pairs, more apparent near apex; apex slightly sloping; aperture wide, rounded anteriorly, with small callus on internal lip.

Remarks: only empty shells of this species are known. The taxonomic placement of this species is uncertain, it is maintained here in the genus *Cylichna* until additional material becomes available for study.

Distribution: Eastern Pacific species only known from its original description based on specimens collected in deep waters (2,300 m) off the Gulf of Panama (Keen 1971).

Genus ***Cylichnella*** Gabb 1873

164. *Cylichnella bidentata* (d'Orbigny 1841) Figure 12e

Diagnosis: shell up to 4 mm in length; body yellow; shell whitish, oval, rounded apically; spiral striae on anterior, posterior area; columella thickened.

Distribution: Atlantic species recorded in the Western Atlantic from New Jersey to Brazil, including the entire Caribbean (Valdés *et al.* 2006; Felder *et al.* 2009; Massemin *et al.* 2009; Rosenberg *et al.* 2009; Miloslavich *et al.* 2010; Yidi & Sarmiento 2011; Caballer *et al.* 2015). In Panama has been cited in the Colon Province (Olsson & McGinty 1958).

165. *Cylichnella tabogaensis* (Strong & Hertlein 1939) Figure 12f

Diagnosis: shell up to 4 mm in length; shell pale brown, small, fragile, with oval outline; apex umbilicated, spiral striations on anterior end; aperture as long as shell with posterior forming rounded; columella thickened with two denticles.

Remarks: only empty shells and preserved animals are known. The specific name derives from the Island of Taboga, Panama, the type locality.

Distribution: Eastern Pacific species common in Costa Rica (Valdés & Camacho-García 2004; Camacho-García *et al.* 2005). In Panama it has been cited in the Gulf of Montijo, Veraguas Province (Vega & González 2002).

Superfamily Haminoeoidea Pilsbry 1895

Family Haminoeidae Pilsbry 1895

Genus ***Haminoea*** Turton & Kingston [in Carrington] 1830

166. *Haminoea elegans* (Gray 1825) Figure 12g

Diagnosis: animal up to 35 mm in length; body yellowish with opaque white, black spots; parapodia completely cover anterior part of shell; shell fragile, with spiral striae, growth lines.

Distribution: this is an amphiatlantic species recorded in the Western Atlantic from Florida to Brazil (Collin *et al.* 2005; Valdés *et al.* 2006; García-García *et al.* 2008; Rosenberg *et al.* 2009; Miloslavich *et al.* 2010; Caballer *et al.* 2015; Ortigosa *et al.* 2015), including the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

167. *Haminoea virescens* (Sowerby II 1833)

Diagnosis: animal up to 11 mm in length; body greenish with yellow, white spots on headshield, parapodia.

Distribution: Eastern Pacific species recorded from southern Alaska to Panama (Keen 1971; Behrens & Hermosillo 2005).

168. *Haminoea antillarum* (d'Orbigny 1841) Figure 12h

Diagnosis: animal up to 40 mm in length; body dark due to black pigment on entire surface, also with white, orange spots; shell semitransparent, lacks spiral striae.

Biology: lives on red algae in the intertidal zone (Goodheart *et al.* 2016).

Distribution: Atlantic species recorded in the Western Atlantic from Florida to Brazil, including the Caribbean islands (Collin *et al.* 2005; Valdés *et al.* 2006; García-García *et al.* 2008; Rosenberg *et al.* 2009; Caballer *et al.* 2015; Ortigosa *et al.* 2015) and Panama (Miloslavich *et al.* 2010) including the Bocas del Toro Archipelago (Goodheart *et al.* 2016).

169. *Haminoea succinea* (Conrad 1846) Figure 13a

Diagnosis: animal up to 20 mm in length; body elongated, greenish-brown with numerous black, white spots; parapodia very short, covering almost no surface of shell; foot very short; shell semi-transparent, revealing viscera with blackish spots.

Biology: lives on soft bottoms in protected areas between the roots of mangroves (Goodheart *et al.* 2016).

Distribution: Atlantic species recorded in the Gulf of Mexico and throughout the Caribbean (Miloslavich *et al.* 2010), including the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

170. *Haminoea vesicula* (Gould 1855)

Diagnosis: animal up to 50 mm in length; body uniform brown, with numerous white spots; eyes surrounded by small gray areas; parapodia short; shell globose, fragile, semitransparent, slightly yellowish; columellar edge thickened;

R*emarks*: Valdés (2019) indicated that this species lives on muddy bottoms inside bays where it can feed on green algae of the genera *Ulva* Linnaeus 1753 and *Polysiphonia* Greville 1823.

Distribution: Pacific species reported from Alaska to Panama (Baker & Hanna 1927; Valdés 2019). In Panama it has been recorded by Strong & Hertlein (1939) and Vega & González (2002).

Genus ***Atys*** Montfort 1810

171. *Atys guildingi* Sowerby II 1869

Diagnosis: animal up to 30 mm in length; body translucent white, with dense brown spots on head, parapodia; parapodia cover anterior part of shell; shell translucent, showing brown digestive gland; shell with spiral striae on anterior, posterior ends.

Distribution: Atlantic species distributed by the Gulf of Mexico, the Caribbean and Brazil, including Panama (Valdés *et al.* 2006; Miloslavich *et al.* 2010; Yidi & Sarmiento 2011; Caballer *et al.* 2015).

172. *Atys riiseanus* Mörch 1875

Diagnosis: animal up to 20 mm in length; body whitish with black spots on head, parapodia; viscera brown visible through shell; shell semi-transparent with spiral striations on anterior, posterior ends.

Distribution: Atlantic species reported in the Eastern Atlantic from Florida to Brazil and the Caribbean islands (Valdés *et al.* 2006; Caballer *et al.* 2015; Ortigosa *et al.* 2015), also Panama (Miloslavich *et al.* 2010).

173. *Atys sandersoni* Dall 1881 Figure 13b

Diagnosis: animal up to 15 mm in length; body translucent white with dark on headshield, parapodia; parapodia short, covering anterior part of shell; shell with no apparent spiral striations.

Distribution: Atlantic species reported in the Western Atlantic from North Carolina to Brazil, including Puerto Rico and Cuba (Valdés *et al.* 2006; Felder & Camp 2009; Miloslavich *et al.* 2010). In Panama it has been recorded in Bocas del Toro (Olsson & McGinty 1958).

174. *Atis defuncta* F. Baker & Hanna 1927

Diagnosis: shell up to 2.6 mm in length; shell translucent-whitish, oval-cylindrical, somewhat narrow at top, thin, smooth, except for growth lines, spiral striae on anterior, posterior ends; apex obliquely truncated, only moderately raised apical lip, thin outer lip, starting at edge of apical umbilicus.

Remarks: Valdés & Camacho-García (2004) include this species in the genus *Atys* based on the morphology of the shell, the gizzard plates, and the radula.

Distribution: Eastern Pacific species very common in Costa Rica (Valdés & Camacho-García 2004). Also reported in the Gulf of California (Baker & Hanna 1927) and Panama (Strong & Hertlein 1939; Vega & González 2002).

Genus ***Weinkauffia*** Weinkauff 1873

175. *Weinkauffia caribaeus* (d'Orbigny 1841)

Diagnosis: animal up to 20 mm in length; body translucent white with opaque white patches, some black, brown dots; shell elongate with spiral striae on anterior, posterior ends.

Remarks: cited in some articles such as *Atys caribaeus* (d'Orbigny 1841).

Distribution: Atlantic species reported in the Western Atlantic from North Carolina to Brazil and the Caribbean islands (Valdés *et al.* 2006; Miloslavich *et al.* 2010; Yidi & Sarmiento 2011; Caballer *et al.* 2015). In Panama it has been collected in the Bocas del Toro Archipelago (Olsson & McGinty 1958; Goodheart *et al.* 2016).

176. *Weinkauffia macandrewii* E.A. Smith 1872

Diagnosis: animal up to 10 mm in length; body whitish, with opaque white spots; parapodia only cover anterior part of shell; viscera visible through shell, with brown spots; shell oval, semitransparent with dark spiral striae all over.

Biology: common in Bocas del Toro, under mangrove roots (Collin *et al.* 2005)

Distribution: amphiatlantic species recorded in the Western Atlantic from the Gulf of Mexico to Brazil, including Panama (Collin *et al.* 2005). In the Eastern Atlantic it has been recorded in the Cabo Verde Archipelago (Valdés 2005) and in the Mediterranean (Toll & Ballesteros 2017).

Genus ***Lamprohaminoea*** Habe 1952

177. *Lamprohaminoea ovalis* (Pease 1868) Figure 13c

Diagnosis: animal up to 12 mm in length; body greenish with numerous oranges, purple spots; head with V-shaped whitish spot; shell white or greenish, thin, fragile, rather oblique-oval, smooth, somewhat rough due to growth lines; opening narrow posteriorly.

Distribution: common, widespread species in the Indo-Pacific, reported in Panama in the Coiba Island National Park (Keen 1971; Hermosillo 2004; Behrens & Hermosillo 2005).

Genus ***Aliculastrum*** Pilsbry 1896

178. *Aliculastrum exaratum* (Carpenter 1857)

Diagnosis: shell up to 6 mm in length; shell whitish, oval, smooth; some visible growth lines; full-length aperture, narrow posteriorly, wider anteriorly, with oblique columellar margin; posterior end aperture protruding beyond apex, forming round wing.

Remarks: only empty shells of this species are known; Strong & Hertlein (1939) cited this species from Panama as *Cylichna stephensae* Strong & Hertlein 1939 and *Cylichna veleronis* Strong & Hertlein 1939 which Valdés (2019) synonymized with *A. exaratum.*

Distribution: Eastern Pacific species known only from the southern California, Mexico, and Panama, where it has been collected in Honda Bay (Strong & Hertlein 1939; Valdés 2019).

Superfamily Philinoidea Gray 1850 (1815)

Family Philinidae Gray 1850 (1815)

Genus ***Philine*** Ascanius 1772

179. *Philine sagra* (d'Orbigny 1841)

Diagnosis: animal up to 6 mm in length; body uniform black; shell white, oblong, translucent, slightly coiled, depressed, anteriorly subtruncated; non-umbilicated spire; thin crenulate lip.

Distribution: Atlantic species reported in the Western Atlantic from Bermuda to Brazil (Turgeon *et al.* 1998; Massemin *et al.* 2009; Yidi & Sarmiento 2011; Caballer *et al.* 2015) also in Panama (Miloslavich *et al.* 2010), including the Bocas del Toro Province (Olsson & McGinty 1958).

180. ***Philine alboides*** Price, Gosliner & Valdés 2011

Diagnosis: animal up to 44 mm in preserved length; color of live animals unknown, preserved body uniformly white; shell lacks sculpture.

Distribution: Atlantic species reported from Florida and the Gulf of Mexico to Brazil, including the Gulf of the Mosquitos, Panama (Price *et al.* 2011).

Family Aglajidae Pilsbry 1895 (1847)

Genus ***Philinopsis*** Pease 1860

181. ***Philinopsis speciosa*** Pease 1860

Diagnosis: animal up to 40 mm in length; body whitish, cream to dark brown, with white, orange spots; headshield well developed, anteriorly rounded; margin of parapodia with alternating black, white spots.

Biology: nocturnal species, feeds on *Bulla punctulata* A. Adams 1850 (Camacho-García *et al.* 2005).

Remarks: in some publications it is reported as *Philinopsis cyanea* (E. von Martens 1879) (Ballesteros *et al.* 2021b).

Distribution: Pacific species distributed in the Eastern Pacific, from Mexico to the Galapagos (Pease 1860; Camacho-García *et al.* 2005) also in the Coiba Island National Park in Panama (Hermosillo 2004; Behrens & Hermosillo 2005).

Genus ***Navanax*** Pilsbry 1895

182. ***Navanax gemmatus*** (Mörch 1863) Figure 13d

Diagnosis: animal up to 50 mm in length; body opaque yellow to dark brown, dorsum with longitudinal white, brown lines, some whitish areas; body elongated with well-formed headshield; edge of parapodia with blue markings; small internal shell; posterior end of body with two tails.

Biology: feeds on other sea slugs (Valdés *et al.* 2006).

Remarks: this species has been reported from the Western Atlantic as *Navanax aenignaticus* (Bergh 1893) but Ornelas-Gatdula *et al.* (2012) using molecular analyses shown that *N. aenignaticus* is a complex of three cryptic species, and that records of this species in the Western Atlantic must refered to *N. gemmatus*. The records of *N. aenigmaticus* from the Eastern Atlantic, according to the same authors, correspond to another species, *N. nyanyanus* (Edmunds 1968).

Distribution: Atlantic species reported in the Western Atlantic from Florida to Brazil and the Caribbean islands (Valdés *et al.* 2006; Ornelas-Gatdula *et al.* 2012; Camacho-García *et al.* 2014; Caballer *et al.* 2015) including the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

183. *Navanax aenigmaticus* (Bergh 1893) Figure 13e

Diagnosis: animal up to 75 mm in length; body dark brown with cream white, turquoise blue spots; calcified internal shell.

Biology: common on rocky bottoms from the intertidal zone to 18 m depth (Camacho-García *et al.* 2005), feeds on other sea slugs.

Remarks: Ornelas-Gatdula *et al.* (2012) confirmed that this species is only found in Eastern Pacific, while the closely related Western Atlantic populations belong to *Navanax gemmatus* (see the previous species).

Distribution: reported from Baja California, Mexico to Chile (Gosliner 1980; Skoglund 2002; Camacho-García *et al.* 2005) also in the Coiba Island National Park, Panama (Hermosillo 2004; Behrens & Hermosillo 2005).

184. *Navanax inermis* (Cooper 1862)

Diagnosis: shell up to 20 mm in length; body black or dark brown with numerous small white, blue, yellow punctuations; live animal is up to 225 mm, dark brown to gray; elongated, narrow; rear end of body with two elongated triangular tails; posterior end with two narrow tails.

Remarks: Valdés (2019) suggested that *Navanax polyalphos* (Gosliner & Williams 1972) is a synonym.

Biology: according to Camacho-García *et al.* (2005) it feeds on other cephalaspideans such as *Haminoea virescens* (G.B. Sowerby II 1833) and *Bulla punctulata* A. Adams 1850.

Distribution: Pacific species reported in the eastern tropical Pacific including Panama (Valdés & Camacho-García 2004; Camacho-García *et al.* 2005).

Genus ***Camachoaglaja*** Zamora-Silva & Malaquias 2017

185. *Camachoaglaja berolina* (Er. Marcus & Ev. Marcus 1970)

Diagnosis: animal up to 12 mm in length; body dark, almost black, with transverse orange band on anterior end of head, along parapodia edges; some specimens with white or orange spots on dorsum; left posterior tail more developed than right one.

Biology: common in shallow sandy areas, crawling among algae during the day (Valdés *et al.* 2006).

Remarks: previously known as *Chelidonura berolina*, the review of the Aglajidae by Zamora-Silva & Malaquias (2018) places this species in the new genus *Camachoaglaja*.

Distribution: Atlantic species reported throughout the Caribbean (Valdés *et al.* 2006; Ornelas-Gatdula *et al.* 2011; Malaquias 2014) including the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

Family Philinorbidae Oskars, Bouchet & Malaquias 2015

Genus ***Philinorbis*** Habe 1950

186. *Philinorbis albus* (Mattox 1958)

Diagnosis: animal up to 60 mm in length; body milky white with tan-yellow to pale pink spots; body oblong, fleshy, extending posteriorly over mantle; shell white, brittle, smooth with faint spiral grooves.

Distribution: Pacific species reported from California, United States to the Galapagos Islands, Ecuador (Price *et al*, 2011; Valdés *et al.*, 2016a).

Family Scaphandridae GO Sars 1878

Genus ***Scaphander*** Montfort 1810

187. *Scaphander punctostriatus* (Mighels & C.B. Adams 1842)

Diagnosis: shell up to 41.2 mm in length; body white; headshield broad; shell ovoid, yellowish.

Distribution: amphiatlantic species, reported in the Western Atlantic from Greenland to the Gulf of Mexico, the Caribbean and the Sargasso Sea (Ev. Marcus 1974; Felder *et al.* 2009), also in Panama (Miloslavich *et al.* 2010). In the eastern Atlantic it has been reported from Norway to the Mediterranean (Lemche 1929; Bouchet 1975; Cervera *et al.* 2004; Eilertsen & Malaquias 2013; Toll & Ballesteros 2017).

188. *Scaphander watsoni* Dall 1881

Diagnosis: shell up to 39.5 mm in length; body white; shell piriform, brown; spiral striae of interconnected rounded punctuations; internal edge of aperture white.

Distribution: Atlantic species reported in the Western Atlantic from the Gulf of Mexico to Brazil and the Caribbean islands (Eilertsen & Malaquias 2013), also Panama (Miloslavich *et al.* 2010).

189. *Scaphander interruptus* Dall 1889

Diagnosis: shell up to 22 mm in length; shell oval with brown spiral lines formed by oval punctuations, with alternate wider, narrower rows; aperture as long as shell, with posterior end slightly protruding from apex.

Remarks: the live animal is unknown.

Distribution: Pacific species reported from California to Chile (Keen 1971; Valdés 2019), also in the Gulf of Montijo, Veraguas Province, Panama (Vega & González 2002).

190. *Scaphander darius* Ev. Marcus & Er. Marcus 1967

Diagnosis: shell up to 23 mm in length; white body; shell thin, solid, piriform, white to light brown; with very conspicuous spiral markings.

Distribution: Atlantic species reported from the Western Atlantic in the Gulf of Mexico, Colombia, and Brazil (Ev. Marcus & Er. Marcus 1967; Eilertsen & Malaquias 2013), also in Panama (Miloslavich *et al.* 2010).

Family Alacuppidae, Oskars, Bouchet & Malaquias 2015

Genus ***Roxania*** Leach 1847

191. *Roxania morgana* (Dall 1908)

Diagnosis: shell up to 5.5 mm in length; shell with oval outline, rather straight; sculpture with growth lines.

Remarks: *Roxania* was included in the family Scaphandridae until the revision of the phylogeny of the Cehalaspidea by Oskars *et al.* (2015).

Distribution: only known from the Gulf of Panama, where it was collected during the expedition of the oceanographic ship Albatross at 2,322 m depth.

Order Aplysiida Pelseneer 1906

Superfamily Aplysioidea Lamarck 1809

Family Aplysiidae Lamarck 1809

Genus ***Aplysia*** Linnaeus 1767

192. *Aplysia dactylomela* Rang 1828 Figure 13f

Diagnosis: animal up to 200 mm in length; body light brown with characteristic black rings of different sizes; branched black lines; parapodia well-developed, with lobed edges; shell thin, membranous plate.

Biology: feeds on a wide variety of algae of the genera *Corallina* [sensu Ellis 1755], *Acanthophora* J.V. Lamouroux 1813*, Laurencia* J.V. Lamouroux 1813*, Ulva* Linnaeus 1753 and *Cladophora* Kützing 1843, among others (Ballesteros *et al.* 2021c). When disturbed, it can produce a defensive reddish ink.

Remarks: based on molecular data Alexander & Valdés (2013) determined that Indo-Pacific populations of *A. dactylomela* should be referred to as *Aplysia argus* (Rüppell & Leuckart 1830).

Distribution: amphiatlantic species reported in the Western Atlantic from Florida to Brazil (Ev. Marcus & Er. Marcus 1960; Camacho-García *et al.* 2005; Valdés 2006; Ríos 2009; Yidi & Sarmiento 2011; Caballer *et al.* 2015; Ortigosa *et al.* 2015), also in Panama (Miloslavich *et al.* 2010) in the Gulf of Montijo, Veraguas Province (Vega & González 2002) and Bocas del Toro (Goodheart *et al.* 2016; present paper). In the Eastern Atlantic has been recorded in Cabo Verde, Senegal, the Canary Islands and the Mediterranean Sea (Ballesteros *et al.* 2021c).

193. *Aplysia californica* J.G. Cooper 1863

Diagnosis: animal up to 750 mm in length; body dark reddish-brown; with white or black spots, reticulate lines well-developed, present parapodia; shell can measure 75 mm, translucent brown, convex; sparsely calcified white.

Biology: commonly active during the day, feeds on red algae such as *Gracilaria* Greville 1830, *Laurencia* J.V. Lamouroux 1813, *Plocamium* J.V. Lamouroux 1813*, Palmaria* Stackhouse 1802 and green algae such as *Ulva* Linnaeus 1753 (Behrens & Hermosillo 2005; Valdés 2019). Found from the intertidal zone to at least 20 m depth.

Distribution: Pacific species reported in the Eastern Pacific from California to Mexico and Panama, including the Coiba Island National Park (Hermosillo & Camacho-García 2006) and El Salao, Aguadulce (Tejera *et al.* 2016).

194. ***Aplysia hooveri*** Golestani, Crocetta, Padula, Camacho-García, Langeneck, Poursanidis, Pola, Yokeş, Cervera, Jung, Gosliner, Araya, Hooker, Schrödl & Valdés 2019

Diagnosis: up to 19 mm in preserved length; color variable from reddish to brown or black, without white spots; edge of parapodia sometimes black, bluish or white; tips of oral tentacles, rhinophores with same color as edge of parapodia; eyes in center of a rounded light spot; shell white semitransparent, small, fragile.

Remarks: Golestani *et al.* (2019) used molecular and morphological data to unravel the taxonomy of the *Aplysia parvula* Mörch 1863 species complex, previously considered a single circumtropical species. In their work they conclude that all the citations in the Eastern Pacific attributed to this species correspond to a new species *A. hooveri.*

Distribution: Pacific species reported in the eastern from Baja California, Mexico to Peru including the Coiba Island National Park, Panama (Hermosillo 2004; Uribe *et al.* 2013; Golestani *et al.* 2019). All records prior to 2019 were cited as *A. parvula.*

Genus ***Dolabella*** Lamarck 1801

195. ***Dolabella auricularia*** (Lightfoot 1786) Figure 13g

Diagnosis: animal up to 500 mm in length; body brown, with patches of green; numerous conical extensions throughout body; head, rhinophores short; calcified ear-shaped internal shell, posterior edge of body forming an oblique disk-shaped shield.

Remarks: Due to its herbivorous diet, this species is used in aquariums to limit the growth of algae. In the Philippines, the egg mass of this species is considered a delicacy called lukot.

Distribution: Indo-Pacific species reported from Panama in the Gulf of Montijo (Vega & González 2002) and also in the Coiba Island National Park (Hermosillo 2004).

Genus ***Bursatella*** Blainville 1817

196. *Bursatella leachii* Blainville 1817 Figure 13h

Diagnosis: animal up to 200 mm in length, but commonly 80-100 mm; body dark green to dark brown or gray, with spots of lighter color, rounded blue "ocelli"; numerous elongated papillae throughout body, ending in pointy tips, generally forked; adults lacking internal shell.

Biology: found in calm, shallow waters, frequently in harbors and bays; feeds on algae and diatoms (Goodheart *et al.* 2016).

Distribution: considered as a pantropical species (Bazzicalupo *et al.* 2018); in the Western Atlantic it has been reported from North Carolina to Brazil and the Caribbean Islands (Collin *et al.* 2005; Valdés *et al.* 2006; Miloslavich *et al.* 2010; Caballer *et al.* 2015) including the Bocas del Toro Archipelago in Panama (Goodheart *et al.* 2016). Since 1940 it has been present in the Mediterranean, where it has colonized all its basins (Bazzicalupo *et al.* 2018; Ballesteros *et al.* 2021d).

Genus ***Dolabrifera*** Gray 1847

197. *Dolabrifera ascifera* (Rang 1828) Figure 14a

Diagnosis: animal up to 90 mm in length; body color variable, brown, green, with spots of different colors; body narrow anteriorly, widening towards posterior end; dorsum with numerous tubercles of different sizes, small ones surrounding large ones, parapodia fused in most posterior part; enrolled oral tentacles, rhinophores; shell internal, oval, flat, narrow nucleus, with growth lines.

Remarks: Valdés *et al.* (2017) carried out a taxonomic review of the species of the genus *Dolabrifera* based on morphological and molecular data.

Distribution: Western Atlantic species, reported from Florida to Brazil; in Panama has been collected in Bocas del Toro (Valdés *et al* 2017).

198. *Dolabrifera nicaraguana* Pilsbry 1896 Figure 14b

Diagnosis: animal up to 50 mm in length; body color variable, greenish, brown, reddish; body wider posteriorly, narrow anteriorly; rhinophores, oral tentacles enrolled; dorsum with numerous tubercles of different sizes, each with papilla at apex; parapodia fused almost completely except in small region; edge of parapodia tuberculated; shell variable, from narrow to very narrow, elongated.

Distribution: Eastern Pacific species reported from Baja California, Mexico to Peru; in Panama it has been recorded from Bahía Honda (Valdés *et al* 2017).

199. *Dolabrifera virens* Verrill 1901

Diagnosis: animal up to 80 mm in length; body greenish to reddish, brown, whitish, with irregular spots of different colors; body oval, flat, somewhat wider posteriorly; dorsal tubercles variable in size; parapodia as in other species; shell flat, elongated, narrow in posterior zone, visible growth lines.

Distribution: Atlantic species reported in the Western Atlantic including Florida, Jamaica, Bermuda, Curaçao and Bocas del Toro, Panama; also recorded from St. Helena in the South Atlantic (Valdés *et al.* 2017).

Genus ***Stylocheilus*** Gould 1852

200. *Stylocheilus longicaudus* (Quoy & Gaimard 1825)

Diagnosis: animal up to 80 mm in length; body pale green or yellow, rounded red spots surrounded by blue circles, sometimes white, blue spots; short white papillae all over body; body elongate; narrow tail reaching half length of animal; shell absent.

Biology: This species lives on floating algae such as *Sargassum* C. Agardh 1820 and *Fucus* Linnaeus 1753, on which it feeds. The foot secretes an adhesive mucus that serves to hold tightly to the algal surface.

Remarks: Controversies over the taxonomic status of *Stylocheilus longicaudus*, *S. citrinus* and *S. striatus* have been widely discussed by Rudman (1999c).

Distribution: considered a circumtropical species, it has been reported in the Pacific Ocean (Spencer *et al.*, 2002) including the Red Sea (Vine 1986), as well as in the Atlantic Ocean (Mozambique, MacNae & Kalk, 1958), including the Caribbean Sea (Cuba, Miloslavich *et al.* 2010), also in Panama, Gulf of Montijo, Veraguas Province (Vega & González 2002).

201. *Stylocheilus striatus* (Quoy & Gaimard 1832) Figure 14c

Diagnosis: animal up to 65 mm in length; translucent specimens with cream, green, brown, gray tones, with dark longitudinal lines, often interrupted, white or blue ocelli surrounded by dark brown area; whole body, including oral, rhinophores tentacles, with conical papillae of different sizes, largest branched; shell absent.

Biology: very common in shallow waters, can produce ink when it is disturbed; feeds on cyanobacteria.

Remarks: this species has often been misidentified with the pelagic species *Stylocheilus longicaudus* (Quoy and Gaimard 1825), which is associated with floating algae according to Valdés *et al.* (2006).

Distribution: Bazzicaluppo *et al.* (2020) suggest that it is a species complex of at least three different species. In the Western Atlantic reported from Florida to Brazil, including the Caribbean Islands (Valdés *et al.* 2006; Camacho-García *et al.* 2014; Caballer *et al.* 2015) and in Panama recorded from the Archipelago of Bocas del Toro (Goodheart *et al.* 2016).

202. *Stylocheilus rickettsi* (MacFarland 1966)

Diagnosis: animal up to 25 mm in preserved length; body elongated; color gray or cream with dark longitudinal lines; numerous tubercles throughout body, including oral tentacles, rhinophores; parapodia reduced, almost completely fused, leaving only two foramina; shell absent.

Distribution: Eastern Pacific species known from Baja California, Mexico, Costa Rica and Panama, where has been collected in Islas Secas and Canal de Afuera (Bazzicaluppo *et al.* 2020).

Genus ***Phyllaplysia*** P. Fischer 1872

203. *Phyllaplysia engeli* Er. Marcus 1955

Diagnosis: animal up to 15 mm in length; body variable in color, green, pink, brown, with white spots; body flattened, oval contour; some animals with irregular longitudinal white lines, small conical papillae; rhinophores short, thick; shell absent.

Biology: in meadows of the marine phanerogams *Thalassia testudinum* K.D. Koenig 1805 and *Halodule sp.* on which it is extremely cryptic living on the leaves.

Distribution: Atlantic species reported in the western Atlantic from Florida, the Gulf of Mexico, the entire Caribbean Sea and Brazil (Valdés *et al.* 2006; Felder *et al.* 2009; Caballer *et al.* 2015) including the Bocas del Toro Archipelago in Panama (Goodheart *et al.* 2016).

204. *Phyllaplysia padinae* Williams & Gosliner 1973

Diagnosis: animal up to 45 mm in length; body olive green or greenish brown with white irregular patches all over; whitish papillae, some simple, others with several pointed apices; rhinophores short; shell absent.

Biology: intertidal and subtidal, feeds on epiphytic diatoms on the alga *Padina durvillaei* Bory de Saint-Vincent 1827 or on the marine sea grass *Zostera* L. (Rudman 2002).

Distribution: Eastern Pacific species reported from the Gulf of California to Costa Rica and Panama, where has been collected in the Coiba Island National Park (Hermosillo, 2004; Behrens & Hermosillo, 2005).

Subcohort Panpulmonata

Order Sacoglossa Ihering 1876

Superfamily Oxynooidea Stoliczka 1868 (1847)

Family Oxynoidae Stoliczka 1868 (1847)

Genus ***Oxynoe*** Rafinesque 1814

205. *Oxynoe antillarum* Mörch 1863 Figure 14d

Diagnosis: animal up to 20 mm in length; body light green or yellow, with white or cream spots on rhinophores, tail; cream line at edge of parapodia, continuing along dorsal crest of tail; conical white tubercles all over body; blue spots on rhinophores, margin of parapodia.

Biology: found in bays and other areas with calm waters, feeds on species of algae of the genus *Caulerpa* Lamouroux, 1809 (Krug *et al.* 2018).

Distribution: Atlantic species reported in the Western Atlantic from Florida to Brazil and the Caribbean islands (Collin *et al.* 2005; Valdés *et al.* 2006; Camacho-García *et al.* 2014; Caballer *et al.* 2015. In Panama it has been reported in the Bocas del Toro Archipelago (Olsson & McGinty, 1958; Miloslavich *et al.*, 2010; Goodheart *et al.* 2016; Krug *et al.* 2018); also collected by us in Adriana Cay, Bocas del Toro Province (present paper).

206. *Oxynoe aliciae* Krug, Berriman & Valdés 2018

Diagnosis: animal up to 13 mm in length; body pale green, with cream-colored lines on edge of parapodia, sometimes on lateral side of parapodia; white or cream conical papillae throughout body; posterior end of rhinophores sometimes pigmented with cream; blue ocelli on parapodia, rhinophores.

Biology: associated with the algae *Caulerpa scalpelliformes* Agardh 1817 (Krug *et al.* 2018).

Remarks: it is very similar morphologically to *O. antillarum*, but Krug *et al.* (2018) demonstrated that they are genetically distinct. Specimens from the Eastern Pacific cited in the literature as *O. panamensis* Pilsbry & Olsson, 1943 (considered a *nomen dubium* by Krug *et al.* 2018) almost certainly belong to *O. aliciae* (Rudman 2009).

Distribution: known only on the Pacific coast of Mexico and Panama (Canal de Afuera and Contreras Island) (Krug *et al.* 2018).

Genus ***Lobiger*** Krohn 1847

207. *Lobiger souverbii* P. Fischer 1857

Diagnosis: animal up to 30 mm in length; body green with yellow-brown papillae on tail, parapodia, mantle; dark green longitudinal line; edge of parapodia extend dorsally, forming 4 characteristic elongated lobes.

Biology: found in association with the green alga *Caulerpa racemosa* (Forsskål) J. Agardh 1873; when disturbed it can release a defensive milky secretion and sometimes autotomizes the parapodial extensions; it can swim using the parapodial lobes.

Distribution: Atlantic species reported in the Western Atlantic from Florida to Brazil and the Caribbean islands (Felder *et al.* 2009; Miloslavich *et al.* 2010); also, in the Bocas del Toro Archipelago, Panama, (Goodheart *et al.* 2016). The reports of this Atlantic species in the Eastern Pacific: Banderas Bay, Mexico

(Rudman 2003) and Coiba Island, Panama (Hermosillo 2004) probably represent a different species described below.

208. *Lobiger cf. souverbii* P. Fischer 1857

Diagnosis: animal up to 30 mm in length; body green with yellow-brown papillae on tail, parapodia, mantle; dark green longitudinal line; edge of parapodia extend dorsally, forming 4 characteristic elongated lobes.

Biology: found in association with the green alga *Caulerpa racemose* Agardh 1873; when disturbed it can release a defensive milky secretion and sometimes autotomizes the parapodial extensions; it can swim using the parapodial lobes.

Distribution: Eastern Pacific: Banderas Bay, Mexico (Rudman 2003) and Coiba Island, Panama (Hermosillo 2004) need confirmation.

Family Juliidae E.A. Smith 1885

Subfamily Juliinae E.A. Smith 1885

Genus ***Julia*** Gould 1862

209. *Julia thecaphora* (Carpenter 1857)

Diagnosis: shell up to 4 mm in length; shell with two heart-shaped valves, green to greenish yellow, ~20 radial lines, characteristic pointed apical protrusion; live animal unknown.

Remarks: only shells collected from subtidal bottoms or on the beach are known.

Distribution: Reported in the Eastern Pacific from Baja California, Mexico to Peru (Camacho-García *et al.* 2005) also in the Coiba Island National Park, Panama (Hermosillo 2004).

Subfamily Bertheliniinae Keen & A.G. Smith 1961

Genus ***Berthelinia*** Crosse 1875

210. *Berthelinia caribbea* Edmunds 1963

Diagnosis: animal up to 4 mm in length; body greenish with some white spots on head, neck, brown longitudinal lines; shell with two semitransparent valves, mantle spots, lines visible through.

Biology: feeds on *Caulerpa verticillata* J. Agardh 1847 (Valdés *et al.* 2006)

Distribution: Atlantic species reported in the Western Atlantic from Florida to Brazil, including Panama (Valdés *et al.* 2006; Felder *et al.* 2009; Miloslavich *et al.* 2010 Ortigosa *et al.* 2015).

Family Volvatellidae Pilsbry 1895

Genus ***Ascobulla*** Ev. Marcus 1972

211. *Ascobulla ulla* (Er. Marcus & Ev. Marcus 1970)

Diagnosis: animal up to 6 mm in length; body cream or slightly orange; shell external, covering 2/3 of body, fragile, cylindrical, with rounded apex; cephalic shield white, well developed, with two elongated lobes.

Biology: lives on sandy bottoms in association with rhizoids of the alga *Caulerpa racemosa* (Forsskål) J. Agardh 1873. Like other sacoglossans, it can produce a defensive milky secretion when disturbed (Goodheart *et al.* 2016).

Distribution: Atlantic species reported in the Western Atlantic from Florida to Brazil and the Caribbean islands (Valdés *et al.* 2006; Felder *et al.* 2009; Miloslavich *et al.* 2010), including the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

Superfamily Plakobranchoidea Gray 1840
Family Plakobranchidae Gray 1840
Genus ***Elysia*** Risso 1818

212. *Elysia ornata* (Swainson 1840) Figure 14e

Diagnosis: animal up to 50 mm in length; body elongated, olive-green, covered with black, white spots; parapodial edge undulated, with black marginal line, submarginal orange diffuse band; rhinophores short, orange on distal half; viscera visible dorsally as two white areas.

Biology: feeds on *Bryopsis plumosa* Agardh 1823 where the animals are extremely cryptic (Goodheart *et al.* 2016).

Remarks: Krug *et al.* (2016) studied the anatomy and taxonomy of the Western Atlantic species of *Elysia*, providing molecular data to clarify their phylogenetic relationships, including some very similar Indo-Pacific species such as *E. marginata*, from which *Elysia ornata* is separated by a COI genetic distance of only 8%.

Distribution: amphiatlantic species recorded in the Western Atlantic from Florida, the Gulf of Mexico, and the Caribbean to Brazil (Felder *et al.* 2009; Miloslavich *et al.* 2010; Krug *et al.* 2016). In the Eastern Atlantic it has been recorded from the Canary Islands and the Azores (Ortea *et al.* 2001; Malaquias *et al.* 2009; Borges *et al.* 2010). In Panama it has been found in the Bocas del Toro Archipelago (Goodheart *et al.* 2016).

213. *Elysia crispata* Mörch 1863 Figure 14f

Diagnosis: animal up to 50 mm in length; body highly variable in color, green, cream, purple, or blue, with or without cream or white spots on mantle; mantle somewhat lighter or darker than rest of body; parapodia very undulated with cream or white margins in most animals; relatively short rolled rhinophores; well defined pericardium.

Biology: very common throughout the Caribbean where it seems to feed on several species of algae of the genera *Bryopsis* J.V. Lamouroux 1809, *Sabella* Linnaeus 1767 (formerly *Penicillus* [Rondelet 1555]), *Halimeda* J.V. Lamouroux 1812, *Acetabularia* J.V. Lamouroux 1812 and *Derbesia* Solier 1846 (Pierce *et al.* 2003; Curtis *et al.* 2004, 2006; Middlebrooks *et al.* 2014; Krug *et al.* 2016).

Remarks: due to its extreme chromatic variability, this species has an extensive list of synonyms that Krug *et al.* (2016) discussed in detail.

Distribution: reported from the Western Atlantic from Florida to Venezuela, including the Caribbean islands (Er. Marcus 1957; Ev. Marcus & Er. Marcus 1960; Ev. Marcus & Er. Marcus 1962; Er. Marcus & Ev. Marcus 1970; Ev. Marcus & Hughes 1974; Ev. Marcus 1977; Thompson 1977; Gavagnin *et al.* 2000; Collin *et al.* 2005; Valdés *et al.* 2006; Felder *et al.* 2009; Miloslavich *et al.* 2010; Caballer *et al* 2015; Ortigosa *et al.* 2015; Krug *et al.* 2016) and the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016), where is very common (present paper).

214. *Elysia diomedea* (Bergh 1894) Figure 14g

Diagnosis: animal up to 100 mm in length; body green, sometimes dark gray, almost bluish; oval white or bluish spots on dorsum, bluish lines on lateral body walls, foot sole; parapodia very short, extremely undulated with orange upper margin; rhinophores well developed with longitudinal white, black or yellow lines.

Distribution: Pacific species recorded in the Eastern Pacific from the Gulf of California to Panama, where has been cited in the Coiba Island National Park (Hermosillo 2004; Behrens & Hermosillo 2005; Camacho-García *et al.* 2005) and the Gulf of Montijo, Veraguas Province (Vega & González 2002).

215. *Elysia flava* Verrill 1901 Figure 14h

Diagnosis: animal up to 20 mm in length; body yellowish-green with digestive gland dark green dendritic branches; parapodia slightly undulated, upper edge white with papillae of same color, also found on lateral body walls; rhinophores short.

Biology: generally found under stones. Marín & Ros (1988) indicate that the Mediterranean specimens may feed on a *Cladophora* Kützing 1843 species.

Distribution: amphiatlantic species that has been recorded throughout the Western tropical Atlantic (Valdés *et al.* 2006; García & Bertsch 2009; Ortigosa *et al.* 2015; Caballer *et al.* 2015), including the Bocas del Toro Archipelago, Panama (Collin *et al.* 2005; Krug *et al.* 2016). In the eastern Atlantic it has been cited in Madeira, the Canary Islands, and the Mediterranean Sea (Thompson & Jaklin 1988; Cervera *et al.* 2004; Valdés 2005; Koukouras 2010; Ballesteros *et al.* 2021e)

216. *Elysia papillosa* A.E. Verrill 1901 Figure 15a

Diagnosis: animal of up to 30 mm in length; body green, brownish, or white; numerous conical or rounded white papillae throughout body, including rhinophores, head, edge of parapodia; parapodia low, scalloped, with short, irregular lobes.

Biology: it is a very common species throughout the Caribbean. It feeds on the green alga *Penicillus capitatus* Lamarck, 1813, from which it sequesters chloroplasts that maintains active for a short time (Curtis *et al.* 2010).

Distribution: Atlantic species distributed throughout the tropical Western Atlantic (Collin *et al.* 2005; Valdés *et al.* 2006; Felder *et al.* 2009; Miloslavich *et al.* 2010; Caballer *et al.* 2015; Ortigosa *et al.* 2015), including the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016; Krug *et al.* 2016). Eastern Atlantic records of this species are misidentifications (see Krug *et al.* 2016).

217. *Elysia subornata* A.E. Verrill 1901 Figure 15b

Diagnosis: animal up to 50 mm in length; body olive-green with numerous conical white papillae of various sizes; parapodia poorly developed with black fine lines, white papillae on edge; rhinophores rolled, short, also papillate.

Remarks: Krug *et al.* (2016) indicate that the development of this species is completely lecithotrophic; adults feed on at least 8 different species of *Caulerpa* J.V. Lamouroux, 1809 (Krug *et al.* 2016).

Distribution: Atlantic species reported in Western Atlantic from Florida to Brazil including almost all the Caribbean islands and the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016; Krug *et al.* 2016).

218. *Elysia velutinus* Pruvot-Fol 1947

Diagnosis: animal up to 15 mm in length; body green with white spots all over, including rhinophores; white spots often larger on edge of parapodia, base of rhinophores; some animals with small papillae all over body; pericardium well-developed; renopericardial vessels with two pairs of branches (one pair on each side of dorsum), two directed forward, two backward, each with lateral branching.

Biology: It feeds on several species of *Halimeda* J.V. Lamouroux 1812 such as *H. incrassata* (J. Ellis) J.V. Lamouroux 1816, *H. monile* (J. Ellis & Solander) J.V. Lamouroux 1816 and *H. discoidea* (Yamada) Hillis-Colinvaux 1968. Krug *et al.* (2016) have studied the egg mass which consists on a zig-zagging ribbon. A fine yellow cord of extra-embryonic yolk enters each of the ovigerous capsules and is consumed by the veliger larvae.

Remarks: Krug *et al.* (2016) discussed the intricate nomenclatorial history of this species and listed its synonyms.

Distribution: Atlantic species reported in Western Atlantic from Florida to Brazil, including the Caribbean islands (Collin *et al.* 2005; Valdés *et al.* 2006; Felder *et al.* 2009; Miloslavich *et al.* 2010; Malaquias 2014; Caballer *et al.* 2015; Ortigosa *et al.* 2015; Krug *et al.* 2016) and the Bocas del Toro

Archipelago, Panama (Goodheart *et al.* 2016), also collected by us in Adriana Cay, Bocas del Toro Province (present paper).

219. *Elysia canguzua* Er. Marcus 1955 Figure 15c

Diagnosis: animal up to 12 mm in length; body green with numerous small white spots throughout body, often forming dashed line on edge of parapodia; some specimens with tiny orange, bluish punctuations; rhinophores very short, rolled; triangular parapodia, wider anteriorly; anterior end of foot with numerous white spots forming transverse line.

Biology: it has planktotrophic larval development, adults' feeds on the green algae such as *Bryopsis plumosa* (Hudson) C. Agardh 1823 and *Codium* sp. (Er. Marcus 1955; Jensen & Clark 1983).

Distribution: Atlantic species reported in Western Atlantic from Florida to Brazil and the Caribbean islands (Krug, *et al.* 2016) including the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

220. *Elysia marcusi* (Ev. Marcus 1972)

Diagnosis: animal up to 5 mm in length; body flattened, green, with white patches of different sizes, some specimens with bluish spots; rhinophores whitish, small, rolled; body elongated while in motion, rounded when resting; parapodia fused forming middorsal line.

Biology: It feeds on the algae *Halimeda opuntia* (Linnaeus) J.V. Lamouroux 1816 and *H. goreaui* W.R. Taylor 1962 (Krug *et al.* 2016). The egg mass consists of a ribbon forming a flat spiral, with few white and yellow eggs.

Remarks: the shape of the specimens of this species is very similar to those of the genus *Bosellia*, in which *E. marcusi* was originally included. Studies on embryonic development and molecular data have shown that *E. marcusi* is more related to *Elysia* than to *Bosellia* (Krug 2009; Krug *et al.* 2015).

Distribution: Atlantic species reported in the Western Atlantic from Florida, Costa Rica, the Caribbean islands, and the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016; Krug *et al.* 2016).

221. *Elysia cornigera* Nuttall 1989 Figure 15d

Diagnosis: animal up to 8 mm in length; specimens can be whitish or greyish with green tones on back, sides of body due to he ramifications of digestive gland; numerous white papillae, red markings all over body; rolled white parapodia also papilous.

Biology: feeds on *Acetabularia crenulata* J.V. Lamouroux 1816 and retains its photosynthetically active chloroplasts for only up to 11 days. (Krug *et al.* 2011 2013).

Remarks: initially considered synonymous with the Mediterranean species *Elysia timida*, Krug *et al.* (2013) have verified that there is a genetic difference of 11.2% between both species, with which they considered *E. cornigera* as valid.

Distribution: Atlantic species Reported in Western Atlantic from Florida and Mexico to the Caribbean Islands, (Valdés *et al.* 2006; Ortigosa *et al.* 2013) and the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

222. *Elysia zuleicae* Ortea & Espinosa 2002

Diagnosis: animal up to 8 mm in length; body olive-green; parapodia with small, conical, white papillae, those on margin more developed, forming white band of groups of 3–5; edge of parapodia with black line in juveniles; parapodia slightly wavy; rhinophores short, brown, or white.

Biology: feeds on the green alga *Udotea flabellum* (Ortea & Espinosa 2002). The egg mass is a flat spiral ribbon with very small white eggs (around 60 μm in diameter) and with extra-embryonic yolk; larvae can be planktotrophic or lecithotrophic (Krug *et al.* 2016).

Distribution: Atlantic species reported in the Western Atlantic from Florida to the Caribbean islands, including Panama, where has been observed in the Bocas del Toro Archipelago (Goodheart *et al.* 2016; Krug *et al.* 2016).

223. *Elysia chavelavargas* Ortea 2017

Diagnosis: animal up to 20 mm in length; body uniformly green; head with white square patch at base of rhinophores; rhinophores whitish or cream.

Biology: the animals are very cryptic on green algae of the genus *Halimeda* Lamouroux 1812 on which they live (Behrens & Hermosillo 2005).

Distribution: Pacific species reported in the Eastern Pacific, including Banderas Bay and Ixtapa, Mexico (Behrens & Hermosillo 2005), Costa Rica (Camacho-García *et al.* 2005) and Canal de Afuera, Coiba Island National Park, Panama (Hermosillo & Camacho-García 2006).

224. *Elysia* sp. 1

Diagnosis: animal up to 8 mm in length; body olive-green, numerous spots, pink, white, yellow; edge of parapodia strongly crenulated, rolled rhinophores.

Biology: lives on green algae of the genus *Caulerpa* Lamouroux, 1809 (Camacho-García *et al.* 2005).

Remarks: it is probably an undescribed species.

Distribution: Pacific species reported in the Eastern Pacific from Baja California, Mexico to Costa Rica and the Revillagigedo Islands, Mexico (Camacho-García *et al.* 2005), also on Granitos de Oro Island and Uva Island in the Coiba Island National Park, Panama (Hermosillo & Camacho-García 2006).

Family Limapontiidae Gray 1847

Genus ***Ercolania*** Trinchese 1872

225. *Ercolania coerulea* Trinchese 1892

Diagnosis: animal up to 16 mm in length; body translucent white or yellowish, digestive branches green, visible all over body, including rhinophores, cerata; white dots on dorsum, rhinophores, cerata; globose cerata covering almost entire body, with bluish tips.

Biology: in the Caribbean it is found on the green algae *Dictyosphaeria cavernosa* (Forsskål) Børgesen 1932 (Goodheart *et al.* 2016) while in the Mediterranean it feeds on *Vallonia utricularis* (Roth) Agardh 1823.

Remarks: specimens of *E. coerulea* reported from the Indo-Pacific (Tanzania, Hong Kong) lack the blue pigment on the cerata (Rudman 2002) and probably belong to a different, cryptic species.

Distribution: amphiatlantic, originally described from the Mediterranean Sea, where it has been cited in the Adriatic and in the western basin (Cervera *et al.* 2004; Ballesteros *et al.* 2021f), also in the Canary Islands, Madeira, and the Azores, it is now considered an amphiatlantic species since it has been reported from the Western Atlantic from Florida to Brazil (Felder *et al.* 2009) including the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

Genus ***Placida*** Trinchese 1876

226. *Placida kingstoni* T.E. Thompson 1977 Figure 15e

Diagnosis: animal up to 15 mm in length; body semi-translucent, green branches of digestive gland visible throughout body, including rhinophores, inside cerata; numerous white, brown spots all over body; rolled rhinophores; elongate cerata, pulsating rhythmically.

Biology: feeds on the green alga *Bryopsis plumosa* (Hudson) C. Agardh 1823 (Jensen 1981).

Distribution: reported in Western Atlantic from Florida to Costa Rica and the Caribbean islands (Felder *et al.* 2009; Miloslavich *et al.* 2010) including the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

Family Hermaeidae H. Adams & A. Adams 1854

Genus ***Hermaea*** Lovén 1844

227. *Hermaea cruciata* Gould 1870

Diagnosis: animal up to 5 mm in length; body translucent with white spots dispersed throughout body, cerata; viscera visible; cerata globose, tuberculate, with digestive gland branches forming cross pattern distally.

Distribution: Atlantic species reported in the Western Atlantic from Massachusetts to Florida, USA, the Caribbean Islands and Brazil (Valdés *et al.* 2006; Turner *et al.* 2012) including the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016). There are reports of this species from the Canary Islands (Cervera *et al.*, 2004), so it could also be an amphiatlantic species.

Genus ***Polybranchia*** Pease 1860

228. *Polybranchia mexicana* Medrano, Krug, Gosliner, Kumar & Valdés 2018

Diagnosis: animal up to 11 mm in length; body semi-translucent, dark brown, with numerous white spots; rhinophores translucent, olive green; cerata pedunculated, leaf-like, with 1–2 black patches, few small black dots.

Remarks: this species has been cited in the Eastern Pacific and Western Atlantic under the name *Polybranchia viridis* (Deshayes, 1857). However, Medrano *et al.* (2018), using molecular and morphological data concluded that the Eastern Pacific specimens of *Polybranchia* constitute a distinct, undescribed species, with COI genetic distances of 4–6% with the Western Atlantic species. Medrano *et al.* (2018) introduced the name *P. mexicana* for the Eastern Pacific species.

Distribution: reported from the Eastern Pacific, from Baja California, Mexico to the Galapagos Islands, including Panama (Medrano *et al.* 2018).

229. *Polybranchia schmekelae* Medrano, Krug, Gosliner, Kumar & Valdés 2018 Figure 15f

Diagnosis: animal up to 14 mm in length; body with different shades of green, brown spots, white spots depending on specimen; lateral sides of body with papillae; cerata greenish, leaf-shaped, largest with two longer papillae on dorsal area, several small papillae on ventral side, black dots on ceratal margin.

Biology: this species is usually found under stones in highly hydrodynamic environments; in Bocas del Toro, Panama it has shown to feed on the green alga *Caulerpa racemosa* (Forsskål) J. Agardh 1873 (Medrano *et al.* 2018).

Remarks: this species has been reported from different locations in the Caribbean under the name of *Polybranchia viridis* (Deshayes 1857). However, Medrano *et al.* (2018) concluded that the name *P. viridis* does not represent a species of *Polybranchia* (see below) and introduced the new name *P. schmekelae* for this species.

Distribution: Atlantic species reported from Florida, the Caribbean Sea including Bocas del Toro, Panama, which is its type locality (Medrano *et al.* 2018). It is possible that it could an amphiatlantic species since there are reports from the Canary Islands (Ortea, 1981 as *P. viridis*).

Genus ***Caliphylla*** A. Costa 1867

230. *Caliphylla viridis* (Deshayes 1857) Figure 15g

Diagnosis: animal up to 80 mm in length; body translucent, viscera giving light green to greenish brown appearance; cerata flattened, translucent, leaf-shaped with opaque white spots.

Biology: found in association with the filamentous green alga *Bryopsis plumosa* (Hudson) C. Agardh 1823 (Goodheart *et al.* 2016).

Remarks: this species was originally described for the Caribbean as *Hermaea viridis*, later assigned to the genus *Polybranchia* and reported from the Eastern Pacific. However, Medrano *et al.* (2018) argued that name *P. viridis* likely corresponds to a species of *Caliphylla*. Thus, Medrano *et al.* (2018) introduced new species names for the Caribbean and Eastern Pacific species of *Polybranchia* (see remarks of *P. mexicana* and *P. schmekelae*). Medrano *et al.* (2018) suggested that the species reported in the western Atlantic as *Caliphylla mediterranea* Costa, 1867 is possibly *C. viridis* and proposed to use the name *C. viridis* for it. However, Medrano *et al.* (2018) did not compare Caribbean specimens assigned to *C. viridis* with Mediterranean specimens.

Distribution: Atlantic species reported in the Western Atlantic from Florida to Brazil and the Caribbean islands, including the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

Genus ***Cyerce*** Bergh 1870

231. *Cyerce antillensis* Engel 1927 Figure 15h

Diagnosis: animal up to 60 mm in length; body translucent with small white spots, viscera green to yellow, visible by transparency; cerata flattened, semitransparent, with rounded tubercles on surface.

Biology: feeds on the green alga *Penicillus dunetosus* Blainville 1830 (Redfern 2001).

Distribution: Atlantic species reported from the Western Atlantic of Florida, the Gulf of Mexico, and the Caribbean (Felder *et al.* 2009; Miloslavich *et al.*,2010; Sanvicente-Añorve *et al.* 2012) including the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016). Also cited in the Azores and Madeira (Cervera *et al.* 2004), so it could be considered an amphiatlantic species.

Family Costasiellidae K.B. Clark 1984

Genus ***Costasiella*** Pruvot-Fol 1951

232. *Costasiella nonatoi* Ev. Marcus & Er. Marcus 1960

Diagnosis: animal up to 4 mm in length; body dark brown, almost completely black, with white spots; cerata fusiform with numerous white spots, covering almost entire body; tail narrow, whitish.

Biology: it feeds on the green algae *Avrainvillea nigricans* Decaisne 1842 and *Cladophora* sp. (Redfern 2001).

Distribution: Atlantic species reported in the Western Atlantic from North Carolina to Brazil, including the Caribbean islands (Valdés *et al.* 2006; Felder *et al.* 2009; Miloslavich *et al.* 2010; Camacho-García *et al.*, 2014; Caballer *et al.* 2015), and in the Bocas del Toro Archipelago, Panama (Goodheart *et al.* 2016).

233. *Costasiella* sp.

Diagnosis: animal up to 3 mm in length; body greenish white, with white spots; red Y-shaped spot just behind rhinophores; rhinophores thick, with purple basal half; cerata short, rounded at tip, purple at base, rest same color as body.

Distribution: reported from the Eastern Pacific of Uva Island, Coiba Island National Park, Panama (Hermosillo & Camacho-García 2006). Possibly it is an undescribed species.

1.5.2. *Sheets of color photographs*

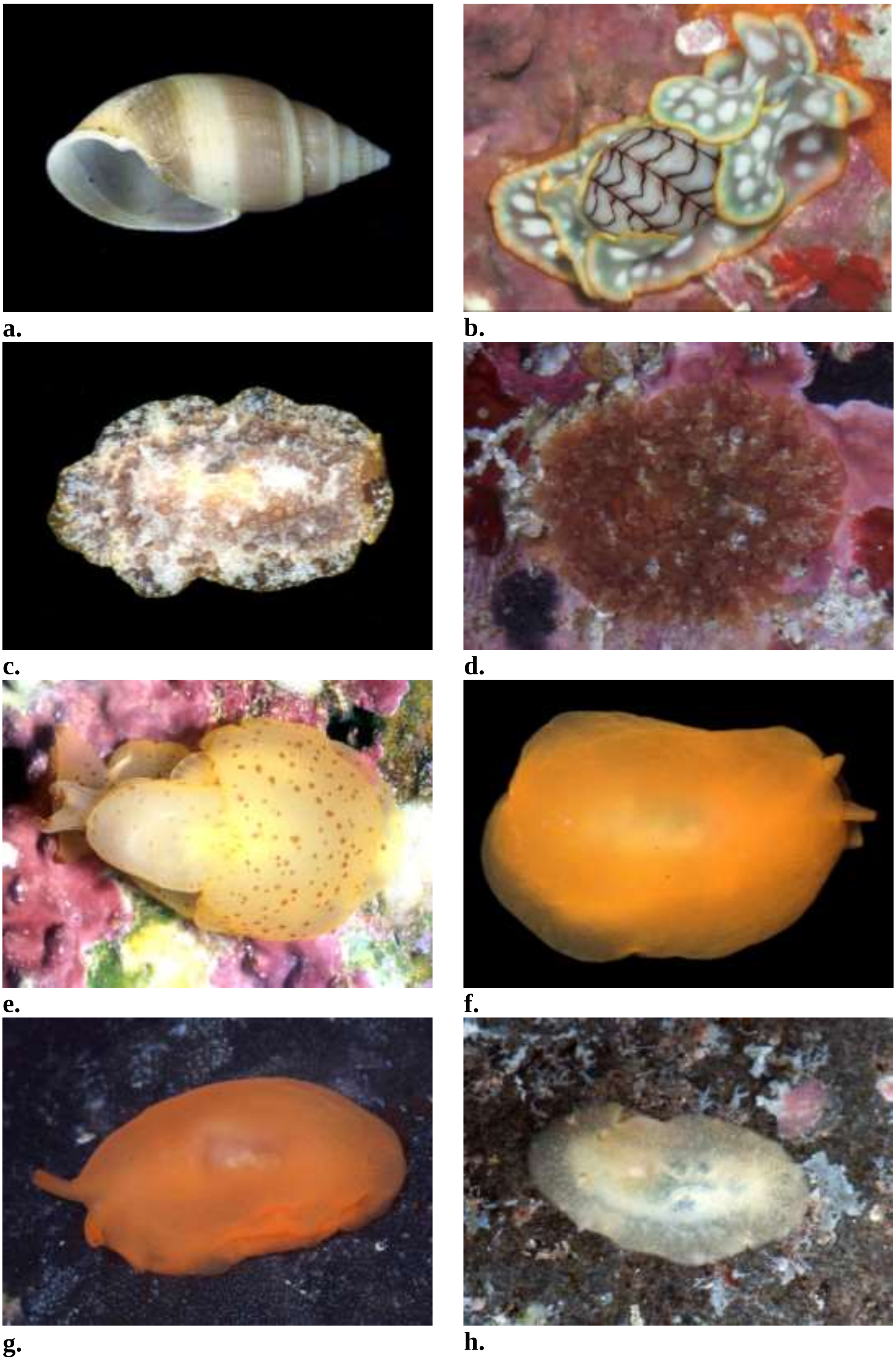
a. b. c. d. e. f. g. h.

Figure 2. a. *Acteon traskii*, b. *Micromelo undatus*, c. *Pleurobranchus areolatus*, d. *P. digueti*, e. *Berthella martensi*, f. *Berthellina quadridens*, g. *B. ilisima*, h. *Doriopsis granulosa*

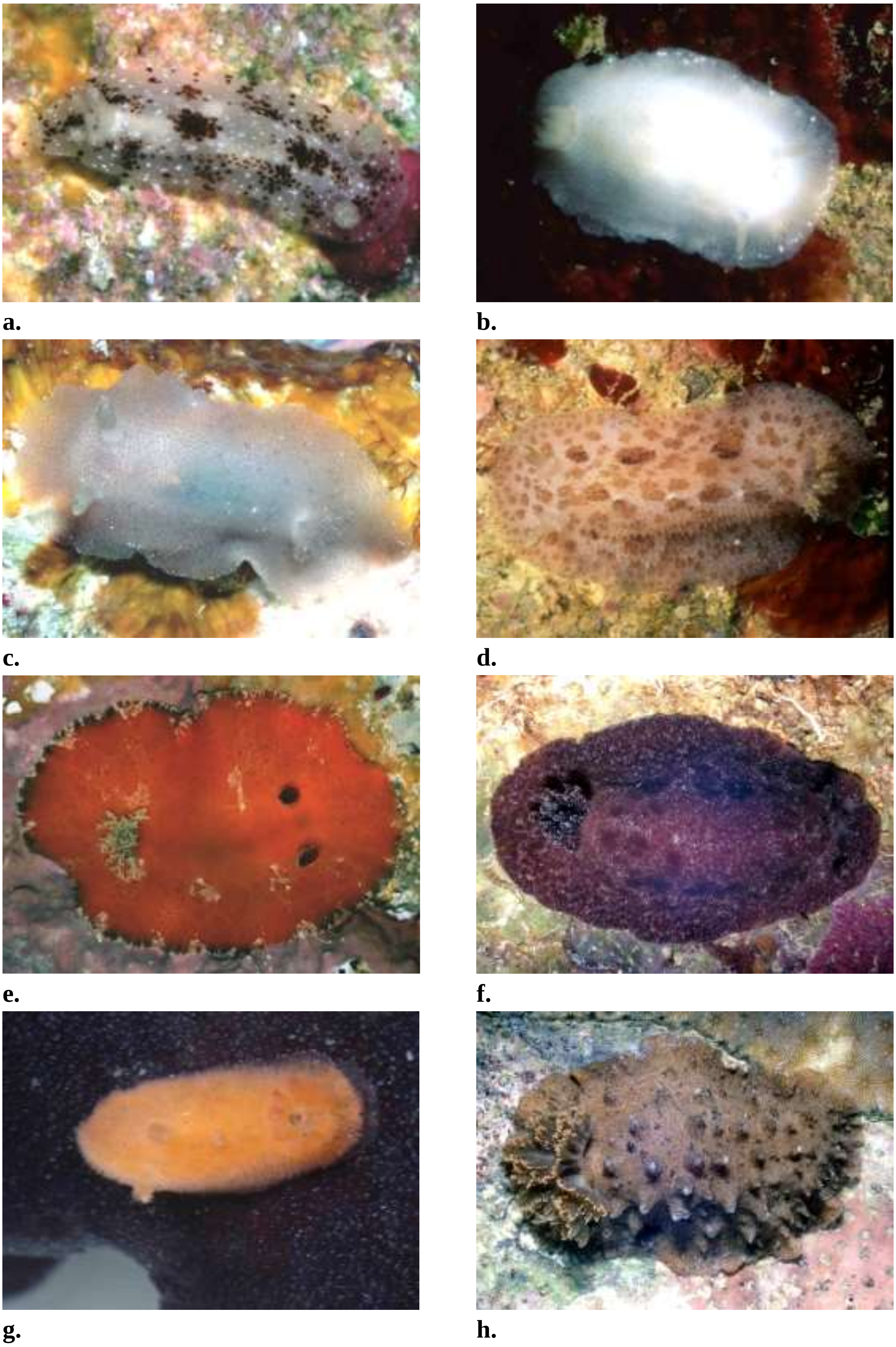

Figure 3. a. *Aphelodoris antillensis* b. *Conualevia alba*, c. *Jorunna spazzola* d. *Discodoris ketos*, e. *Platydoris angustipes*, f. *Diaulula phoca*, g. *Rostanga pulchra*, h. *Paradoris adamsae*

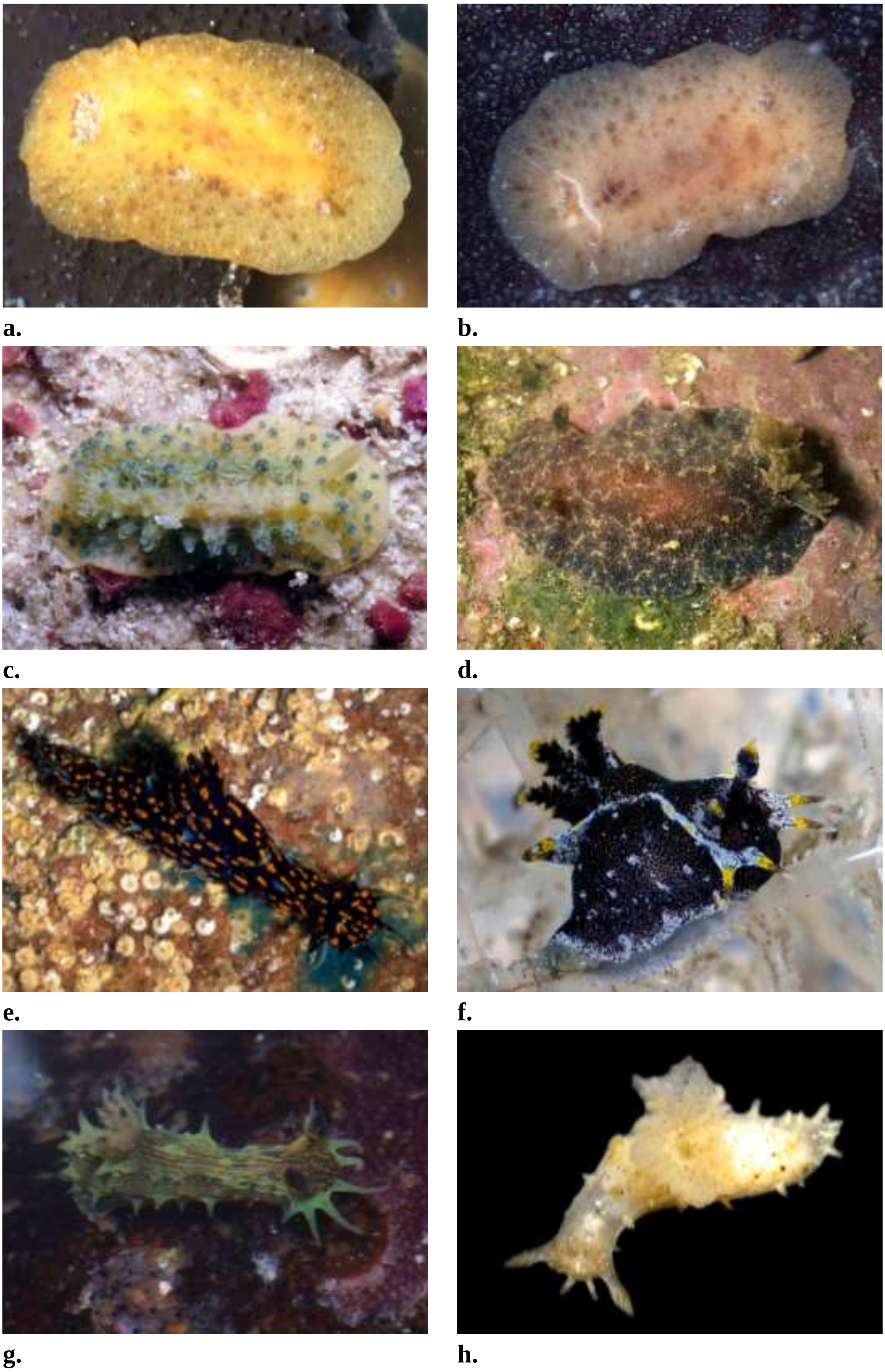
a.
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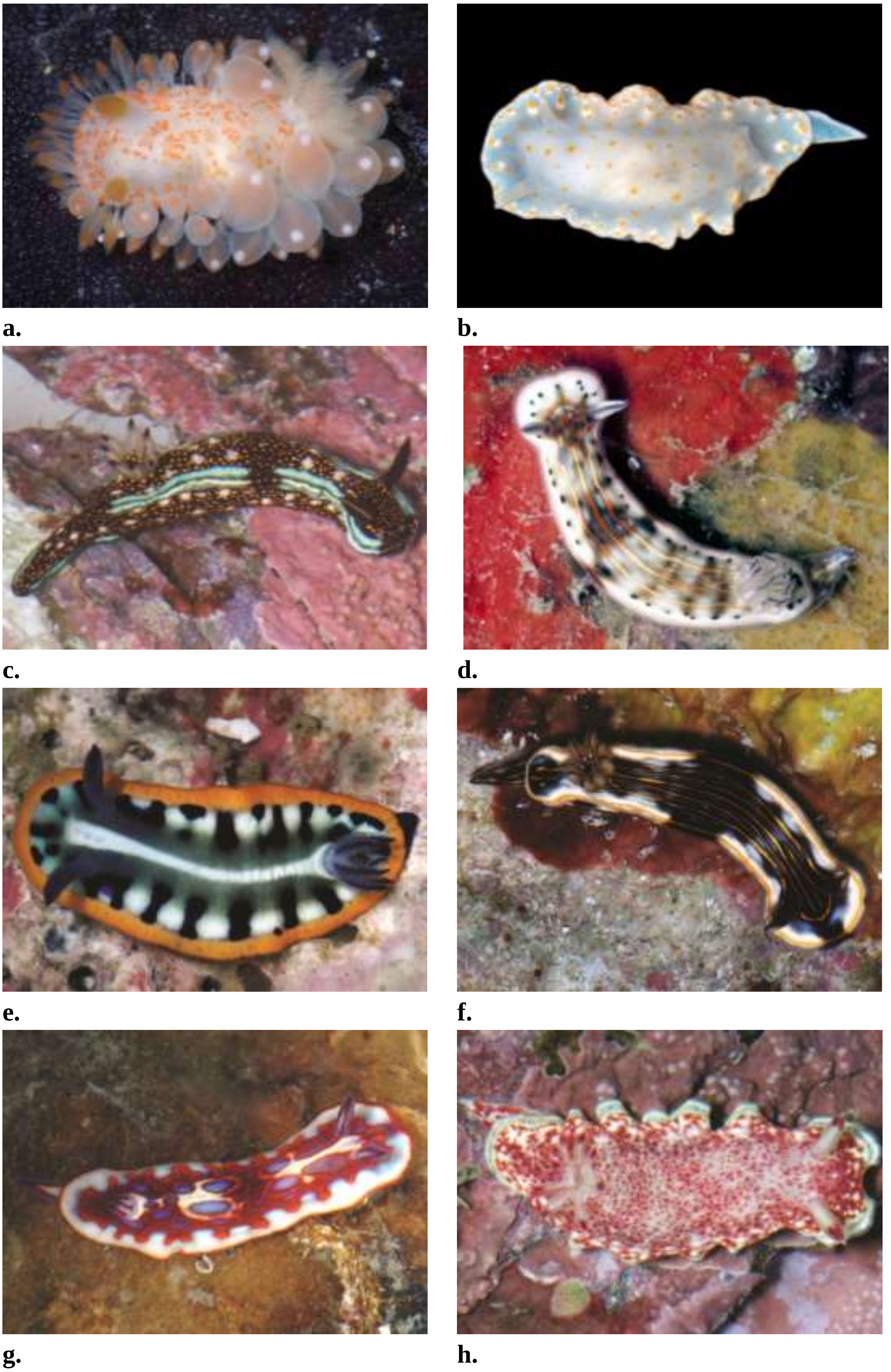
Figure 4. a. *Geitodoris planata*, b. *G. immunda*, c. *Sclerodoris prea*, d. *Taringa aivica, e. Polycera alabe*, f. *P. hedgpethi*, g. *P. anae,* h. *Polycerella glandulosa*



a. b. c. d. e. f. g. h.

Figure 5. a. *Limacia janssi*, b. *Tyrinna evelinae*, c. *Felimare agassizii*, d. *F. bayeri*, e. *F. kempfi*, f. *Felimare ruthae*, g. *Felimida clenchi*, h. *F. baumanni*

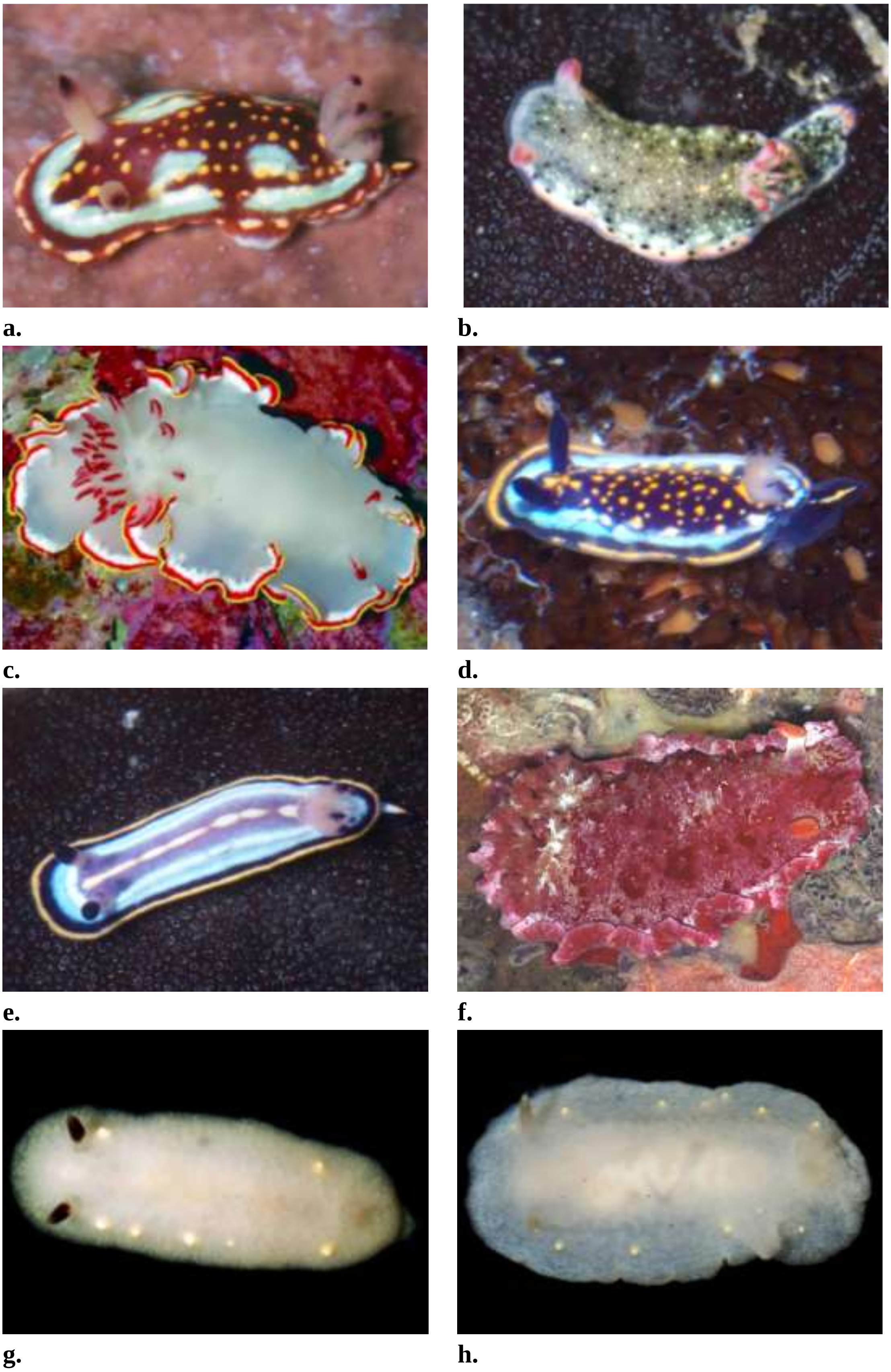
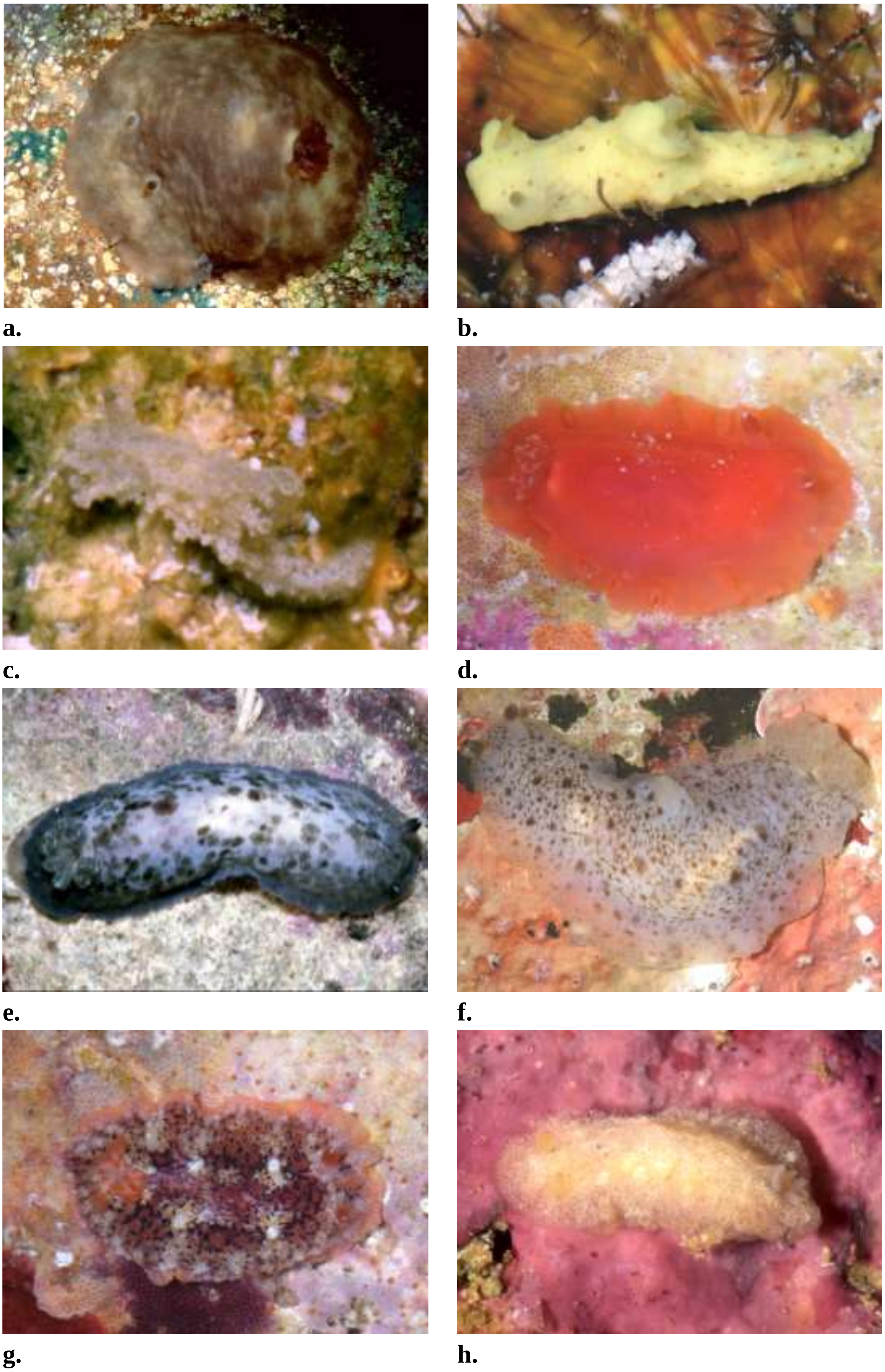


Figure 6. a. *Felimida sphoni*, b. *Chromolaichma dalli*, c. *Ch. sedna*, d. *Mexichromis tura*, e. *M. antonii*, f. *Hexabranchus morsomus*, g. *Cadlina sparsa*, h. *C. rumia*



a. b. c. d. e. f. g. h.

Figure 7. a. *Cadlina luarna*, b. *Aegires sublaevis*, c. *A. ortizi*, d. *Dendrodoris fumata*, e. *D. krebsii*, f. D. *albobrunnea*, g. *Doriopsilla janaina*, h. *D. rowena*

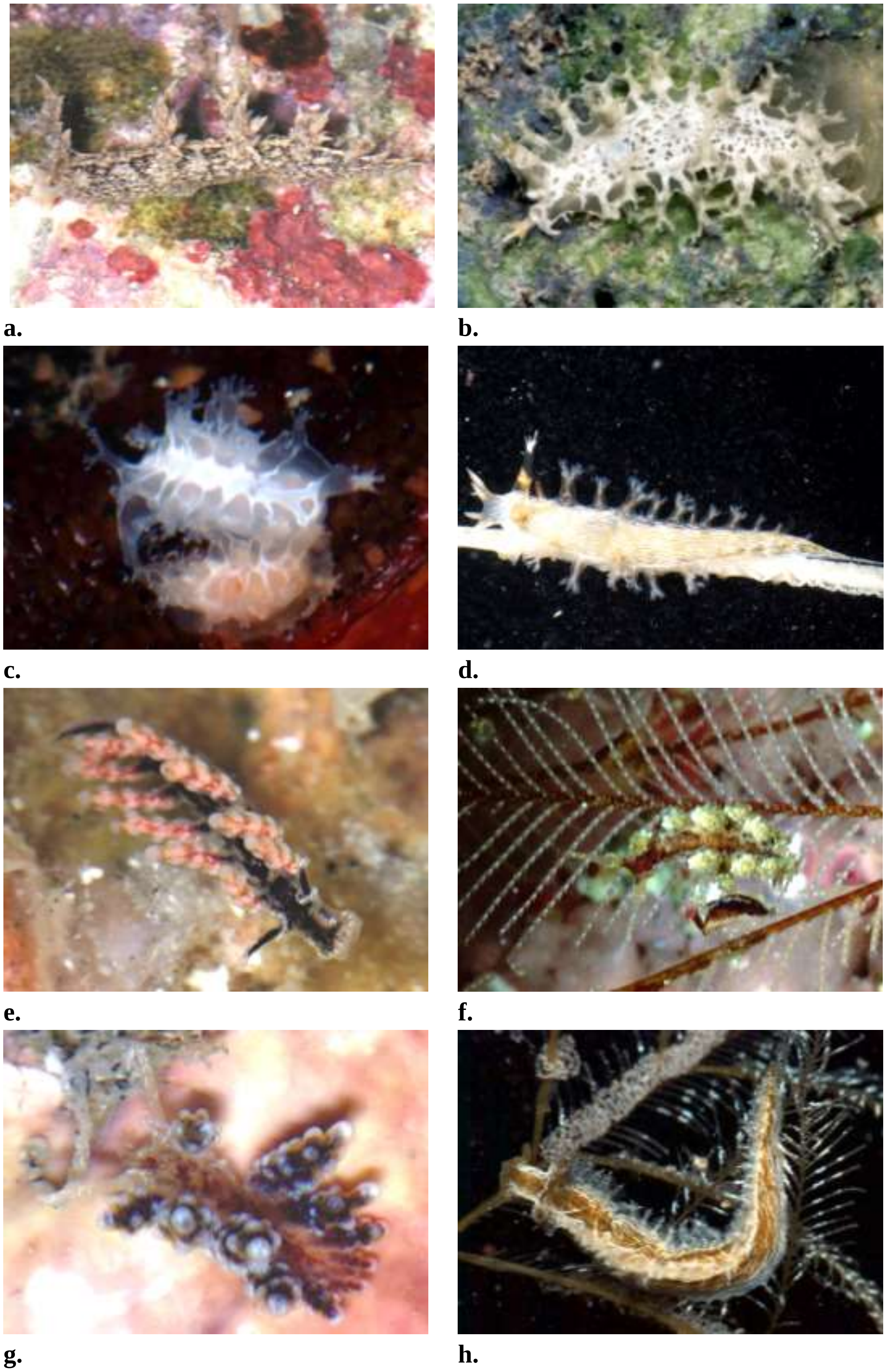


Figure 8. a. *Bornella sarape*, b. *Tritonicula bayeri*, c. *T. pickensi*, d. *T. hamnerorum*, e. *Doto chica*, f. *D. lancei*, g. *D. escatllari*, h. *Lomanotus vermiformis*

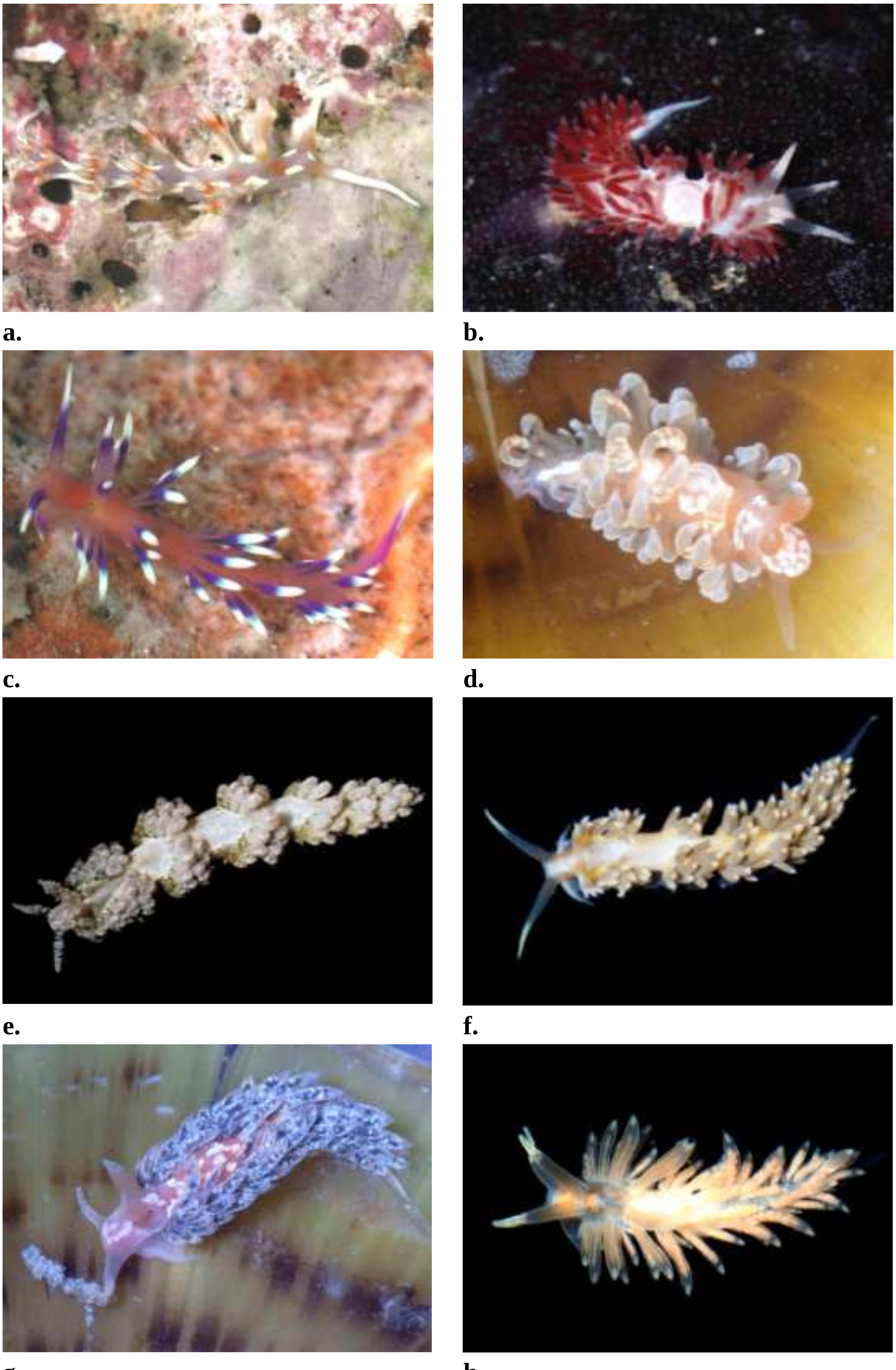


Figure 9. a. *Flabellina engeli*, b. *F. bertschi*, c. *Coryphellina marcusorum*, d. *Spurilla braziliana*, e. *Berghia creutzbergi*, f. *B. rissodominguezi*, g. *Anteaeolidiella chromosoma*, h. *A. lurana*

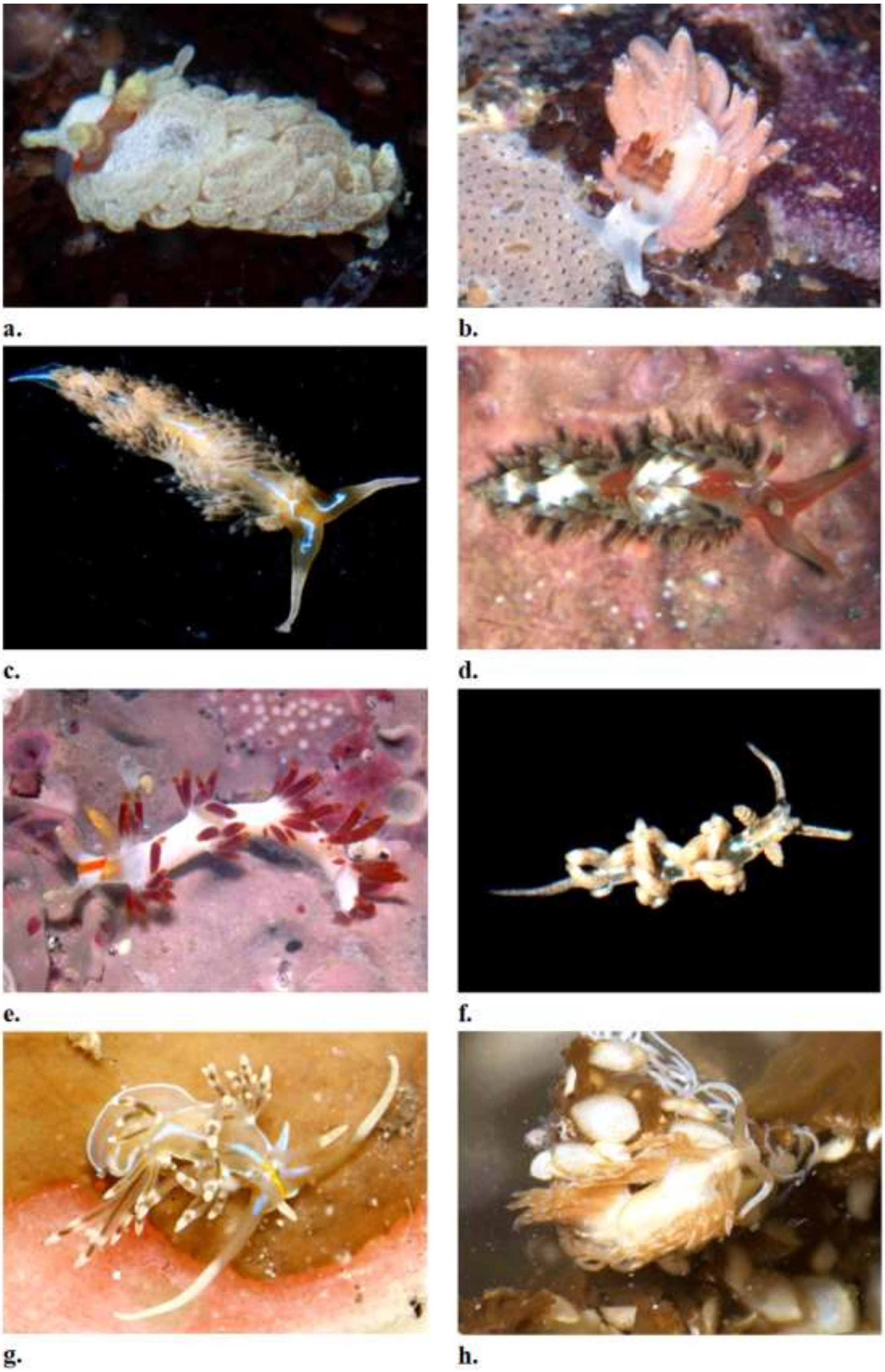


Figure 10. a. *Bulbaeolidia alba*, b. *Favorinus elenalexiae*, c. *Phidiana lynceus*, d. *P. lascrucensis*, e. *Noumeaella rubrofasciata*, f. *Nanuca sebastiani*, g. *Dondice occidentalis*, h. *D. parguerensis*

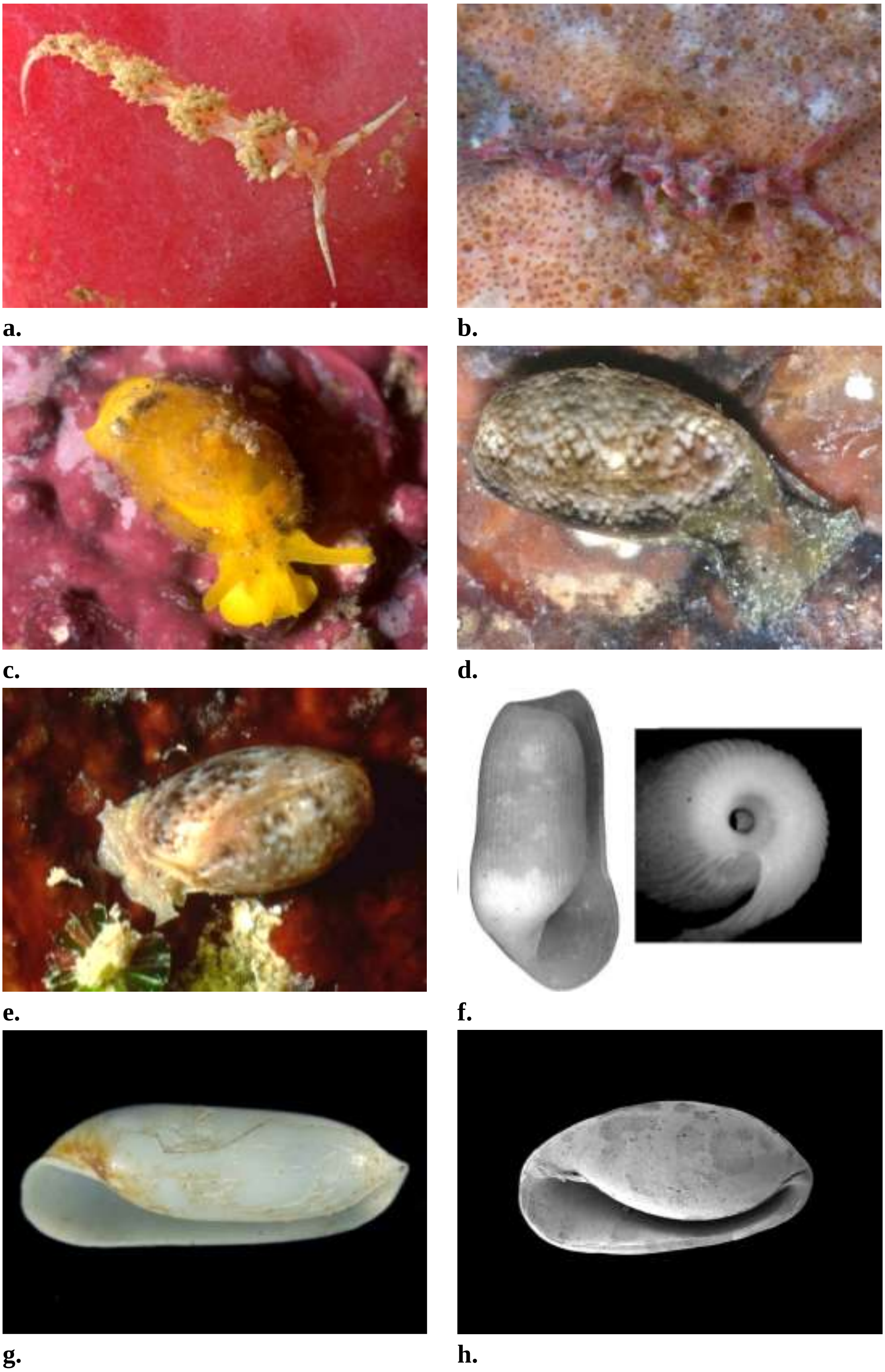


Figure 11. a. *Palisa papillata*, b. *Bajaeolis bertschi*, c. *Tylodina fungina*, d. *Bulla occidentalis*, e. *B. punctulata*, f. *Retusa sulcata*, g. *Volvulella cylindrica*, h. *V. catharia*

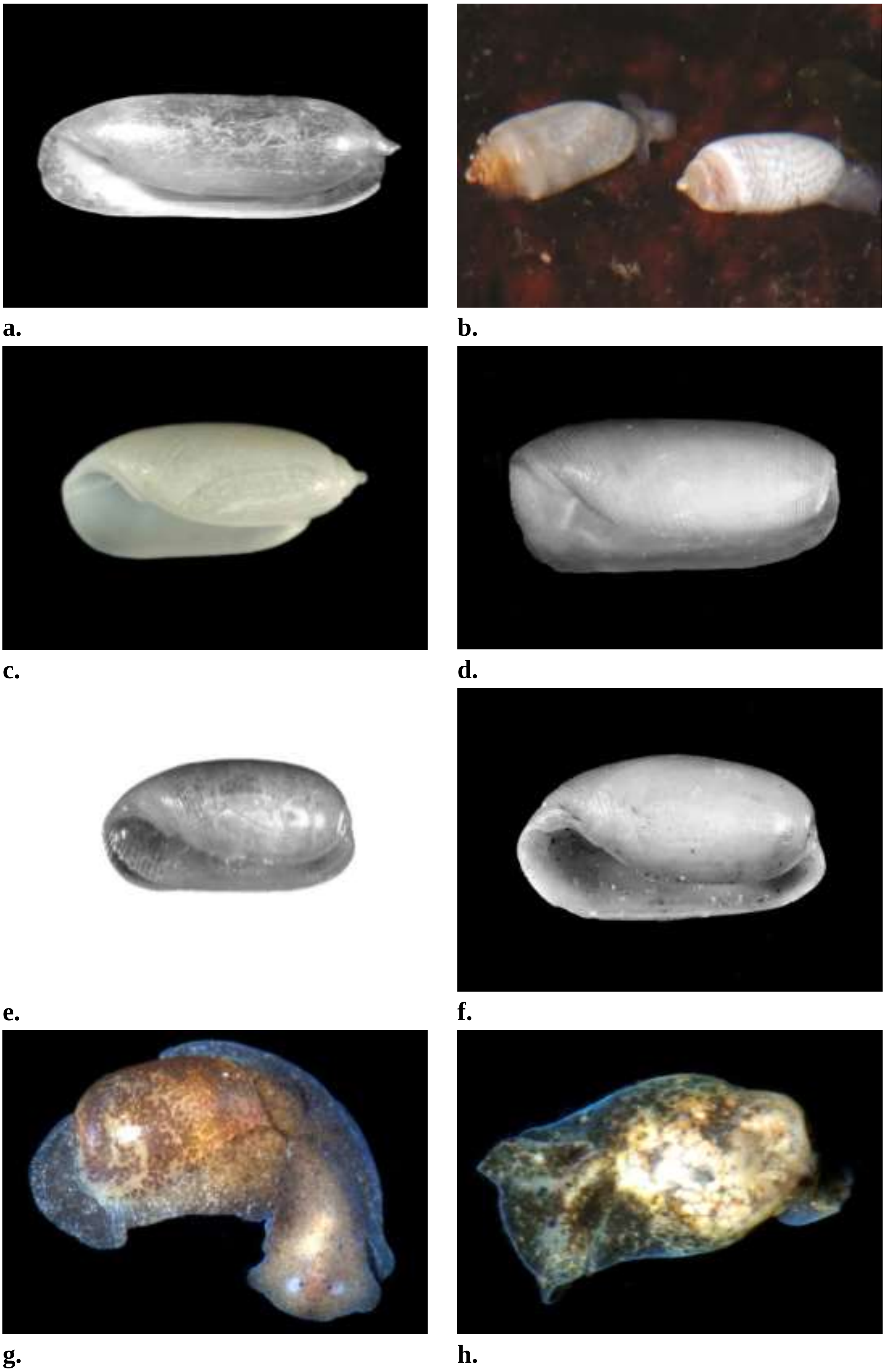


Figure 12. a. *Volvulella panamica*, b. *Acteocina candei*, c. *Acteocina infrequens*, d. *Cylichna atahualpa*, e. *Cylichnella bidentata*, f. *C. tabogaensis*, g. *Haminoea elegans*, h. *H. antillarum*

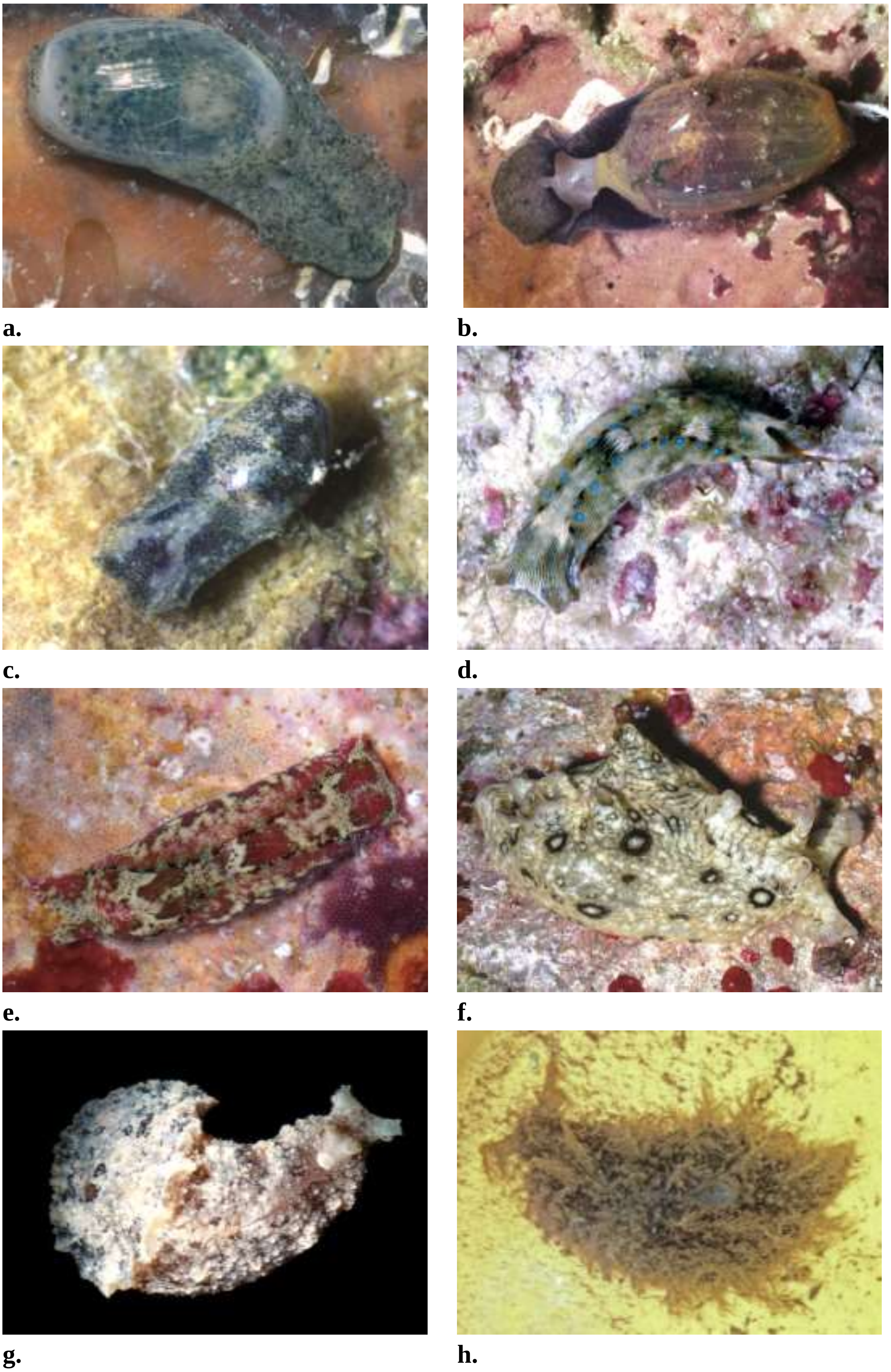


Figura 13. a. *Haminoea succinea*, *b. Atys sandersoni*, c. *Lamprohaminoea ovalis*, d. *Navanax gemmatus*, e. *N. aenigmaticus*, f. *Aplysia dactylomela*, g. *Dolabella auricularia*, h. *Bursatella leachii*

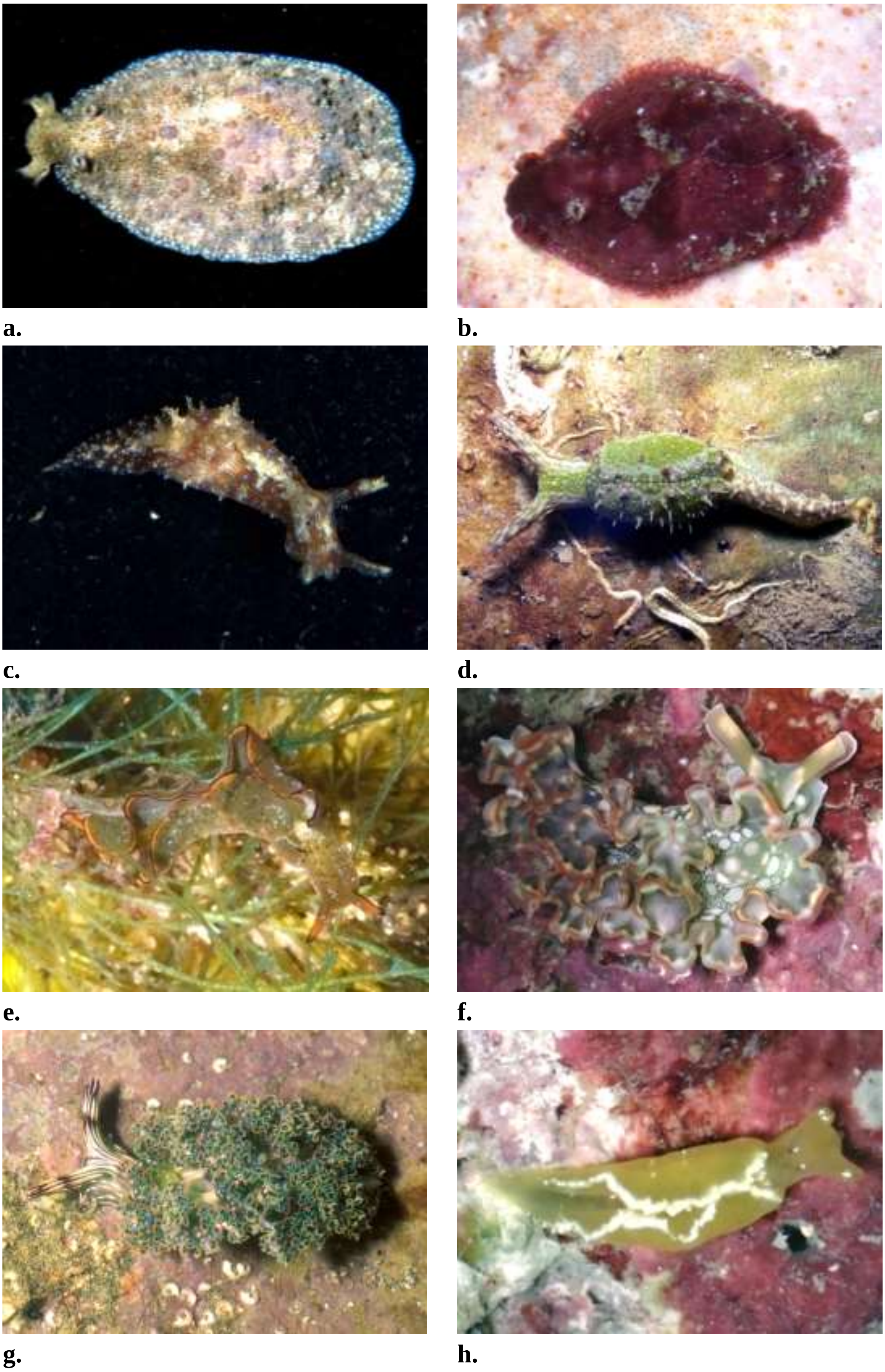


Figure 14. a. *Dolabrifera ascifera*, b. *D. nicaraguana*, c. *Stylocheilus striatus*, d. *Oxynoe antillarum*, e. *Elysia ornata*, f. *E. crispata*, g. *E. diomedea*, h. *E. flava*

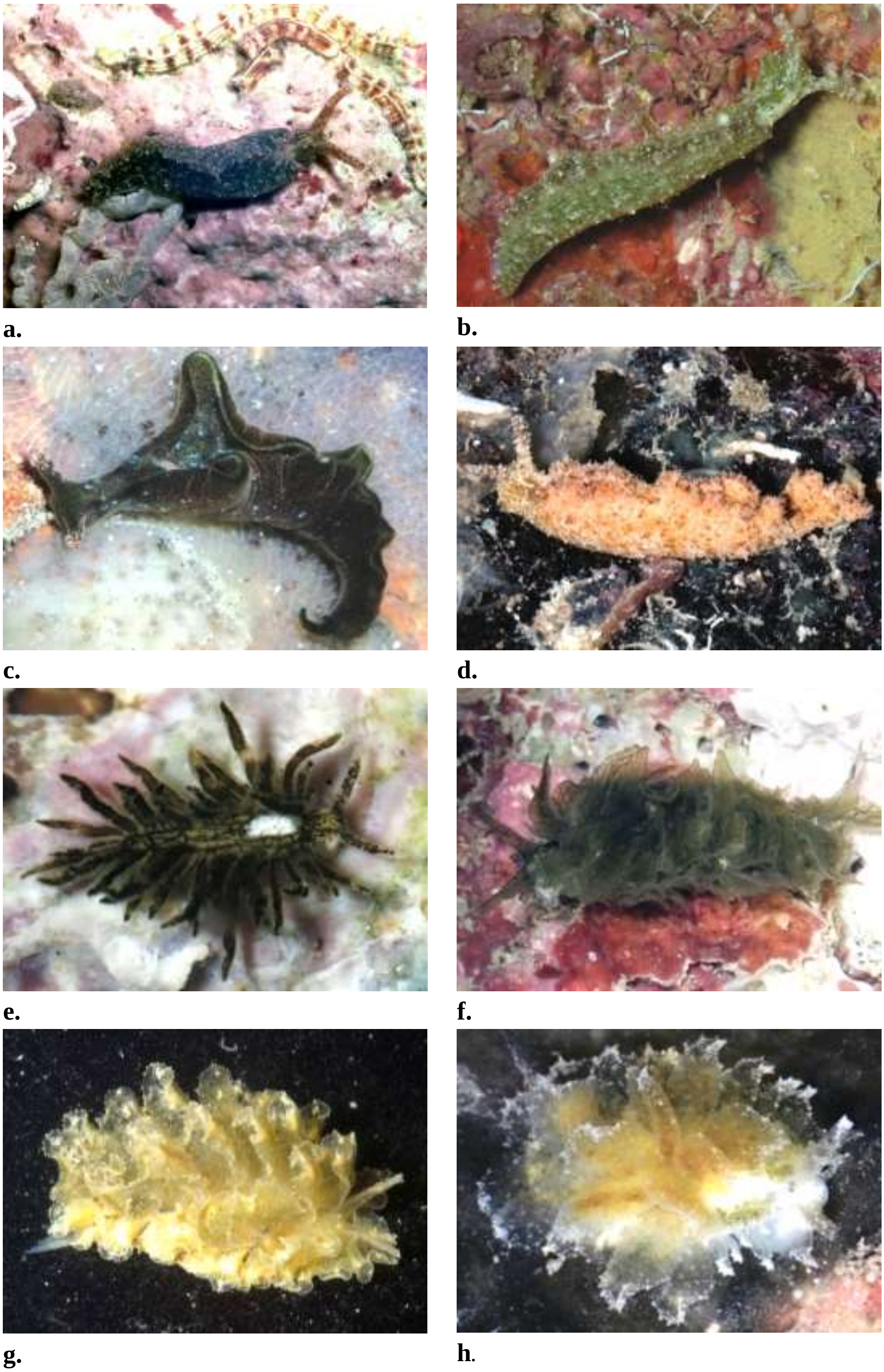


Figure 15. a. *Elysia papillosa*, b. *E. subornata*, c. *E. canguzua*, d. *E. cornigera*, e. *Placida kingstoni*, f. *Polybranchia schmekelae*, g. *Caliphylla viridis*, h. *Cyerce antillensis*

1.6. Discussion

Biodiversity research on sea slugs has often been hampered by the lack of up-to-date field guides. This is particularly problematic for the study of sea slugs, because their taxonomy and systematics have changed drastically in recent years due to new data resulting from molecular studies. For this reason, a new illustrated species list, including all past and recent bibliographic information is here provided to support research projects dealing with sea slug species from the Panamanian coasts.

The majority of marine research in Panama has been carried out in the Caribbean around Isla Colon, Bocas del Toro, primarily because the marine station of the Smithsonian Tropical Research Institute (STRI) is located there. Another area that has attracted the attention of marine scientists is the island of Coiba in the Coiba Island National Park, located in Pacific waters and where STRI also has a small research laboratory.

Whereas many publications cite species of Panamian heterobranch sea slugs, only 9 articles deal more or less exclusively with Panamanian species (Strong & Hertlein 1939; Olsson & McGinty 1958; Meyer 1977; Vega & González 2002; Hermosillo 2004; Hermosillo & Camacho-García 2006; Collin *et al.* 2005; Aviles 2010; Goodheart *et al.* 2016). Although no exhaustive work has been done in the coasts of Panama to document the total diversity of heterobranch sea slugs, in this work a total of 233 species are compiled from the literature, numerous online records and personal collections. Of the total number of species, 118 are from the Caribbean representing 35.87% of the 329 species reported in the entire Caribbean (Valdés *et al.*, 2006, García & Bertsch, 2009). This is a somewhat low number compared to those reported from the Caribbean coast of Costa Rica according to Camacho-García *et al.* (2014), which currently stands at 152. Another 127 species are recorded from the Pacific coast, same as the neighboring country Costa Rica, which has 127 species recorded (Camacho-García 2009); these 127 species constitute 32.07% of the 396 heterobranch sea slugs present in the Eastern Pacific between Point Concepción (California) and the Galapagos Islands (García & Bertsch 2009) and 57.73% of the 220 species recorded by these authors for the Pacific in the Panamic Province.

Recent studies have focused on the biodiversity of sea slugs in Panama's neighboring countries. For example, Ardila *et al.* (2007) compiled a list of 109 species in Colombia, 83 of them for the Caribbean coast and 29 for the Pacific; *Navanax aenigmaticus* also recorded one species for both coasts; those have now been determined to be species complexes. In Venezuela, Caballer *et al.* (2015), sampled 52 localities between 1993 and 2015, recording 134 species. Considering these data and the previous studies, it can be concluded that the biodiversity of Panamanian heterobranch sea slugs is relatively well known, despite the fact that exhaustive or long-term studies have not been carried out.

Of the total species recorded in Panama, seven (3.00%) belong to Acteonoidea, ten (4.29%) to Pleurobranchida, 127 (54.51%) to Nudibranchia (68 Doridina, 29.18% and 59 Cladobranchia, 25.32%), two (0.86%) to Umbraculida, 45 (19.31%) to Cephalaspidea, 13 (5.58%) to Aplysiida and 29 (12.45%) to Sacoglossa. These percentages are similar to those found by Bertsch (2008) in the Northeast Pacific region between Point Conception (California, United States) and Punta Aguja (Piura, Peru) and those by García & Bertsch (2009) in the Caribbean.

In the Panamanian Pacific, the best-known area in terms of heterobranch sea slug biodiversity is the island of Coiba in the Coiba National Park, Veraguas province. Hermosillo (2004) recorded 75 species for Coiba Island, expanding the distribution of some species such as *Haminoea ovalis, Philinopsis speciosa* (as *Philinopsis cyanea*), *Berthella agassizii* and *Phyllaplysia padinae*. Subsequently, Hermosillo & Camacho-García (2006) recorded another 14 species on Coiba Island that had not been previously mentioned, bringing the total number of heterobranch sea slug species in the Coiba National Park to 89.

In the photographic guide of common marine invertebrates of Bocas del Toro (Caribbean Area) by Collin *et al.* (2005), 19 species of heterobranch sea slugs are illustrated. Later, Goodheart *et al.* (2016) conducted a major study on heterobranch sea slug diversity (307.5 h/person of searching) on the surroundings of the Smithsonian Institute Station in Isla Colon, where for the first-time molecular markers were used in the identification and comparison of the species. In this publication Goodheart *et al.* (2016) cited in total 82 species.

Of the species recorded in the present paper, 18 have amphiatlantic distributions or are widely distributed (seven Nudibranchia, one Cephalaspidea, four Aplysiida and six Sacoglossa); species like *Geitodoris planata, Tyrinna evelinae, Cadlina rumia, Aegires sublaevis, Okenia evelinae, Doto escatllari, Limenandra nodosa, Anteaeolidiella lurana, Phidiana lynceus, Haminoea elegans, Weinkauffa macandrewii, Scaphander punctostriatus, Aplysia dactylomela, Bursatella leachii, Elysia ornata, Elysia flava, Ercolania coerulea* and *Cyerce antillensis*.

The following species have been cited in both the Panamanian Pacific and the Caribbean and some of them possibly belong to cryptic species complexes, as indicated in the remarks of each of them: *Berthella agassizii*, *Tyrinna evelinae*, *Chromolaichma edmundsi*, *Adisa sp.* 1, *Lomanotus vermiformis*, *Coryphellina marcusorum*, *Spurilla braziliana* and *Stylocheilus longicaudus*.

There is no doubt that molecular analyses have contributed substantially to improvements in the taxonomy and classification of the species of marine slugs of Panama. For example, here we cite papers such as Valdés *et al.* (2017) that separate the species *Dolabrifera dolabrifera* into a complex of five cryptic species of which three are present in Panama (*Dolabrifera nicaraguana* in the Pacific, *D. ascifera* and *D. virens* in the Caribbean); or Golestani *et al.* (2019) that separate *Aplysia parvula* into four genetically distinct lineages of which *A. hooveri* is found in the Pacific of Panama; or Bazzicalupo *et al.* (2020) that separates *Stylocheilus striatus* into three cryptic species of which two are in Panama (*Stylocheilus striatus* in the Caribbean and *S. rickettsi* in the Pacific).

As general conclusion, it can be said that although a relatively large number of species of sea slugs are known from Panama, it is necessary to extend the study to additional localities, mainly on the Pacific coast but also to others on the Caribbean coast and especially on substrates where sea slugs can potentially be fund, such as the underside of stones and coral debris, among algae (for herbivorous species), the surface of sponges and corals, on hydroid colonies or soft substrates for species that have ability to bury themselves into the sediment.

1.7. Acknowledgments

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1.8. References

Adams C.B. 1852. *Catalogue of shells collected of Panama with notes on their synonymy, station and geographical distribution*. R. Craighead printer, New York, United State, Annals of Lyceum of Natural History of New York, volume V, 303 pp.

Alexander J. & Valdés A. 2013. The ring doesn't mean a thing: Molecular data suggest a new taxonomy for two Pacific species of sea hares (Mollusca: Opisthobranchia, Aplysiidae). *Pacific Scientific*, 67:283-94.

Alvim J. & Pimenta A. 2013. Taxonomic review of the family Discodorididae (Mollusca: Gastropoda: Nudibranchia) from Brazil, with descriptions of two new species. *Zootaxa*, 3745(2): 152-198.

Alvim J. & Pimenta A.D. 2016. Comparative morphology and redescription of Pleurobranchus species (Gastropoda, Pleurobranchoidea) from Brazil. *Zoological Studies,* 55: 15.

Anderson E.S. 1971. The association of the nudibranch *Rostanga pulchra* MacFarland 1905 with the sponges *Ophlitaspongia pennata, Esperiopsis originalis*, and *Plocamia karykina*. PhD. Dissertation. University of California, Santa Cruz, Biology, Santa Cruz, CA, 302 pp.

Angulo-Campillo O. 2005. A four-year survey of the opisthobranch fauna (Gastropoda, Opisthobranchia) from Baja California Sur, Mexico. *Vita Malacologica*, 3: 43–50.

Angulo-Campillo O. & Valdés Á. 2003. A new species of Cuthona Alder & Hancock, 1855, from the Gulf of California, Mexico (Opisthobranchia: Nudibranchia: Tergipedidae). *The Veliger*, 46 (2): 179-182.

Angulo-Campillo O. & Bertsch H. 2013. *Marionia kinoi* (Nudibranchia: Tritoniidae): A new species from the tropical eastern Pacific. *The Nautilus.* 127(2): 85-89. Available from https://www.biodiversitylibrary.org/page/50437509

Ardila N., Baez D.P. & Valdés A. 2007. Babosas y liebres de mar (Mollusca: Gastropoda: Opisthobranchia) de Colombia. Biota Colombiana, 8(2): 185-197.

Avilés M.C. 2010. Listado preliminar de moluscos opistobranquios de la República de Panama. *MUMAUP*, 3: 1-23.

Báez D.P., Ardila N., Valdés A. & Acero A. 2011. Taxonomy and phylogeny of *Armina* (Gastropoda: Nudibranchia: Arminidae) from the Atlantic and Eastern Pacific. *Journal of the Marine Biological Association of the United Kingdom*, 91(5): 1107–1121.

Baker F. & Hanna G.D. 1927. Expedition of the California Academy of Sciences to the Gulf of California in 1921. Marine Mollusca of the order Opisthobranchia. *Proceedings of the California Academy of Sciences*, 16: 123-135.

Ballesteros M. 2007. Lista actualizada de los opistobranquios (Mollusca: Gastropoda: Opisthobranchia) de las costas catalanas. *Spira*, 2(3): 163-188.

Ballesteros M., Madrenas E. & Pontes M. 2016. Actualización del catálogo de los moluscos opistobranquios (Gastropoda: Heterobranchia) de las costas catalanas. *Spira*, 6: 1-28.

Ballesteros M., Pontes M. & Madrenas E. 2019. *Els nudibranquis del mar catalá.* Número. 3, 190 pp.

Ballesteros, Manuel, Enric Madrenas, Miquel Pontes (2012-2020) *"Dendrodoris fumata"* in *OPK-Opistobranquis*, published: 19/09/2014, 02/10/2020. Available from(https://opistobranquis.info/es/bIoGf)

Ballesteros M., Madrenas E. & Pontes M. 2021a. *"Limenandra nodosa"* in *OPK-Opistobranquis*. Published: 16/05/2012. Accessed: 22/01/2021. Available from (https://opistobranquis.info/en/mB1If)

Ballesteros M., Madrenas E. & Pontes M. 2021b "*Philinopsis speciosa*" in OPK-Opistobranquis. Published: 01/05/2015. Accessed: 12/12/2021. Available from (https://opistobranquis.info/en/vfvvU)

Ballesteros M., Madrenas E. Pontes M. 2021c. *"Aplysia dactylomela"* in *OPK-Opistobranquis*. Published: 15/05/2012. Accessed: 25/10/2021. Available from (https://opistobranquis.info/en/R2dRy

Ballesteros M., Madrenas E. & Pontes M. 2021d. *"Bursatella leachii"* in *OPK-Opistobranquis*. Published: 15/05/2012. Accessed: 26/10/2021. Available from (https://opistobranquis.info/en/NNgfg)

Ballesteros M., Madrenas E. & Pontes M. 2021e. "*Elysia flava*" in *OPK-Opistobranquis*. Publicado: 14/05/2012. Accedido: 30/10/2021. Available from(https://opistobranquis.info/es/AnLgr)

Ballesteros M., Madrenas E. & Pontes M. 2021f. "*Ercolania coerulea*" in *OPK-Opistobranquis*. Published: 14/05/2012. Accessed: 01/11/2021. Available from (https://opistobranquis.info/en/R33vJ)

Bazzicalupo E., Crocetta F., Estores-Pacheco K., Golestani H., Bazairi H., Giacobbe S., Jaklin A., Poursanidis Chandran D.B.; Cervera J.L. & Valdés Á. 2018. Population genetics of *Bursatella leachii* (De Blainville, 1817) and implications for the origin of the Mediterranean population. *Helgoland Marine Research*, 72: 19.

Bazzicalupo E., Crocetta F., Gosliner T., Berteaux-Lecellier V., Camacho-García Y., Sneha B. & Valdés Á. 2020. Molecular and morphological systematics of *Bursatella leachii* de Blainville, 1817 and *Stylocheilus striatus* Quoy & Gaimard, 1832 reveal cryptic diversity in pantropically distributed taxa (Mollusca: Gastropoda: Heterobranchia). *Invertebrate Systematics*, 34: 535–568.

Belmonte T., Alvim J., Padula V. & Muricy G. 2015. Spongivory by nudibranchs on the coast of Rio de Janeiro state, southeastern Brazil. *Spixiana*, 38:187-95.

Behrens D.W. 2004. Pacific Coast Nudibranchs, Supplement II. New Species to the Pacific Coast and New Inforfmation on the Oldies. *Proceedings of the Califorfnia Academy of Sciences*, 55 (2): 11-54.

Behrens D.W. 2005. *Nudibranch behavior*. New World Publication Inc, 176 pp.

Behrens D.W. & Hermosillo A. 2005. *Eastern Pacific nudibranchs. A guide to the opisthobranchs from Alaska to central America*. Monterey, CA: Sea Challengers, 143 pp.

Bergh L.S.R. 1888. Malacologische Untersuchungen. In: Semper, C. (Ed.), Reisen im Archipel der Philippinen. Zweiter Theil, *Wissenschaftliche Resultate*, Band 2, Heft 16, pp 755–814.

Bertsch H. 1972. Two additions to the opisthobranch fauna of the Southern Gulf of California. *Veliger*, 15:103–106.

Bertsch H. 1977. The Chromodoridinae nudibranchs from the Pacific Coast of America – Part I. Investigating methods and supra-specific taxonomy. *Veliger*, 202: 107–118.

Bertsch H. 1980. A new species of *Bornella* from tropical west-America (Mollusca, Opisthobranchia). *Spixiana*, 3: 33-42.

Bertsch H. 1988. Anatomy and zoogeography of *Glossodoris sedna* and *Chromodoris grahami* (Opisthobranchia, Nudibranchia) in the tropical Western Atlantic and Caribbean. *The Veliger*, 30(4): 395-399.

Bertsch H. & Ferreira A.J. 1974. Four new species of nudibranchs from tropical West America. *The Veliger*, 16(4): 343-353.

Bertsch H. & Kerstitch A. 1984. Distribution and radular morphology of various nudibranchs (Gastropoda: Opisthobranchia) from the Gulf of California, Mexico. *The Veliger*, 26: 264-273.

Bertsch H., Campillo O.A. & Arreola J.L. 2000. New distributional records of opisthobranchs from Punta Eugenia region of the Baja California, Mexico peninsula, a record based on 1997-1998 CONABIO sponsored expeditions. *The Festivus*, 32(7): 99-104.

Borges P.A.V., Costa A., Cunha R., Gabriel R., Gonçalves V., Martins A.F., Melo I., Parente M., Raposeiro P., Rodrigues P., Santos R.S., Silva L., Vieira P. & Vieira V. (Eds.). 2010. A *list of the terrestrial and marine biota from the Azores. Princípia, Oeiras*, 432 pp.

Bouchet P. 1975. Opisthobranches de profondeur de l'Océan Atlantique. I.- Cephalaspidea. *Cahiers de Biologie Marine,* 16: 317-365.

Bouchet P., Rocroi J.P., Hausdorf B., Kaim A., Kano Y., Nützel A., Parkhaev P., Schrödl M. & Strong E.E. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia*. 61(1-2): 1-526.

Brodie G. 2000. *Comments on Dendrodoris krebsi. [Message in] Sea Slug Forum. Australian Museum, Sydney.* Available from http://www.seaslugforum.net/find/3188

Bruguière J.G. 1792. *Histoire naturelle des vers.* Vol. 1. In: Encyclopédie Méthodique. Paris: Panckoucke, 794 pp.

Caballer Gutiérrez M., Ortea J.A., Rivero N., Tucker G.C., Malaquias M.A.E. & Narciso S. 2015. The opisthobranch gastropods (Mollusca: Heterobranchia) from Venezuela: An annotated and illustrated inventory of species. *Zootaxa*, 4034: 201-56.

Camacho-García Y. 2009. *Benthic opisthobranchs*. In Wehrtmann, I. & Cortes, J. *Marine biodiversity of Costa Rica*. Springe Science, pp 371-386.

Camacho-García Y. & Gosliner T. 2007. The genus *Paradoris* Bergh, 1884 (Nudibranchia: Discodorididae) in the Tropical Americas, and South Africa with the description of a new species. *The Veliger*, 49(3): 105-119. Available from http://biodiversitylibrary.org/page/42498056

Camacho-García Y. & Gosliner T. 2008. Systematic revision of *Jorunna* Bergh, 1876 (Nudibranchia: Discodorididae) with a morphological phylogenetic analysis. *Journal of Molluscan Studies*, 74: 143-181.

Camacho-García Y. & Ortea J. 2000. New species of *Trapania* (Nudibranchia: Goniodorididae) from the Pacific coast of Central America. Revista Biología Tropical, 48(2/3): 317-322.

Camacho-García Y. & Valdés A. 2003. Caryophyllidia-bearing dorid nudibranchs (Mollusca: Nudibranchia: Doridacea) from Costa Rica. *Proceedings of the California Academy of Sciences*, 54: 65-79.

Camacho-García Y., Gosliner T. & Valdés A. 2005. *Guía de Campo de las babosas marinas del Pacífico Este Tropical Field Guide to the sea slugs of the Tropical Eastern Pacific*. United State: California Academy of Sciences, 129 pp.

Camacho-García Y., Pola M., Carmona L., Padula V., Villani G. & Cervera L. 2014. Diversity and distribution of the heterobranch sea slug fauna on the Caribbean of Costa Rica. *Cahiers de Biologie Marine Journal*, 55:109-127.

Camps-Castellà J., Ballesteros M., Trobajo R., Pontes M. & Prado P. 2020. Not all nudibranchs are carnivorous: trophic ecology of *Polycerella emertoni* in the Ebro Delta. *Marine Ecology Progress Series*, 645. 67-82.

Carmona L., Pola M., Gosliner T.M. & Cervera J.L. 2013. A tale that morphology fails to tell: A molecular phylogeny of Aeolidiidae (Aeolidida, Nudibranchia, Gastropoda). *PLoS ONE* 8(5): e63000.

Carmona L., Pola M., Gosliner T.M. & Cervera J.L. 2014b. The Atlantic-Mediterranean genus *Berghia* Trinchese, 1877 (Nudibranchia: Aeolidiidae): taxonomic review and phylogenetic analysis. *Journal of Molluscan Studies*, 80:482-498.

Carmona L., Pola M., Gosliner T.M. & Cervera J.L. 2014c. Review of *Baeolidia*, the largest genus of Aeolidiidae (Mollusca: Nudibranchia), with the description of five new species. *Zootaxa*, 3802 (4): 477–514.

Carmona L., Pola M., Gosliner T.M. & Cervera J.L. 2014d. The end of a length controversy: systematics of the genus *Limenandra* (Mollusca: Nudibranchia: Aeolidiidae). *Helgoland Marine Research*, 68(1), 37.

Carmona L., Bhave V., Salunkhe R., Pola M., Gosliner T.M. & Cervera J.L. 2014e. Systematic review of *Anteaeolidiella* (Mollusca, Nudibranchia, Aeolidiidae) based on morphological and molecular data, with a description of three new species. *Zoological Journal of the Linnean Society*. 171(1): 108-132.

Carmona L., Lei B.R., Pola M., Gosliner T.M., Valdés A. & Cervera J.L. 2014a Untangling the *Spurilla neapolitana* (Delle Chiaje, 1841) species complex: a review of the genus *Spurilla* Bergh, 1864 (Mollusca: Nudibranchia: Aeolidiidae). *Zoological Journal of the Linnean Society*, 170(1), 132-154.

Cem C., Cavas L., Erguden D. & Turan C. 2012. A second observation of *Dendrodoris fumata* (Rüppell & Leuckart, 1830) from the Mediterranean Sea (Nudibranchia: Dendrodorididae). *Zoology in the Middel East*, 56: 148-149.

Cervera J.L., Calado G., Gavaia C., Malaquias M.A., Templado J., Ballesteros M., García-Gómez J.C. & Megina C. 2004. An annotated and updated checklist of the opisthobranchs (Mollusca: Gastropoda) from Spain and Portugal (including islands and Archipelagos). *Boletín Instituto Español de Oceanografía*, 20(1-4): 1-122.

Chia F.S. & Koss R. 1977. Development and metamorphosis of the long planktotrophic larvae of R*ostanga pulchra* MacFarland (Mollusca: Nudibranchia). *Mar. Biol.*, 46: 109-119.

Collin R. 2008. Development of *Tylodina fungina* Gabb, 1865 (Gastropoda: Notaspidea) from the Pacific Coast of Panama. *The Veliger*, 50(1): 51-56.

Collin R., Díaz M.C., Norenburg J., Rocha R.M., Sánchez J.A. & Schulze A. 2005. Photographic identification guide to some common marine invertebrates of Bocas Del Toro, Panama. *Caribbean Journal of Science*, 41: 638-707.

Cronin G., Hay M.E., Fenical W. & Lindquist N. 1995. Distribution, density, and sequestration of host chemical defenses by the specialist nudibranch *Tritonia hamnerorum* found at high densities on the sea fan *Gorgonia ventalina*. *Mar Ecol Prog Ser.*, 119: 177-89.

Curtis N.E., Massey S.E., Schwartz J.A., Tagihof H. & Pierce S.K. 2004. The intracellular, functional chloroplasts in adult *Elysia crispata* come from several algal species and are different from those in juvenile slugs. *Integr Comp Biol.*, 44: 686.

Curtis N.E., Massey S.E. & Pierce S.K. 2006. The symbiotic chloroplasts in the sacoglossan *Elysia clarki* are from several algal species. *Invertebr. Biol.*, 125: 336–345.

Curtis N.E., Schwartz J.A. & Pierce S.K. 2010. Ultrastructure of sequestered chloroplasts in sacoglossan gastropods with differing abilities for plastid uptake and maintenance. *Invertebrate Biology*, 129, 297–308. Available from http://dx.doi.org/10.1111/j.1744-7410.2010.00206.x

Dall W.H. 1908. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer "Albatross," during 1891, Lieut.-Commander Z.L. Tanner, U.S.N., commanding. XXXVIII. Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross," from October, 1904, to March, 1905, Lieut.-Commander L.M. Garrett, U.S.N., commanding. XIV. The Mollusca and the Brachiopoda. *Bulletin of the Museum of Comparative Zoölogy,* 43: 205-487.

Dayrat B. 2006. A taxonomic revision of *Paradoris* sea slugs (Mollusca, Gastropoda, Nudibranchia, Doridina). *Zoological journal of the Linnean Society*, 147(2): 125–238.

Dayrat B. 2010. A monographic revision of basal discodorid sea slugs (Gastropoda, Opisthobranchia, Nudibranchia, Doridina). *Proceedings of the California Academy of Sciences*. Series 4, vol. 61, suppl. I: 1-403, 382.

Debelius H. & Kulter R. 2007. *Nudibranchs of the world.* Alemania: IKAN-Unterwasserarchiv, Frankfurt, 360 pp.

Diaz J.M. & Puyana M. 1994. *Moluscos del Caribe Colombiano*. Un catalogo Ilustrado. Colciencias, Funacion Natura, Invemar. Colombia: Santafe de Bogota, 291 pp.

Dinapoli A. & Klussmann-Kolb A. 2010. The length way to diversity – Phylogeny and evolution of the Heterobranchia (Mollusca: Gastropoda). *Molecular Phylogenetics and Evolution*, 55: 60-76.

Edmunds M. 1981. Opisthobranchiate Mollusca from Ghana: Chromodorididae. *Zoological Joumal ofthe Linnean Society*, 72: 175-201.

Eilertsen M.E. & Malaquias M.A.E. 2013. Systematic revision of the genus *Scaphander* (Gastropoda, Cephalaspidea) in the Atlantic Ocean with a molecular phylogenetic hypothesis. *Zoological Journal of the Linnean Society*, 167: 389 429.

Eliot C.N.E. 1903. On some nudibranchs from east Africa and Zanzibar, part II. *Proceedings of the Zoological Society of London*, 1, 250–257.

Felder D.L. & Camp D.K. 2009. *Gulf of Mexico Origin, Waters, and Biota*. Volume 1: Biodiversidad. Texas A & M University Press, 1449 pp.

Feliciano K., Malaquias M.A., Stout C., Bastian Brenzinger B., Gosliner T.M. & Valdés Á. 2021. Molecular and morphological analyses reveal pseudocryptic diversity in *Micromelo undatus* (Bruguiere, 1792) (Gastropoda: Heterobranchia: Aplustridae). *Systematics and Biodiversity*, 0(0): 1–25.

Fritts-Penniman A.L., Gosliner T.M., Ngurah Mahardika G. & Barber P.H. 2020. Cryptic ecological and geographic diversification in coralassociated nudibranchs. *Mol. Phylogenet. Evol.* 144:106698. 10.1016/j.ympev.2019.106698.

Furfaro G. & Mariottini P. 2021a. "Looking at the Nudibranch Family Myrrhinidae (Gastropoda, Heterobranchia) from a Mitochondrial '2D Folding Structure' Point of View" *Life,* 11(6): 583. Available from https://doi.org/10.3390/life11060583

Furfaro G. & Mariottini P. 2021b. Nemesignis, a Replacement Name for Nemesis Furfaro & Mariottini, 2021 (Mollusca, Gastropoda, Myrrhinidae), Preoccupied by Nemesis Risso, 1826 (Crustacea, Copepoda). Life, 11. 809. 10.3390/life11080809.

García F.J. & Bertsch H. 2009. Diversity and distribution of the Gastropoda Opisthobranchia from the Atlantic Ocean: A global biogeographic approach. *Scientia Marina*, 73: 153-160.

García-García F.J., Domínguez M. & Troncoso J.S. 2008. *Opistobranquios de Brasil: descripción y distribución de opistobranquios del litoral de Brasil y del Archipiélago Fernando de Noronha*. Vigo: Feito, S.L., 215 pp.

García F.J. & Troncoso J.S. 2001. *Favorinus elenalexiae*, a new species (Opisthobranchia: Aeolidiidae) from the Eastern Pacific Ocean. *The Nautilus*, 115(2): 55-61.

Gavagnin M., Mollo E., Montanaro D., Ortea J. & Cimino G. 2000. Chemical studies on Caribbean Sacoglossans: Dietary relationships with green algae and ecological implications. *Journal of Chemical Ecology*, 26: 1563-1578.

Ghanimi H., Goddard J., Chichvarkhin A., Gosliner T.M., Jung D-W. & Valdés A. 2020a. An integrative approach to the systematics of the *Berthella californica* species complex (Heterobranchia: Pleurobranchidae). *Journal of Molluscan Studies*, 86: 186-200.

Ghanimi H., Schrödl M., Goddard J., Ballesteros M., Gosliner T.M., Buske Y. & Valdés A. 2020b. Stargazing under the sea: Molecular and morphological data reveal a constellation of species in the *Berthella stellata* (Risso, 1826) species complex (Mollusca, Heterobranchia, Pleurobranchidae). Mar. Biodivers, 50(11): 1-32.

Göbbeler K. & Klussmann-Kolb A. 2011. Molecular phylogeny of the Euthyneura (Mollusca, Gastropoda) with special focus on Opisthobranchia as a framework for reconstruction of evolution of diet. *Thalassas*, 27 (2): 121-154.

Goddard J.H.R. 2007. *Conualevia alba* from Monterey, California. *[Message in] Sea Slug Forum.* Australian Museum, Sydney. Available from http://www.seaslugforum.net/find/19683

Goddard J.H.R. & Hermosillo A. 2008. Developmental mode in opisthobranch molluscs from the tropical Eastern Pacific Ocean. *The Veliger*, 50: 83–96.

Goddard J.H.R. & Valdés A. 2015. *Reviving a cold case: two northeastern Pacific dendrodorid nudibranchs reassessed (Gastropoda: Opisthobranchia). The Nautilus*, 129(1):31–42.

Golestani H., Crocetta F., Padula V., Camacho-García Y., Langeneck J., Poursanidis D., Pola M., Yokeş M.B., Cervera J.L., Jung D-W., Gosliner T., Araya J.F., Hooker Y., Schrödl M. & Valdés A. (2019) The little Aplysia coming of age: from one species to a complex of species complexes in *Aplysia parvula* (Mollusca: Gastropoda: Heterobranchia). *Zoological Journal of the Linnean Society,* XX, 1–52.

Gonzalez L., Hanson D. & Valdés A. 2013. Molecular divergence between two sympatric species of *Dondice* (Mollusca: Nudibranchia) with distinct feeding specializations. *J Mar Biol Assoc U.K.*, 93:1887-93.

Goodheart J., Camacho-García Y., Padula V., Schrödl M., Cervera J., Gosliner T. & Valdés A. 2015. Systematics and biogeography of *Pleurobranchus* Cuvier, 1804, sea slugs (Heterobranchia: Nudipleura: Pleurobranchidae). Zoological Journal of the Linnean Society, 174: 322-362.

Goodheart J., Ellingson R., Vital X., Galvão H., McCarthy J., Medrano S., Bhave V., García-Méndez K., Jiménez L., López G., Hoover C., Awbrey J., De Jesus J., Gowacki W., Krug P. & Valdés A. 2016. Identification guide to the heterobranch sea slugs (Mollusca: Gastropoda) from Bocas del Toro, Panama. *Marine Biodiversity Records*, 9:1-31.

Gosliner T.M. 1980. Systematics and phylogeny of the Aglajidae (Opisthobranchia: Mollusca). *Zoological Journal of the Linnean Society*, 68: 325-360.

Gosliner T.M. & Bertsch H. 1988. A review of the genus *Berthella* (Opisthobranchia: Notaspidea) from the Pacific coast of North America. *Veliger*, 31:46–67.

Gosliner T.M. & Williams G. 1972. A new species of Chelidonura from Bahia San Carlos, Gulf of California, with a synonomy of the family Aglajidae. *The Veliger*, 14: 424-436. Available from https://biodiversitylibrary.org/page/42413643

Gosliner T.M., Behrens D.W. & Valdés Á. 2008. *Indo-Pacific nudibranchs and sea slugs.* Sea Challengers/California Academy of Sciences, Gig Harbor, San Francisco, CA, Gosliner T.M., Valdés Á. & Behrens D. 2015. *Nudibranch & Sea Slug Identification - Indo-Pacific*. Editorial: New World Publications Inc., U.S., 408 pp.

Hamatani I. 2000. A new recorded species of the genus *Spurilla* Bergh, 1864 from Osaka Bay, Middle Japan (Opisthobrachia, Aeolidacea). *Venus*, 59: 263–265.

Haefelfinger H.R. & Stamm R.A. 1958. *Limenandra nodosa* gen. et spec. nov. (Nudibranchia, Aeolidiidae prop.), un opisthobranche nouveau de la Mediterranee. *Vie Milieu*, 9:418–423.

Hermosillo A. 2003. Re: Aeolid from Ecuador. *[Message in] Sea Slug Forum*. Australian Museum, Sydney. Available from http://www.seaslugforum.net/find/10822

Hermosillo A. 2004. Opisthobranch mollusks of Parque Nacional de Coiba, Panama (tropical eastern Pacific). *The Festivus*, 36: 105-117.

Hermosillo A. & Camacho-García Y. 2006. A note on the opisthobranchs of Parque Nacional de Coiba, Panama (Tropical Eastern Pacific). *The Festivus*, Vol. 38(9): 95-98.

Hermosillo. A. & Valdés Á. 2007. Five new species of aeolid nudibranchs (Mollusca, Opisthobranchia) from the tropical eastern Pacific. *Amer. Malac. Bull.,* 22: 119-137.

Hermosillo A., Behrens D.W. & Rios E. 2006. *Opistobranquios de Mexico. Guia de babosas marinas del pacifico, Golfo de california y las islas oceanicas*. Guadalajara, Mexico: CONABIO, 144 pp.

Hildering J. & Miller G. 2007. *Berthella californica - mating & egg-laying. [Message in] Sea Slug Forum. Australian Museum, Sydney*. Available from http://www.seaslugforum.net/find/20109

Jensen K.R. 1981. Observations on feeding methods in some Florida ascoglossans. *Journal of Molluscan Studies, 47*: 190-199.

Jensen K. & Clark K.N. 1983. Annotated checklist of Florida ascoglossan Opisthobranchia. *Nautilus*, 97:1-13.

Johnson R. & Gosliner T. 2012. Traditional taxonomic groupings mask evolutionary history: A molecular phylogeny and new classification of the chromodorid nudibranchs. *PLoS ONE* 7(4): e33479.

Jörger K.M., Stöger I., Kano Y., Fukuda H., Knebelsberger T. & Schrödl M. 2010. On the origin of Acochlidia and other enigmatic euthyneuran gastropods and implications for the systematics of Heterobranchia. *BMC Evolutionary Biology*, 10, Art. 323.

Kay E.A. 1979. Hawaiian marine shells, reef and shore fauna of Hawaii, section 4: Mollusca. *Bernice P. Bishop Museum Special Publication*, 64(4).

Keen A.M. 1971. *Sea Shells of Tropical West America. Marine mollusks from Baja California, Mexico to Peru*. United States: Stanford University Press, 1080 pp.

Keppel E., Sigovini M. & Tagliapietra D. 2012. A new geographical record of *Polycera hedgpethi* Er. Marcus, 1964 (Nudibranchia: Polyceridae) and evidence of its established presence in the Mediterranean Sea, with a review of its geographical distribution. *Marine Biology Research*, 8(10): 969-981.

Kocot K.M., Halanych K.M. & Krug P.J. 2013. Phylogenomics supports Panpulmonata: Opisthobranch paraphyly and key evolutionary steps in a major radiation of gastropod molluscs. *Molecular Phylogenetics and Evolution*, 69, 764-771.

Korshunova T. & Martynov A. 2020. Consolidated data on the phylogeny and evolution of the family Tritoniidae (Gastropoda: Nudibranchia) contribute to genera reassessment and clarify the taxonomic status of the neuroscience models Tritonia and Tochuina. *PLOS ONE*, 15(11): e0242103. Available from https://doi.org/10.1371/journal.pone.0242103

Korshunova T., Picton B., Furfaro G. & Mariottini P. 2019. Multilevel fine-scale diversity challenges the 'cryptic species' concept. *Sci. Rep* **9,** 6732 Available from https://doi.org/10.1038/s41598-019-42297-5

Korshunova T., Martynov A., Bakken T., Evertsen J., Fletcher K., Mudianta W.I., Saito H., Lundin K., Schrödl M. & Picton B. 2017. Polyphyly of the traditional family Flabellinidae affects a major group of Nudibranchia: aeolidacean taxonomic reassessment with descriptions of several new families, genera, and species (Mollusca, Gastropoda). *ZooKeys* 717: 1–139. Available from https://doi.org/10.3897/zookeys.717.21885

Krug P.J. 2009. Not my "type": Larval dispersal dimorphisms and bet-hedging in opisthobranch life histories. *The Biological Bulletin*, 216: 355–372.

Krug P.J., Händeler K. & Vendetti J.E. 2011. Genes, morphology, development and photosynthetic ability support the resurrection of *Elysia cornigera* (Heterobranchia: Plakobranchoidea) as distinct from the 'solar–powered' sea slug, *E. timida. Invertebr Syst.*, 25:477-489.

Krug P.J., Vendetti J.E. & Valdés A. 2016. Molecular and morphological systematics of *Elysia* Risso, 1818 (Heterobranchia: Sacoglossa) from the Caribbean region. *Zootaxa*, 4148: 1-137.

Krug P.J., Berriman J. & Valdés A. 2018. Phylogenetic systematics of the shelled sea slug genus Oxynoe Rafinesque, 1814 (Heterobranchia: Sacoglossa), with integrative descriptions of seven new species. *Invertebrate Systematics*, 32, 950-1003.

Krug P.J., Vendetti J.E., Rodriguez A.K., Retana J.N., Hirano Y.M. & Trowbridge C.D. 2013. Integrative species delimitation in photosynthetic sea slugs reveals twenty candidate species in three nominal taxa studied for drug discovery, plastid symbiosis or biological control. *Mol Phylogenet Evol.*, 69:1101-119.

Krug P.J., Vendetti J.E., Ellingson R.A., Trowbridge C.D., Hirano Y.M. & Trathen D.Y. 2015. Species selection favors dispersive life histories in sea slugs, but higher peroffspring investment drives shifts to short-lived larvae. *Syst Biol.*, 64:983-99.

Lemche H. 1929. Gastropoda Opisthobranchiata. *The Zoology of the Faroes* 3: 1–35. Andr. Fred. Høst og søn. Lipej L., Acevedo I, Akel E., Anastasopoulou A., Angelidis A., Azzurro E., Castriota L., Çelik M., Cilenti L., Crocetta F., Deidun A., Dogrammatzi A., Falautano M., Fernández-Álvarez

F.A., Gennaio R., Insacco G., Katsanevakis S., Langeneck J., Lombardo B.M., Mancinelli G., Mytilineou Ch., Papa L., Pitacco V., Pontes M., Poursanidis D., Prato E., Rizkalla S.I., Rodríguez-Flores P.C., Stamouli C., Tempesti J., Tiralength O., Tirnetta S., Tsirintanis K., Turan C., Yaglioglu D., Zaminos G. & Zava B. 2017. "New Mediterranean Biodiversity Records". *Mediterranean Marine Science*, 18: 179-201.

Macedo M.C.C., Macedo M.I.C. & Borges, J.P. 1999. *Conchas Marinhas de Portugal.* Lisboa: Verbo, 516 pp.

Macfarland F.M. 1909. *The opisthobranchiate Mollusca of the Branner-Agassiz expedition to Brazil.* Leland Stanford Junior University Publications, University Series (2):1–104, pls. 1–19.

MacNae W. & Kalk M. 1958. *A natural history of Inhaca Island, Mozambique*. Witwatersrand Univ. Press, Johannesburg. I-IV, 395 pp.

Malaquias M.A.E. 2014. New data on the heterobranch gastropods ('opisthobranchs') for the Bahamas (tropical Western Atlantic Ocean). *Marine Biodiversity Records*, 7: e27.

Malaquias M.A.E. & Reid D.G. 2008. Systematic revision of the living species of Bullidae (Mollusca: Gastropoda: Cephalaspidea), with a molecular phylogenetic analysis. *Zoological Journal of the Linnean Society*, 153: 453-543.

Malaquias M.A.E., Calado G., Padula V., Villani G. & Cervera J. 2009. Molluscan diversity in the North Atlantic Ocean: new records of opisthobranch gastropods from the Archipelago of the Azores. *JMBA2 - Biodiversity Records*, e38.

Marcus Er. 1955. Opisthobranchia from Brazil. Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo. *Zoologia*, 20: 89–200, pl. 1–30.

Marcus Er. 1957. On Opisthobranchia from Brazil (2). *Journal of the Linnean Society of London Zoology*, 43: 390-486.

Marcus Er. 1961. Opisthobranch Mollusks from California. *The Veliger*, 3: 1–85.

Marcus Er. & Marcus Ev. 1970. Opisthobranchs from Curaçao and faunistically related regions. *Studies on the Fauna of Curaçao and other Caribbean Islands*, 33: 1-129.

Marcus Ev. 1972. On some Acteonidae (Gastropoda, Opisthobranchia). *Papéis Avulsos de Zoologia*, 25:167-188.

Marcus Ev. 1974. On some Cephalaspidea (Gastropoda: Opisthobranchia) from the western and middle Atlantic warm waters. *Bulletin of Marine Science*, 24: 300-371.

Marcus Ev. 1976. Opisthobranchia von Santa Marta, Colombia. *Studies on the Neotropical Fauna & Environment*, 11: 119-150.

Marcus Ev. 1977. An annotated checklist of the Western Atlantic warm water Opisthobranchs. *Journal of Molluscan Studies*, 4 (Supplement): 1-22.

Marcus Ev. & Hughes H.P.I. 1974. Opisthobranchs mollusks from Barbados. *Bulletin of Marine Science*, 24: 498-532.

Marcus Ev. & Marcus Er. 1960. Opisthobranchs from American Atlantic warm waters. *Bulletin of Marine Science*, 10: 129-203.

Marcus Ev. & Marcus Er. 1962. Opisthobranchs from Florida and the Virgin Islands. *Bulletin of Marine Science*, 12: 450-488.

Marcus Ev. & Marcus Er. 1967. Opisthobranchs from the gulf of California. *Studies in Tropical Oceanography*, 6:1-137.

Mariño J., Farfán E. & Caballer M. 2011. Primer registro de *Dondice parguerensis* (Mollusca: Favorinidae) para Venezuela. *Revista Mexicana de Biodiversidad*, 82:709-12.

Martynov A.V. & Korshunova T.A. 2012. *Opisthobranch molluscs of Vietnam (Gastropoda: Opisthobranchia)*. In: Britayev T.A. & Pavlov D.S. (Eds.). Benthic fauna of the Bay of Nhatrang, Southern Vietnam. Vol. 2. Moscow, KMK: pp 142-257.

Massemin D., Lamy D., Pointier J.P. & Gargominy O. 2009. *Coquillages et escargots de Guyane. Seashells and snails from French Guiana*. Biotope editions, Meze (Collection Parthenope). Francia: Museum nacional d'Histoire naturelle, Paris, 1188 pp.

Matsuda S. & Gosliner T.M. 2018. Molecular phylogeny of *Glossodoris* (Ehrenberg, 1831) nudibranchsand related genera reveals cryptic and pseudocryptic species complexes. *Cladistics*, 34: 41–56.

McDonald G.R. 1983. A review of the nudibranchs of the California coast. *Malacologia*, 24, 114-276.

McDonald G.R. & Nybakken J.W. 1997. List of the worldwide food habits of nudibranchs. *Veliger*, 40:157-9.

McDonald G.R. & Nybakken J.W. 1999. A worldwide review of the food of nudibranch mollusks. II. The suborder Dendronotacea. *Veliger*, 42:62–6.

Medrano S., Krug P., Gosliner T. Kumar A. & Valdés Á. 2018. Systematics of Polybranchia Pease, 1860 (Mollusca: Gastropoda: Sacoglossa) based on molecular and morphological data. *Zoological Journal of the Linnean Society*, 2018, XX, 1-40.

Meyer K.B. 1977. Dorid nudibranchs of the Caribbean coast of the Panama Canal Zone. *Bulletin of Marine Science*, 27: 299-307.

Middlebrooks M.L., Bell S.S., Curtis N.E. & Pierce S.K. 2014. Atypical plant–herbivore association of algal food and a kleptoplastic sea slug (Elysia clarki) revealed by DNA barcoding and field surveys. *Mar Biol.*, 161:1429-40.

Millen S. & Hermosillo A. 2012. Three new species of aeolid nudibranchs (Opisthobranchia) from the Pacific coast of Mexico, Panama and the Indopacific, with a redescription and redesignation of a fourth species. *The Veliger*. 51(3): 145-164.

Miloslavich P., Díaz J.M., Klein E., Alvarado J.J., Díaz C., Gobin J., Escobar-Briones E., Cruz-Motta J.J., Weil E., Cortés J., Bastidas A.C., Robertson R., Zapata F., Martín A., Castillo J., Kazandjian A. &

Ortiz M. 2010. Marine Biodiversity in the Caribbean: Regional Estimates and Distribution Patterns. *PLoS ONE*, 5: e11916.

Möbius K. 1880. *Beitrage zur meeresfauna der Inseln Mauritius und der Seychellen*. Berlin, Germany, 352 pp.

Moretzsohn F., Brenner J., Michaud P., Tunnell J.W. & Shirley T. 2011. *Biodiversity of the Gulf of Mexico Database (BioGoMx).* Version 1.0. Corpus Christi: Harte Research Institute for Gulf of Mexico Studies, Texas A&M University-Corpus Christi, 1393 pp.

Nakano R. 2004. *Opisthobranchs of Japan Islands*. Tokyo: Rutles, Inc, 304 pp.

Odhner N. 1932. Beiträge zur malakozoologie der Kanarischen Inseln, Lamellibranchien, Cephalopoden, Gastropoden. *Arkiv för Zoologi*, 23A(14): 1–116.

Olsson A. & McGinty T.L. 1958. Recent marine mollusks from the caribbean coast of Panama with the description of some new genera and species. *Bulletins of American Paleontology*, 39(177): 5-59.

Orbigny A.d'. 1835–1843. *Voyage dans l'Amérique Méridionale (le Brésil, la République Orientale de l'Uruguay, la République Argentine, La Patagonie, la République du Chili, la République de Bolivia, la République du Pérou*), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833. Volume 5, Partie 3: Mollusques. Bertrand, Paris, 258 pp.

Ornelas-Gatdula E., DuPont A. & Valdés A. 2011. The tail tells the tale: taxonomy and biogeography of some Atlantic *Chelidonura* (Gastropoda: Cephalaspidea: Aglajidae) inferred from nuclear and mitochondrial gene data. *Zoological Journal of the Linnean Society*, 163: 1077-95.

Ornelas-Gatdula E., Camacho-García Y., Schrödl M., Padula V., Hooker Y. & Gosliner T.M. 2012. Molecular systematics of the '*Navanax aenigmaticus*' species complex (Mollusca, Cephalaspidea): coming full circle. *Zoologica Scripta*, 41: 374-85.

Ortea J.A. 1995. Estudio de las especies atlánticas de *Paradoris* Bergh, 1884 (Mollusca: Nudibranchia: Discodorididae) recolectadas en las Islas Canarias. *Avicennia*, 3: 5–27.

Ortea J.A. 2001. El género *Doto* Oken, 1815 (Mollusca: Nudibranchia) en el mer Caribe: Historia natural y descripción de nuevas especies. *Avicennia*. Supplement 3: 1-46.

Ortea J.A. & Llera E. 1981. Un nuevo dórido (Mollusca: Nudibranchiata) de la isla Isabel, Nayarit, México. *Iberus*, 1: 47-51.

Ortea J.A. & Moro L. 2017. Nuevas citas y nuevos datos sobre las lesmas do mar (Mollusca: Heterobranchia) de las islas de Cabo Verde, con el restablecimiento de *Tritonia pallescens* (Eliot, 1906). *Avicennia*, 21: 1-10.

Ortea J.A., Caballer M. & Espinosa J. 2003. Nuevos Aeolidaceos (Mollusca: Gastropoda) de Costa Rica. *Avicennia,* 16: 129-142.

Ortea J.A., Moro L. & Caballer M. 2014. Contribución al estudio de la famila Pleurobranchidae Gray, 1827 (Mollusca: Opisthobranchia) en la Macaronesia y las islas Galapagos. *Vieraea*, 42: 117-148.

Ortea J., Moro L. & Espinosa J. 2009. El género *Okenia* Menke, 1830 (Mollusca: Nudibranchia) en las islas Canarias con notas sobre *Okenia zoobotryon* (Smallwood, 1910) una especie en controversia permanente. *Vieraea*, 37: 75-83. Available from http://www.azoresbioportal.angra.uac.pt/files/publicacoes_06%20El%20genero%20Okenia%20en%20Canarias%20Vieraea37%202009.pdf

Ortea J.A., Moro L., Bacallado J. & Herrera R. 2000. Catálogo actualizado de los moluscos opistobranquios de las islas canarias. *Revista de la Academia Canaria de Ciencias*, XII. 105-134.

Ortea J.A., Espinosa J., Buske Y. & Caballer M. 2013. Additions to the inventory of the sea slugs (Opisthobranchia and Sacoglossa) from Guadeloupe (Lesser Antilles, Caribbean Sea). *Revista de la Academia Canaria de Ciencias*, 25:163-94.

Ortigosa D., Lemus-Santana E. & Simöes N. 2015. New records of 'opisthobranchs' (Gastropoda: Heterobranchia) from Arrecife Alacranes National Park, Yucatan, Mexico. *Marine Biodiversity Records*, 8: e117.

Padula V. & Valdés Á. 2012. Phylogeny and Biogeography of *Paradoris* (Nudibranchia, Discodorididae), with the Description of a New Species from the Caribbean Sea. *The Veliger*, 51(3):165-176.

Padula V., Bahia J., Stöger I., Camacho-García Y., Malaquias M.A.E., Cervera J.L. & Schrödl M. 2016. A test of color-based taxonomy in nudibranchs: molecular phylogeny and species delimitation of the *Felimida clenchi* (Mollusca: Chromodorididae) species complex. *Molecular Phylogenetics and Evolution*, vol. 103: 215-229. Available from http://dx.doi.org/10.1016/j.ympev.2016.07.019

Parera A., Pontes M., Salvador X. & Ballesteros M. 2020. Sea slugs (Mollusca, Gastropoda, Heterobranchia) the other inhabitants of the city of Barcelona (Spain). *Butlleti de la Institució catalana d'Historia Natural*, 84: 75-100.

Paz-Sedano S., Tanduo V., Yonow N., Yokeş M.B., Kletou D. & Crocetta F. 2019. *Baeolidia moebii* Bergh, 1888 (Mollusca: Gastropoda: Nudibranchia) is spreading in the eastern Mediterranean Sea. *Regional Studies in Marine Science.* 32: 100830.

Pease W.H. 1860. Descriptions of new species of Mollusca from the Sandwich Islands. *Proceedings of the Zoological Society of London*. 28: 18-36, 141-148.

Pereira F.R., Santos M., Williams D., Andersen R., Padula V., Ferreirad A. & Berlinck R. 2014. Rodriguesic Acids, Modified Diketopiperazines from the Gastropod Mollusc Pleurobranchus areolatus. *Journal of the Brazilian Chemical Society*, 25: 788-794.

Pierce S.K., Massey S.E., Hanten J.J. & Curtis N.E. 2003. Horizontal transfer of functional nuclear genes between multicellular organisms. *Biol Bull.*, 204: 237-40.

Pittman C. & Fiene P. 2012. *Baeolidia nodosa*. [Message in] Sea Slugs of Hawaii. Available from http://seaslugsofhawaii.com/species/Baeolidia-nodosa-a.html.

Pola M., Camacho-García Y.E. & Gosliner T.M. 2012. Molecular data illuminate cryptic nudibranch species: the evolution of the Scyllaeidae (Nudibranchia: Dendronotina) with a revision of *Notobryon*. *Zoological Journal of the Linnean Society* 165: 311-336.

Pola M., Sánchez-Benítez M. & Ramiro B. 2014. The genus *Polycera* Cuvier, 1817 (Nudibranchia: Polyceridae) in the Eastern Pacific Ocean, with redescription of *Polycera alabe* Collier & Farmer, 1964. *Journal of Molluscan Studies*, 80: 551–561 and description of a new species.

Poorman F.L. & Poorman L.H. 1978. Additional molluscan records from Bahia de los Angeles, Baja California Norte. *The Veliger*, 20: 369–374.

Poppe G.T. & Goto Y. 1991. *European seashells (Polyplacophora, Caudofoveata, Solenogastra, Gastropoda)*, Vol. 1. Wiesbaden: Christa Hemmen, 352 pp.

Price R., Gosliner T. & Valdés A. 2011. Systematics and Phylogeny of *Philine* (Gastropoda: Opisthobranchia), with Emphasis on the *Philine aperta* Species Complex. *The Veliger*, 51(2): l-58.

Princz D. 1982. Lista y bibliografía de los gastropodos marinos vivos de los mares de Venezuela, Trinidad e Islas de Sotavento. *Boletín de la Sociedad Venezolana de Ciencias Naturales*, 37 (140):103-147.

Redfern C. 2001. *Bahamian Seashells: a Thousand Species from Abaco, Bahamas*. Bahamianseashells.com Inc: Boca Raton, Florida. 1-280.

Ríos E.C. 1985. *Sea Shells of Brazil*. Brazil: Fundacao Cidade do Rio Grande, Fundagao Universidade do Rio Grande, Museu Oceanografico, 328 pp.

Ríos E.C. 2009. *Compendium of Brazilian Sea Shells*. Brazil: Evangraf, Rio Grande, 668 pp.

Rosenberg G., Moretzsohn F. & García E.F. 2009. Gastropoda (Mollusca) of the Gulf of Mexico. In Felder, D.L. & D.K. Camp (eds.), Gulf of Mexico–Origins, Waters, and Biota. United States: Texas A&M Press, College Station, Texas, pp 579-699.

Rudman W.B. 1999a. *Lomanotus vermiformis* Eliot, 1908. *[In] Sea Slug Forum*. Australian Museum, Sydney. Available from http://www.seaslugforum.net/find/lomaverm

Rudman W.B. 1999b. *Umbraculum mediterraneum* (Lamarck, 1819). *[In] Sea Slug Forum*. Australian Museum, Sydney. Available from http://www.seaslugforum.net/factsheet/umbrmedi

Rudman W.B. 1999c. *Stylocheilus longicauda & Stylocheilus citrina* Nomenclatural discussion. *[In] Sea Slug Forum*. Australian Museum, Sydney. Available from http://www.seaslugforum.net/find/stylnome

Rudman W.B. 2002 *Phyllaplysia padinae* Williams & Gosliner, 1973. *[In] Sea Slug Forum*. Australian Museum, Sydney. Available from http://www.seaslugforum.net/factsheet/phylpadi

Rudman W.B. 2003. Comment on *Lobiger souverbii* from Bahia de Banderas by Alicia Hermosillo. *[Message in] Sea Slug Forum*. Australian Museum, Sydney. Available from http://www.seaslugforum.net/find/9209

Rudman W.B. 2005. *Hypselodoris bayeri* (Marcus & Marcus, 1967). [In] Sea Slug Forum. Australian Museum, Sydney. Available from http://www.seaslugforum.net/factsheet/hypsbaye

Rudman W.B. 2009. *Oxynoe panamensis* Pilsbry & Olsson, 1943. *[In] Sea Slug Forum*. Australian Museum, Sydney. Available from http://www.seaslugforum.net/factsheet/oxynpana

San Martín G., López E., Redondo M.S., Capa M., Cladera P. & Laborda A.J. 1997. *El bento marino del Parque Nacional de Coiba (Panamá)*. In S. Castroviejo (ed.). Flora y Fauna del Parque Nacional de Coiba (Panamá), pp p. 33-55.

Santander M. & Valdés Á. 2013. Genetic structure of *Polycera alabe* and *P. atra* (Mollusca: Opistobranchia: Nudibranchia) in the Pacific coast of North America. *Bull. Southern California Acad. Sci.,* 112(3): 176–184.

Sanvicente-Añorve L., Solís-Weiss V., Ortigosa J., Hermoso-Salazar M. & Lemus-Santana E. 2012. Opisthobanch fauna from the National Park Arraecife Alacranes, southern Gulf of Mexico. *Cah. Biol. Mar.*, 53: 447-460.

Schrödl M. 2000. Revision of the nudibranch genus Cadlina (Gastropoda: Opisthobranchia) from the Southern Ocean. *Journal of the Marine Biological Association of the United Kingdom*, 80: 299-309.

Schrödl M., Jörger K., Klussmann-Kolb A. & Wilson N.G. 2011. Bye bye "Opisthobranchia"? A review on the contribution of mesopsammic sea slugs to euthyneuran systematics. *Thalassas*, 27: 101-112.

Skoglund C. 2002. Panamic Province molluscan literature. Additions and changes from 1971 through 2001. III Gastropoda. *The Festivus* 23(supplement): i–xi, 1-286.

Spencer H.G., Marshall B.A. & Willan R.C. 2002. *Phylum Mollusca: clams, snails, chitons, squids, octopuses and kin*. In: Gordon, D.P. (ed.) New Zealand inventory of biodiversity. Volume one. Kingdom Animalia: Radiata, Lophotrochozoa, Deuterostomia. Canterbury University Press, Christchurch, pp .161-254.

Stearns R.E.C. 1897. Description of a new species of Actaeon from the Quaternary bluffs at Spanish Bight, San Diego, California. *Proceedings of the United States National Museum*, 21:297-299.

Streftaris N., Zenetos A. & Papathanassiou E. (2005. Globalisation in marine ecosystems: the story of non-indigenous marine species across European seas. Oceanogr. *Mar. Biol. Ann. Rev.*, 43: 419-453.

Strong A.M. & Hertlein L.G. 1939. *Marine mollusks from Panama collected by the Allan Hancock Expedition to the Galapagos Islands, 1931-1932. Allan Hancock Pacific Expeditions*, 2: 177-246.

Templado J., Luque A. A. & Ortea J. 1987. A new species of Aegires Lovén, 1844 (Opisthobranchia, Doridacea, Aegiretidae) from the Caribbean Sea: *Aegires ortizi* n. sp. with comparative descriptions of the North Atlantic species of this genus. *The Veliger*. 29(3): 303-307.

Tejera V.H., Avilés M.C. & Córdoba D.E. 2016. *Moluscos intermareales del Distrito de Aguadulce*. Panama: Imprenta Color Group International, 184 pp.

Thompson T.E. 1977. Jamaican Opisthobranch mollusks I. *Journal of Molluscan Studies*, 43: 93-140.

Thompson T.E. 1981. Redescription of a rare north Atlantic doridacean nudibranch, *Aegires sublaevis* Odhner. *The Veliger,* 23(4): 315–316.

Thompson T.E. & Brown G.H. 1984. Biology of Opisthobranch Molluscs, Volume 2. Ray Society, London, 229 pp.

Thompson T.E. & Jaklin A. 1988. Eastern Mediterranean Opisthobranchia: Elysiidae (Sacoglossa: Ascoglossa). *Journal of Molluscan Studies*, 54: 59-69.

Toll L. & Ballesteros M. 2017. "Opistobranquios" (Mollusca: Gastropoda) de la colección malacológica Lluis Dantart. *Spira*, 6:171-184.

Turgeon D., Quinn Jr. J.F., Bogan A.E., Coan E.V., Hochberg F.G. & Lyons W.G. 1998. *Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks*. 2nd ed. United States: American Fisheries Society Special Publication, 536 pp.

Turk T. & Furlan B. 2011. New records of Indo-Pacific and Atlantic mollusc species (Opisthobranchia) in the Eastern Mediterranean and Adriatic Sea. *Annales Series Historia Naturalis*, 21, 5–10.

Turner E.M., Evans E. & Abgarian C. 2012. *Cayman nudibranchs. A photographic collection of seaslugs found by the authors while diving Grand Cayman*. Turner, Evans & Abgarian, C. (eds.), Gran Cayman, Cayman Islands, 216 pp.

Uribe R. & Pacheco A. 2012. First record of *Spurilla neapolitana* (Mollusca: Nudibranchia: Aeolidiidae) on the central coast of Peru (Humboldt Current Upwelling Ecosystem). *Marine Biodiversity Records*, 5. 10.1017/S1755267211001138.

Uribe R.A., Nakamura K., Indacochea A., Pacheco A.S., Hooker Y. & Schrödl M. 2013. A review on the diversity and distribution of opisthobranch gastropods from Peru, with the addition of three new records (Gastropoda, Heterobranchia). *Spixiana*, 36: 43–60.

Valdés Á. 2002. How many species of *Hexabranchus* (Opisthobranchia: Dorididae) are there? *Molluscan Research*, 22(3): 289-301.

Valdés Á. 2003. "Preliminary Molecular Phylogeny of the Radula-less Dorids (Gastropoda: Opisthobranchia), Based on 16S mtDNA Sequence Data". *J. Moll. Stud.*, 69(1): 75–80.doi:10.1093/mollus/69.1.75.

Valdés Á. 2004. Tropical western Atlantic species of *Diaulula* Bergh,1878 (Mollusca, Nudibranchia) with the description of a new species. *Contributions in Science*, 501: 1-7.

Valdés Á. 2005. *Subclass Opisthobranchia s.* 1. In: Rolán, E. *Malacological Fauna from The Cape Verde Archipelago*. Part 1, *Polyplacophora and Gastropoda*. ConchBooks. Klaus & Christina Groh, Mainzer Str. 25, Germany, pp 201-248.

Valdés Á. 2019. Northeast Pacific benthic shelled sea slugs. *Zoosymposia, 13: 242–304.*

Valdés Á. & Camacho-García Y. 2004. “Cephalaspidean” Heterobranchs (Gastropoda) from the Pacific Coast of Costa Rica. *Proceedings of the California academy of Sciences*, 55(26): 459-497.

Valdés Á. & Hamann J. 2008. Two new species of *Doriopsilla* from the tropical Western Atlantic with remarks on Cariopsillidae Ortea & Espinosa, 2005. *Veliger*, 50:210-218.

Valdés Á. & Ortea J. 1997. Review of the genus *Doriopsilla* Bergh, 1880 (Gastropoda: Nudibranchia) in the Atlantic Ocean. *Veliger*, 40: 240-54.

Valdés Á., Cadien D.B. & Gosliner T.M. 2016a. Philinidae, Laonidae and Philinorbidae (Gastropoda: Cephalaspidea: Philinoidea) from the northEastern Pacific Ocean and the Beaufort Sea (Arctic Ocean). *Zootaxa*. 4147(5): 501-537.

Valdés Á., Medrano S. & Bhave V. 2016b. A new species of *Cuthona* Alder and Hancock, 1855 (Gastropoda: Heterobranchia: Nudibranchia: Tergipedidae) from the Caribbean Sea. *The Nautilus, 130(2):72-78.*

Valdés Á., Hamann J., Behrens D.W. & DuPont A. 2006. *Caribbean Sea Slugs: A field guide to the opisthobranch mollusks from the tropical northWestern Atlantic*. United States: Gig Harbor, Sea Challengers Natural History Books, 289 pp.

Valdés Á., Breslau E., Padula V., Schrödl M., Camacho-García Y., Malaquias M.A., Alexander J., Bottomley M., Vital X., Hooker Y. & Gosliner T. 2017. Molecular and morphological systematics of *Dolabrifera* Gray, 1847 (Mollusca: Gastropoda: Heterobranchia: Aplysiomorpha). *Zoological Journal of the Linnean Society*, 184(1); 31-65.

Vega A. & González A. 2002. Moluscos del pacífico veragüense, parte II (Gasteropoda). *Tecnociencia*, 4(1): 23-45.

Vermeij G.J. & Rosenberg G. 1993. Giving and receiving: the tropical Atlantic as donor and recipient region for invading species. *American Malacological Bulletin*, 10: 181–194.

Vine P. 1986. *Red Sea Invertebrates*. Immel Publishing, Londron, 224 pp.

Willan RC. 1984. A review of diets in the Notaspidea (Mollusca: Opisthobranchia). *J Malacological Soc Aust,* 6:125-42.

Willan R.C. 2006. Globe-trotting nudibranch arrives in Australia. *Australian shell news,* 130: 1–3.

WoRMS Editorial Board. 2021. World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. Accessed 2020/X/09.

Yidi E. & Sarmiento V. 2011. *Colombian Seashells from the Caribbean Sea*. Italia: L’Informatore Piceno, Ancona, 400 pp.

Young D.K. 1967. New records of Nudibranchia from the Central and West-Central Pacific with a description of a new species. *The Veliger*, 10:159-173.

Zamora-Silva A. & Malaquias M.A.E. 2018. Molecular phylogeny of the Aglajidae head-shield sea slugs (Heterobranchia: Cephalaspidea): new evolutionary lineages revealed and proposal of a new classification. *Zoological Journal of the Linnean Society*, 183(1): 1-51. Available from https://doi.org/10.1093/zoolinnean/zlx064/4584517

Zetek J. 1918. Los moluscos de la República de Panama, *REVISTA NUEVA*, Números 1 y 2: 1-37.

Table 1. List of the heterobranch sea slugs of the Panamanian coasts
Legend: C = Caribbean, P = Pacific, AF = amphiatlantic.

Actenimorpha
1. *Acteon traskii* Stearns, 1898 P
2. *A. panamensis* Dall, 1908 P
3. *A. candens* Rehder, 1939 C
4. *Crenilabium venustus* (d'Orbigny, 1840) P
5. *Rictaxis punctocaelatus* (Carpenter, 1864) P
6. *Japonactaeon punctostriatus* (C.B. Adams, 1840) C
7. *Micromelo undatus* (Bruguière, 1792) C

Pleurobranchida
8. *Pleurobranchus areolatus* Mörch, 1863 C
9. *P. digueti* Rochebrune, 1895 P
10. *Berthella martensi* (Pilsbry, 1896) P
11. *B. californica* (Dall, 1900) P
12. *B. agassizii* (MacFarland, 1909) P, C
13. *B. nebula* Ghanimi, Schrödl, Goddard, Ballesteros, Gosliner, Buske & Valdés, 2020 C
14. *Berthella* sp. 1 P
15. *Berthellina quadridens* (Mörch, 1863) C
16. *B. ilisima* Ev. Marcus & Er. Marcus, 1967 P
17. *B.* grovesi Hermosillo & Valdés, 2008 P

Nudibranchia Doridina
18. Dorid sp. 1 P
19. Dorid sp. 2 P
20. Dorid sp. 3 P
21. *Doriopsis granulosa* Pease, 1860 P
22. *Aphelodoris antillensis* Bergh, 1879 C
23. *Conualevia alba* Collier & Farmer, 1964 P
24. *Atagema notacristata* Camacho-García & Gosliner, 2008 P
25. *Jorunna spazzola* (Er. Marcus, 1955) C
26. *J. tempisquensis* Camacho-García & Gosliner, 2008 P
27. *Jorunna* sp. 1 P
28. *Discodoris branneri* MacFarland, 1909 C
29. *Discodoris ketos* (Ev. Marcus & Er. Marcus, 1967) P
30. *Discodoris* sp. 1 P
31. *Platydoris angustipes* (Mörch, 1863) C
32. *Thordisa* sp. 1 P
33. *Diaulula aurila* (Marcus & Marcus, 1967) P
34. *D. phoca* (Ev. Marcus & Er. Marcus, 1967) C
35. *D. nayarita* (Ortea & Llera, 1981) P
36. *Rostanga pulchra* MacFarland, 1905 P
37. *Paradoris mulciber* (Ev. Marcus, 1971) C
38. *P. adamsae* Padula & Valdés, 2012 C
39. *Carminodoris bramale* (Fahey & Gosliner, 2003) P
40. *Geitodoris planata* (Alder & Hancock, 1846) C, AF
41. *G. immunda* Bergh, 1894 C
42. *Sclerodoris prea* (Ev. Marcus & Er. Marcus, 1967) C
43. *Taringa aivica* Ev. Marcus & Er. Marcus, 1967 P
44. *Polycera alabe* Collier & Farmer, 1964 P
45. *P. hedgpethi* Er. Marcus, 1964 P
46. *P. anae* Pola, Sánchez-Benítez & Ramiro, 2014 P
47. *Polycera* sp. 1 C
48. *Polycerella glandulosa* Behrens & Gosliner, 1988 P
49. *Martadoris oliva* (K.B. Meyer, 1977) C
50. *Limacia janssi* (Bertsch & Ferreira, 1974) P
51. *Tyrinna evelinae* (Er. Marcus, 1958) C, P, AF
52. *Felimare agassizii* (Bergh, 1894) P
53. *F. bayeri* Ev. Marcus & Er. Marcus, 1967 C
54. *F. kempfi* (Ev. Marcus, 1971) C
55. *F. ruthae* (Ev. Marcus & Hughes, 1974) C
56. *F. fregona* (Ortea & Caballer, 2013) C
57. *Felimida clenchi* (Russell, 1935) C
58. *F. baumanni* (Bertsch, 1970) P
59. *Felimida sphoni* Ev. Marcus, 1971 P
60. *F. marislae* (Bertsch, 1973) P
61. *F. grahami* (T.E. Thompson, 1980) C
62. *Chromolaichma dalli* (Bergh, 1879) P
63. *Ch. sedna* (Ev. Marcus & Er. Marcus, 1967) P
64. *Ch. cf. sedna* (Ev. Marcus & Er. Marcus, 1967) C
65. *Ch. edmundsi* (Cervera, García-Gómez & Ortea, 1989) C, P
66. *Mexichromis tura* (Marcus & Marcus, 1967) P
67. *M. antonii* (Bertsch, 1976) P
68. *Hexabranchus morsomus* Ev. Marcus & Er. Marcus, 1962 C
69. *Aldisa* sp. 1 C, P
70. *Cadlina sparsa* (Odhner, 1921) P
71. *C. rumia* Er. Marcus, 1955 C, AF
72. C. *luarna* (Er. Marcus & Ev. Marcus, 1967) P
73. *Cadlina* sp. 1 P
74. *Aegires sublaevis* Odhner, 1932 C, AF
75. *A. ortizi* Templado, Luque & Ortea, 1987 C
76. *Okenia evelinae* Er. Marcus, 1957 C, AF
77. *Trapania inbiotica* Camacho-García & Ortea, 2000 P
78. *Trapania* sp. 1 C
79. *Phyllidiella molaensis* (Meyer, 1977) C
80. *Dendrodoris fumata* (Rüppell & Leuckart, 1830) P
81. *D. krebsii* (Mörch, 1863) C
82. *D. albobrunnea* Allan, 1933 P
83. *Doriopsilla janaina* Er. Marcus & Ev. Marcus, 1967 P
84. *D. nigrolineata* Meyer, 1977 C
85. *Doriopsilla rowena* Er. Marcus & Ev. Marcus, 1967 P

Nudibranchia Cladobranchia
86. *Bornella sarape* Bertsch, 1980 P
87. *Armina californica* (J.G. Cooper, 1863) P
88. *Armina* sp. 1 P
89. *Histiomena marginata* (Mörch, 1859) P
90. *Tritonia exsulans* Bergh, 1894 P
91. *Tritonicula bayeri* (Ev. Marcus & Er. Marcus, 1967) C
92. *T. pickensi* (Marcus & Marcus, 1967) P
93. *T. myrakeenae* (Bertsch & Mozqueira, 1986) P
94. *T. hamnerorum* (Gosliner & Ghiselin, 1987) C
95. *Marionia kinoi* Angulo & Bertsch, 2013 P
96. *Doto caramella* Er. Marcus, 1957 C
97. *D. chica* Ev. Marcus & Er. Marcus, 1960 C
98. *D. lancei* Ev. Marcus & Er. Marcus, 1967 P

99. *D. wildei* Er. Marcus & Ev. Marcus, 1970 C
100. *D. escatllari* Ortea, Moro & Espinosa, 1998 C, AF
101. *Doto* sp. 1 P
102. *Doto* sp. 2 C
103. *Crosslandia daedali* Poorman & Mulliner, 1981 P
104. *Notobryon panamicum* Pola, Camacho-García & Gosliner, 2012 P
105. *Lomanotus vermiformis* Eliot, 1908 C, P
106. *Flabellina engeli* Ev. Marcus & Er. Marcus, 1968 C
107. *F. bertschi* Gosliner & Kuzirian, 1990 P
108. *Coryphellina marcusorum* (Gosliner & Kuzirian, 1990) C, P
109. *Edmundsella vansyoci* (Gosliner, 1994) P
110. *Kynaria cynara* (Ev. Marcus & Er. Marcus, 1967) P
111. *Tenellia lugubris* (Bergh, 1870) P
112. *T. tina* (Er. Marcus, 1957) C
113. *T. lizae* Angulo-Campillo & Valdés, 2003 P
114. *Tenellia behrensi* Hermosillo & Valdés, 2007 P
115. *T. destinyae* Hermosillo & Valdés, 2007 P
116. *T. luciae* Valdés, Medrano & Bhave, 2016 C
117. *Tenellia* sp. 1 P
118. *Eubranchus conicla* (Er. Marcus, 1958) C
119. *E. cucullus* Behrens, 1985 P
120. *Eubranchus* sp. 1 P
121. *Eubranchus* sp. 2 P
122. *Unidentia angelvaldesi* Millen & Hermosillo, 2012 P
123. *Spurilla braziliana* MacFarland, 1909 C, P
124. *Berghia creutzbergi* Er. Marcus & Ev. Marcus, 1970 C
125. *Berghia rissodominguezi* Muniain & Ortea, 1999 C
126. *Baeolidia moebii* Bergh, 1888 P
127. *Limenandra nodosa* Haefelfinger and Stamm, 1958 C, AF
128. *Limenandra cf. confusa* Carmona, Pola, Gosliner & Cervera, 2014, P
129. *Anteaeolidiella chromosoma* (Cockerell & Eliot, 1905) P
130. *A. lurana* (Ev. Marcus & Er. Marcus, 1967) C, AF
131. *A. ireneae* Carmona, Bhave, Salunkhe, Pola, Gosliner & Cervera, 2014 P
132. *Bulbaeolidia alba* (Risbec, 1928) P
133. *Favorinus elenalexiae* García F. & Troncoso, 2001 P
134. *Phidiana lynceus* Bergh, 1867 C y AF
135. *P. lascrucensis* Bertsch & Ferreira, 1974 P
136. *Noumeaella isa* Ev. Marcus & Er. Marcus, 1970 P
137. *N. rubrofasciata* Gosliner, 1991 P
138. *Herviella* sp. 1 P
139. *Nanuca sebastiani* Er. Marcus, 1957 C
140. *Dondice occidentalis* Engel, 1925 C
141. *D. parguerensis* Brandon & Cutress, 1985 C
142. *Palisa papillata* Edmunds, 1964 C
143. *Bajaeolis bertschi* Gosliner & Behrens, 1986 P
144. *Hermosita hakunamatata* (Ortea, Caballer & Espinosa, 2003) P

Umbraculida

145. *Tylodina fungina* Gabb, 1865 P
146. *Umbraculum ovale* (Carpenter, 1856) P

Cephalaspidea

147. *Bulla solida* Gmelin, 1791 C
148. *B. occidentalis* A. Adams, 1850 C
149. *B. punctulata* A. Adams in Sowerby, 1850 P
150. *Retusa sulcata* (d'Orbigny, 1841) C
151. *Volvulella cylindrica* (Carpenter, 1864) P
152. *V. persimilis* (Mörch, 1875) C
153. *V. minuta* (Bush, 1885) C
154. *V. catharia* Dall, 1919 P
155. *V. panamica* Dall, 1919 P
156. *Acteocina candei* (d'Orbigny, 1841) C
157. *A. recta* (d'Orbigny, 1841) C
158. *A. infrequens* (C.B. Adams, 1852) P
159. *Acteocina inculta* (Gould, 1855) P
160. *A. inconspicua* Olsson & McGinty, 1958 C
161. *Cylichna atahualpa* (Dall, 1908) P
162. *C. inca* (Dall, 1908) P
163. *C. pizarro* (Dall, 1908) P
164. *Cylichnella bidentata* (d'Orbigny, 1841) C
165. *C. tabogaensis* (Strong & Hertlein, 1939) P
166. *Haminoea elegans* (Gray, 1825) C, AF
167. *H. virescens* (Sowerby II, 1833) P
168. *H. antillarum* (d'Orbigny, 1841) C
169. *H. succinea* (Conrad, 1846) C
170. *H. vesicula* (Gould, 1855) P
171. *Atys guildingi* Sowerby II, 1869 C
172. *A. riiseanus* Mörch, 1875 C
173. *A. sandersoni* Dall, 1881 C
174. *A. defuncta* F. Baker & Hanna, 1927 P
175. *Weinkauffia* caribaeus (d'Orbigny, 1841) C
176. *W. macandrewii* E.A. Smith, 1872 C, AF
177. *Lamprohaminoea ovalis* Pease, 1868 P
178. *Aliculastrum exaratum* (Carpenter, 1857) P
179. *Philine sagra* (d'Orbigny, 1841) C
180. *P. alboides* Price, Gosliner & Valdés, 2011 C
181. *Philinopsis speciosa* Pease 1860 P
182. *Navanax gemmatus* (Mörch, 1863) C
183. *N. aenigmaticus* (Bergh, 1893) P
184. *N. inermis* (Cooper, 1862) P
185. *Camachoaglaja berolina* (Er. Marcus & Ev. Marcus, 1970) C
186. *Philinorbis albus* (Mattox, 1958) P
187. *Scaphander punctostriatus* (Mighels & C.B. Adams, 1842) C, AF
188. *Scaphander watsoni* Dall, 1881 C
189. *S. interruptus* Dall, 1889 P
190. *S. darius* Ev. Marcus & Er. Marcus, 1967 C
191. *Roxania morgana* (Dall, 1908) P

Aplysiida

192. *Aplysia dactylomela* Rang, 1828 C, AF
193. *A. californica* J.G. Cooper, 1863 P
194. *A. hooveri* Golestani, Crocetta, Padula, Camacho-García, Langeneck, Porsanidis, Pola, Yokeş, Cervera, Jung, Gosliner, Araya, Hooker, Schrödl & Valdés, 2019 P
195. *Dolabella auricularia* (Lightfoot, 1786) P
196. *Bursatella leachii* Blainville, 1817 C, AF
197. *Dolabrifera ascifera* (Rang, 1828) C

198. *D. nicaraguana* Pilsbry, 1896 P
199. *D. virens* Verrill, 1901 C
200. *Stylocheilus longicaudus* (Quoy y Gaimard, 1825) C, P
201. *S. striatus* (Quoy & Gaimard, 1832) C
202. *S. rickettsi* (MacFarland, 1966) P
203. *Phyllaplysia engeli* Er. Marcus, 1955 C
204. *P. padinae* Williams & Gosliner, 1973 P

Sacoglossa

205. *Oxynoe antillarum* Mörch, 1863 C
206. *O. aliciae* Krug, Berriman & Valdés, 2018 P
207. *Lobiger souverbii* P. Fischer, 1857 C
208. *Lobiger cf. souverbii* P. Fischer, 1857 P
209. *Julia thecaphora* (Carpenter, 1857) P
210. *Berthelinia caribbea* Edmunds, 1963 C
211. *Ascobulla ulla* (Er. Marcus & Ev. Marcus, 1970) C
212. *Elysia ornata* (Swainson, 1840) C, AF
213. *E. crispata* Mörch, 1863 C
214. *E. diomedea* (Bergh, 1894) P
215. *E. flava* Verrill, 1901 C, AF
216. *E. papillosa* A.E. Verrill, 1901 C
217. *E. subornata* A.E. Verrill, 1901 C
218. *E. velutinus* Pruvot-Fol, 1947 C
219. *E. canguzua* Er. Marcus, 1955 C
220. *E. marcusi* (Ev. Marcus, 1972) C
221. *E. cornigera* Nuttall, 1989 C
222. *E. zuleicae* Ortea & Espinosa, 2002 C
223. *E. chavelavargas* Ortea, 2017 P
224. *Elysia* sp. 1 P
225. *Ercolania coerulea* Trinchese, 1892 C, AF
226 *Placida kingstoni* T.E. Thompson, 1977 C
227. *Hermaea cruciata* Gould, 1870 C
228. *Polybranchia mexicana* Medrano, Krug, Gosliner, Biju Kumar & Valdés, 2018 P
229. *P. schmekelae* Medrano, Krug, Gosliner, Biju Kumar & Valdés, 2018 C
230. *Caliphylla viridis* (Deshayes, 1857) C
231. *Cyerce antillensis* Engel, 1927 C, AF
232. *Costasiella nonatoi* Ev. Marcus & Er. Marcus, 1960 C
233. *Costasiella* sp. 1 P

CHAPTER II. Where do I come from? Phylogenetic analysis of *Bursatella leachii* Blainville, 1817 (Mollusca: Gastropoda: Heterobranchia) from the Catalonian coasts.

Where do I come from? Phylogenetic analysis of *Bursatella leachii* Blainville, 1817 (Mollusca: Gastropoda: Heterobranchia) from the Catalonian coasts.

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2.1. Abstract

Climate change and other human activities have contributed to the dispersal of species from the tropical to temperate waters. This is the case of the sea hare *Bursatella leachii* a species whose type locality is unknown, considered pantropical, that adapts very well to shallow bays and to less than favorable conditions inside ports and marinas. This species was first reported in the Mediterranean Sea in the 1940s, with increasing observation records since then. The most accepted idea, based on molecular data, is that this species entered the Mediterranean via the Straits of Gibraltar rather than the Suez Canal (Lessepsian migration) as postulated in earlier works. To confirm these ideas, we collected specimens of *B. leachii* from two locations (Ebro Delta, Tarragona and Fòrum bathing area, Barcelona) on the coast of Catalonia, Spain (NW Mediterranean) and carried out molecular analysis so we could compare their sequences with specimens from the Atlantic, Indian, Pacific and other areas of the Mediterranean, obtained from the GenBank. Our results show that specimens from Catalonia share haplotypes with specimens from both shores of the Atlantic and other locations of the Mediterranean Sea, but not with those from the Indo-Pacific, which confirms the hypothesis that they entered the Mediterranean Sea through the Gibraltar Straits.

2.2. Keywords: *Bursatella leachii*, species, Mediterranean, Atlantic, Indo-pacific, coasts, Catalonian

2.3. Introduction

Introduction of exotic species to the marine environment is often contributed by human activities. Main factors could be discharge of ballast water by commercial shipping boats, breeding of commercial species, activities of marine laboratories and trade of exotic species (Molnar *et al.* 2008; Sylvester *et al.* 2011; Nunes *et al.* 2014). The Mediterranean Sea is one of the most affected regions because it is connected to the Atlantic Ocean by the Straits of Gibraltar, allowing the entry of Atlantic species, and to the Red Sea by the Suez Canal, allowing the entry of Indo-Pacific species (Streftaris *et al.* 2005; Katsanevakis *et al.* 2013). International trade of exotic species is also an important contributing factor (Rilov & Galil 2009), as is climate change (Bianchi & Morri 2003).

One of the species that has been experiencing a rapid expansion in the Mediterranean in recent decades is the ragged sea hare *Bursatella leachii* Blainville 1817. First Mediterranean record was reported by O'Donoghue and White (1940) off the coast of Israel, and since then it has been colonizing all the Mediterranean shores towards the west, thanks to its adaptability to local environmental conditions. Ibáñez-Yuste *et al.* (2012) produced a map with all the reports of *B. leachii* in the region, later updated by Selfati *et al.* (2017) and Bazzicalupo *et al.* (2018).

As the colonization of the Mediterranean Sea proceeded from east to west, many researchers initially thought that *B. leachii* was a Lessepsian species coming from the Red Sea (Zenetos *et al.* 2004). However, this hypothesis was questioned by Bazzicalupo *et al.* (2018) with the remark that *B. leachii* is a pantropical species living in both the tropical Atlantic and Indo-Pacific, but they expressed doubts regarding the Indo-Pacific origin because they did not find shared haplotypes between specimens from the Mediterranean and from the Indo-Pacific, but they did find them between those individuals from the Atlantic and those from the Mediterranean. They concluded that the Mediterranean specimens arrived naturally through the Straits of Gibraltar, as a result of an alteration in oceanic currents favored by climate change, thus managing to cross the Atlantic Ocean that was previously considered a geographical barrier for such type of species.

In a more recent paper Bazzicalupo *et al.* (2020) considered that *B. leachii* is a complex of two widely distributed species with records from the Atlantic, Mediterranean and parts of the Indo-Pacific region, where it retains its name. The other species, *Bursatella ocelligera* (Bergh 1902), can be found in the Indo-Pacific, coexisting with *B. leachii* in that zone. However, another species *Bursatella hirsuta* Nimbs & Wilson 2020 was recently described at Southern Australia where it also co-exists with *B. leachii*.

With the data obtained by Bazzicalupo *et al.* (2020), it cannot be proven whether *B. leachii* and *B. ocelligera* have evolved allopatrically in the Atlantic and Indo-Pacific, and sympatrically in the latter, but it can be inferred that *B. leachii* has managed to keep a gene flow between the two oceans, thanks to the Agulhas Leakage process and its ability to adapt to changes in water temperature.

The best assumption of the introduction and spread of this species in the Mediterranean is indicated by Bazzicalupo *et al.* (2018) indicating that, after crossing the Straits of Gibraltar, the larvae are transported by the Algerian current towards the central and eastern basins of the Mediterranean in a natural effect, taking advantage of the warmer waters facilitating larval distribution throughout the Mediterranean. It would be similar to what has happened with the Mediterranean dispersion of the sea hare *Aplysia dactylomela* Rang 1828, according to Valdés *et al.* (2013).

The first record of *B. leachii* on the Catalonian coast (NE Spain) was registered by Weitzmann *et al.* (2007) in the Ebro Delta, where it has managed to adapt very well, due to its high incidence in the area. There are later reports of its presence at the fish farm cages of Vilanova i la Geltrú (Barcelona) in 2011, at the Fòrum bathing area (Barcelona) in 2012, at Cubelles (Barcelona) in 2015 (Ballesteros & Weitzmann 2016) and at the small natural brackish ponds of the Creixell - Gorg beach (Tarragona) in 2020 (Carlos San Vicente, pers. comm.). It is likely that its presence in Catalonia is more extensive than is reported, given its cryptic appearance and the absence of data from areas where this species could potentially live, such as inside ports and marinas (Córdoba & Ballesteros 2019).

As there is doubt on the origin of specimens of *B. leachii* found in the Catalonian coasts, we have considered necessary to carry out a morphological and molecular analysis of *B. leachii* from two Catalonian coastal sectors (Fòrum bathing area, Barcelona and Ebro Delta, Tarragona), and compare them with other *B. leachii* from different world regions in order to assess the origin of the specimens of *B. leachii* found at the Western Mediterranean, and to know if the Atlantic Ocean is a natural barrier for the dispersal of this type of species.

2.4. Materials and methods

2.4.1. *Taxon sampling*

We have collected 10 individuals of *B. leachii* from two localities (Fòrum bathing area, Barcelona and Ebro Delta, Tarragona) on the coast of Catalonia, Spain (NW Mediterranean). The specimens were collected by hand on freediving between 1 and 4.5 m depth.

Specimens were collected alive in the field and immediately transferred to absolute ethanol, then stored at -20 ºC for the subsequent morphological study and DNA extraction. In total, all these observation data correspond to approximately 50 hours of freediving or scuba by different divers, where the number of specimens, the substrates where they have appeared, both from the observations themselves and from the photographs, were recorded.

2.4.2. *Anatomical analysis*

We followed the taxonomical study approach by Eales and Engel (1935), reviewed and updated with the systematics of sea hares by Valdés *et al.* (2017) and Cunha & Simone (2019).

A binocular Olympus SZ-PT dissecting microscope was used to study their internal anatomy. A dorsal incision was made on the anterior portion of the animal to dissect the distal anterior part of the digestive tract, which includes the buccal bulb, radula, and jaws. The buccal mass was immersed in a potassium hydroxide (KOH) solution (10%) for three hours to dissolve the organic tissues and then rinsed with distilled water. The radula was mounted on a metal stub with bio adhesive tabs, coated with a carbon layer, and examined under a FEI Quanta 200 scanning electron microscope (SEM).

2.4.3. *Molecular procedures*

Total genomic DNA was extracted from the foot of each specimen using the Sigma-Aldrich REDExtract-N-Amp™ TissuePCR Kit protocol.

Partial fragment of one mitochondrial gene was sequenced in the present study: COI (cytochrome c oxidase subunit I). The LCO1490/HCO2198 was the preferred primer combination, while Nancy was used as a replacement for HCO2198 and specific primers designed for *B. leachii* (Table 1) (forward 5'-GGGATGTGATGTGGTCTAGTAGGAAC-3', reverse 5' - ATAGGATCTCCTCCTCCCGCAGGATC Bazzicalupo *et al.* 2018 and 2020). COI was amplified as follows: 3 min at 95ºC followed by 35 cycles of denaturation at 94ºC for 45 s, annealing temperature range of 45ºC for 45 s, 72ºC for 90 s and final extension at 72ºC for 10 s. min. Polymerase chain reaction (PCR) was performed using 5 µl MyTaq 5x reaction buffer (BIOLINE), 0.4 µl forward and reverse primers (10 µM), 0.2 µl MyTaq red DNA polymerase (BIOLINE), 4 µl of ultrapure distilled and diluted DNA. water to a total reaction volume of 20 µL.

Table 1. Primers used for each gene

Gene	Primers Name	Direction	Sequence	Reference
COI	LCO1490	Forward	5'-GGTCAACAAATCATAAAGATATTGG-3'	Folmer *et al.* 1994
COI	HCO2198	Reverse	5'-TAAACTTCAGGGTGACCAAAAAATCA-3'	Folmer *et al.* 1994
COI	Nancy	Reverse	5'-CCCGGTAAAATTAAAATATAAACTTC-3'	Simon *et al* 1994
COI	Designed *B. leachii*	Forward	5'-GGG ATG TGATGT GGT CTA GTA GGA AC-3',	Bazzicalupo *et al.* 2018
COI	Designed *B. leachii*	Reverse	5'-ATA GGATCT CCT CCT CCC GCA GGA TC-3'	Bazzicalupo *et al.* 2018

The fragments were visualized by agarose gel electrophoresis at a concentration of 1% (w/v) in 1X TBE buffer (0.89 M Tris, 0.89 M boric acid, 0.02 M EDTA) (Panreac AppliChem, Barcelona, Spain) at 120 V for 45 min. The PCR products were sequenced in both directions using one of the respective amplification primers on the Macrogen services (www.macrogen.com). Chromatograms were assembled and edited in Geneious v. 5.3.6 (Drummond *et al.* 2010).

2.4.4. *Phylogenetic analysis*

Phylogenetic analyses were conducted under Maximum Likelihood (ML). The best partition scheme and evolutionary model for each partition was selected with Partition Finder v2.1.1. (Lanfear *et al.* 2017). ML analyses were performed with RAxML 8.0 (Stamatakis 2014) with 10000 replicates, random initial trees, and estimated parameters evolutionary models. Branches with bootstrap values above 70% were considered supported (Hillis & Bull 1993). The resulting trees were visualized with iToL (https://itol.embl.de/itol.cgi). One specimen of *Akera bullata* O. F. Müller 1776 from Sweden and one of *Aplysia californica* J. G. Cooper 1863 from California (USA) obtained from the GenBank were used as outgroups. To complete the dataset, we retrieved all the available sequences of the genus from GenBank (see Table 2).

Table 2. Table with information on all the specimens used in this study, including the species, location, voucher (collection code) and the COI GenBank accession number.

Species	DNA Code	Location	Region	COI
Akera bullata	GenBank	Sweden	Northern-Atlantic	AF156143
Aplysia californica	GenBank	California, USA	Eastern-Pacific	AF077759
Bursatella leachii	GenBank	Forum, Barcelona, Spain	B1: Mediterranean	OK066363
B. leachii	GenBank	Forum, Barcelona, Spain	B2: Mediterranean	OK066356
B. leachii	GenBank	Forum, Barcelona, Spain	B3: Mediterranean	OK066357
B. leachii	GenBank	Forum, Barcelona, Spain	B4: Mediterranean	OK066364
B. leachii	GenBank	Forum, Barcelona, Spain	B5: Mediterranean	OK066361
B. leachii	GenBank	Delta del Ebro, Tarragona, Spain	B6: Mediterranean	OK066355
B. leachii	GenBank	Delta del Ebro, Tarragona, Spain	B7: Mediterranean	OK066359
B. leachii	GenBank	Forum, Barcelona, Spain	B8: Mediterranean	OK066358
B. leachii	GenBank	Forum, Barcelona, Spain	B9: Mediterranean	OK066362
B. leachii	GenBank	Forum, Barcelona, Spain	B10: Mediterranean	OK066360
B. leachii	CASIZ 176327	Western Cape Province, South Africa	South-Africa	MH837965
B. leachii	GenBank	Sakai city, Otsaka, Japan 1	Indo-Pacific	MH837966
B. leachii	GenBank	Sakai city, Otsaka, Japan 2	Indo-Pacific	MH837967
B. leachii	GenBank	Sakai city, Osaka, Japan 3	Indo-Pacific	MH837968
B. leachii	CASIZ 202048(b)	Luzon Island, Batangas Province, Mabini, Philippines	Indo-Pacific	MH837969
B. leachii	CPIC 00647	Iberostar Rose Hall Beach, Jamaica	Western-Atlantic	MH837970
B. leachii	CPIC 02031	Marchica Lagoon, Morocco 1	Mediterranean	MH837971
B. leachii	CPIC 01430	Bocas del Toro, Panama 1	Western-Atlantic	MH837972

B. leachii	CPIC 02023	Marchica Lagoon, Morocco 2	Mediterranean	MH837973
B. leachii	CPIC 00482(b)	Bocas del Toro, Panama 2	Western-Atlantic	MH837974
B. leachii	CPIC 02035	Marchica Lagoon, Morocco 3	Mediterranean	MH837975
B. leachii	CPIC 02025	Marchica Lagoon, Morocco 4	Mediterranean	MH837976
B. leachii	CPIC 00482(a)	Bocas del Toro, Panama 3	Western-Atlantic	MH837977
B. leachii	GenBank	Vrsar, Croatia 1	Mediterranean	MH837978
B. leachii	GenBank	Marchica Lagoon, Morocco 5	Mediterranean	MH837979
B. leachii	CPIC-02034	Marchica Lagoon, Morocco 6	Mediterranean	MH837980
B. leachii	CPIC-02036	Marchica Lagoon, Morocco 7	Mediterranean	MH837981
B. leachii	GenBank	Gulf of Naples, Italy	Mediterranean	MH837982
B. leachii	GenBank	Vrsar, Croatia 2	Mediterranean	MH837983
B. leachii	GenBank	Vrsar, Croatia 3	Mediterranean	MH837984
B. leachii	GenBank	Sicily, Italy 1	Mediterranean	MH837985
B. leachii	GenBank	Lesvos island, Greece 1	Mediterranean	MH837986
B. leachii	GenBank	Lesvos island, Greece 2	Mediterranean	MH837987
B. leachii	GenBank	Lesvos island, Greece 3	Mediterranean	MH837988
B. leachii	GenBank	Lesvos island, Greece 4	Mediterranean	MH837989
B. leachii	GenBank	Lesvos island, Greece 5	Mediterranean	MH837990
B. leachii	GenBank	Lesvos island, Greece 6	Mediterranean	MH837991
B. leachii	GenBank	Lesvos island, Greece 7	Mediterranean	MH837992
B. leachii	GenBank	Sicily, Italy 2	Mediterranean	MH837993
B. leachii	GenBank	Dhalavapuram, India 1	Indo-Pacific	MH837994
B. leachii	GenBank	Dhalavapuram, India 2	Indo-Pacific	MH837995
B. leachii	GenBank	Mar Menor, Múrcia, Spain coastal 1	Mediterranean	KJ187403
B. leachii	GenBank	Mar Menor, Múrcia, Spain coastal 2	Mediterranean	KJ187404
B. leachii	GenBank	Mar Menor, Múrcia, Spain coastal 3	Mediterranean	KJ187405
B. leachii	GenBank	Florida, USA	Western-Atlantic	AF156146
B. ocelligera	CASIZ 201161	Luzon Island, Batangas Province, Mabini, Philippines 1	Indo-Pacific	MT025965
B. ocelligera	CASIZ 200587	Luzon Island, Batangas Province, Mabini, Philippines 2	Indo-Pacific	MT025966

2.4.5. *Species delimitation under the ASAP algorithm and Haplotype network*

COI sequences were used for species delimitation analyses with Assemble Species by Automatic Partitioning (ASAP; Puillandre *et al.* 2021). Jukes Cantor (JC69), Kimura (K80) and Simple Distance substitution models were tested. Finally, we constructed a haplotype for the COI using the TCS algorithm (Clement *et al.* 2002) as implemented in the PopArt 1.7 program version 4.8.4 (Leigh & Bryant 2015).

2.4.6. *Biological data*

A table has also been compiled with all the georeferenced records of *B. leachii* from different parts of the world (Table 3).

Table 3. Citations of *Bursatella leachii* in different parts of the world based on bibliographic references or public access databases.

Locality	Observer, museum | reference [source database]	year	month	day
Krusadai Island, India	IndOBIS (2022)	1817	7	2
Kingston Harbor, South of, Jamaica	United States Fish Commission, GBIF (2022)	1884	3	11
Rose Bay, NSW, Austràlia	Australian Museum Malacology Collection, GBIF (2022)	1893	1	1
Hillsborough County, Florida, USA	Yale Peabody Museum - Invertebrate Zoology, GBIF (2022)	1932	3	29
Toroneos Kolpos, Greece	Koukouras (2000), OBIS (2022)	1937	7	2
Triglia, Nea Propontida, Greece	Koukouras (2000), OBIS (2022)	1937	7	2
Jupiter, Florida, USA	Lyman, F. B., Florida Museum of Natural History - Invertebrate Zoology, GBIF (2022)	1938	5	20
Angourie Point, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)	1940	9	7
Flinders, Victòria, Austràlia	Museums Victoria - Marine Invertebrates Collection GBIF (2022)	1958	3	2

Mascot, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)	1958	7	2
Plettenberg Bay, South Africa	F.H. Zalbot, GBIF (2022)	1961	1	30
S of Nature's Valley, South Africa	Iziko South African Museum - Mollusc Collection, OBIS (2022)	1961	7	2
Lakeside, Capetown, South Africa	Iziko South African Museum - Mollusc Collection, OBIS (2022)	1964	9	15
Eden, NSW, Austràlia	Australian Museum Malacology Collection, GBIF (2022)	1966	1	1
Goodwood Island, NSW, Austràlia	F. Ryan Chatsworth, Australian Museum - Malacology, GBIF (2022)	1967	1	1
Nadgee, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)	1967	4	25
Guajira Peninsula, Off Puerto Estrella, Colombia	United States National Museums - Invertebrate Zoology, GBIF (2022)	1968	7	28
Muizenberg, South Africa	Iziko South African Museum - Mollusc Collection, OBIS (2022)	1968	9	15
Carrabelle, Florida, USA	Academy of Natural Sciences of Philadelphia, Malacology, GBIF (2022)	1970	1	30
Carrabelle, Florida, USA	Academy of Natural Sciences of Philadelphia, Malacology, OBIS (2022)	1970	7	2
Galeta Island, Colón, Panamá	United States National Museums - Invertebrate Zoology, GBIF (2022)	1971	11	9
Royal National Park, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)	1972	9	24
Micalo Island, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)	1972	10	18
Canada Island, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)	1973	6	26
Shoal Bay, N of Darwin, NT, Australia	Museum and Art Gallery of the Northern Territory - Malacology Collection GBIF (2022)	1973	8	9
Tin Can Bay, QLD, Australia	Australian Museum Malacology Collection, OBIS (2022)	1976	10	22
Watsons Bay, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)	1977	2	19
Royal National Park, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)	1978	9	17
Watsons Bay, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)	1979	8	20
Ashqelon, Israel	Gil Gat, OPK (2022)	1979	9	28
Angourie Point, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)	1979	10	6
Bari Harbor, Italy	Vaccarella and Pastorelli (1983) in Zenetos *et al.* (2016)	1982	1	1
North Stradbroke Island, QLD, Austràlia	Queensland Museum Molluscs - Marine records, OBIS (2022)	1982	4	14
S. Padre Is. Texas, United States	D. Hockaday, Texas Cooperative Wildlife Collection - Marine Invertebrates, GBIF (2022)	1983	7	12
Bari Harbor, Italy	Vaccarella (1986) in Zenetos et al. (2016)	1984	1	1
Laguna di Venezia, Italy	Cesari et al. (1986); Cesari (1990; 1994) in Zenetos *et al.* (2016)	1985	1	1
Sorgenti di Aurisina, Trieste, Italy	Jaklin and Vio (1989) in Zenetos et al. (2016)	1985	1	1
Timavo River stuary, Trieste, Italy	Jaklin and Vio (1989) in Zenetos et al. (2016)	1985	1	1
Laguna di Grado-Marano, Italy	Jaklin and Vio (1989); De Min and Vio (1998) in Zenetos *et al.* (2016)	1985	1	1
Rovinj, Croatia	Jaklin and Vio (1989) in Zenetos et al. (2016)	1986	1	1
Margherita di Savoia, Italy	Vaccarella (1986) in Zenetos et al. (2016)	1986	1	1
Harbour Heights, Florida, USA	Florida Museum of Natural History - Invertebrate Zoology, GBIF (2022)	1986	7	12
Fukeko, Osaka, Japan	Ryohei YAMANISHI, Oklahoma Museum of Natural History, GBIF (2022)	1986	10	6
Bird Island, Basin Padre Is., Texas, USA	Shaver, D., Texas Cooperative Wildlife Collection - Marine Invertebrates, GBIF (2022)	1987	10	10
Bird Island Basin, Padre Island, Texas, USA	Chaney and Shaver, Texas Cooperative Wildlife Collection - Marine Invertebrates, GBIF (2022)	1987	10	19
Canale dei Marani, Venezia, Italy	Cesari (1990) in Zenetos et al. (2016)	1988	1	1
Bird Island Basin, Padre Island, Texas, USA	Chase Chaney, Texas Cooperative Wildlife Collection - Marine Invertebrates, GBIF (2022)	1988	1	7
Great Mercury Islands, New Zealand	Australian Institute of Marine Science - Bioresources Library, OBIS (2022)	1988	12	6
Cedar Key, Florida, USA	R.W. Portell, Florida Museum of Natural History - Invertebrate Zoology, GBIF (2022)	1989	1	28
Hvar Island, Croatia	Despalatović et al. 2008 in Zenetos *et al.* 2016	1990	1	1
Split, Croatia	Despalatović et al. 2008 in Zenetos *et al.* 2016	1990	1	1
Pontal do Sul, Brasil	Centro de Estudos do Mar, Universidade Federal do Paraná, OBIS (2022)	1990	6	26
Angourie Point, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)	1990	11	30
Baia di Panzano, Trieste, Italy	Vio and De Min (1996); De Min and Vio (1998) in Zenetos *et al.* (2016)	1996	1	1
Muggia, Trieste, Italy	Vio and De Min (1996); De Min and Vio (1998) in Zenetos *et al.* (2016)	1996	1	1
Nightcliff reef, Darwin, NT, Australia	Museum and Art Gallery of the Northern Territory - Malacology Collection GBIF (2022)	1996	6	3
Diamond Beach, Serakaki, Okinawa, Japan	R.F. Bolland, California Academy of Sciences - Invertebrate Zoology, GBIF (2022)	1997	6	11

Lazzaro, Reggio Calabria, Italy	Gianni Neto, Medslugs (2022)	1998	1	1
Laguna di Venezia, Italy	Mizzan (1999) in Zenetos et al. (2016)	1998	1	1
Patres, Greece	Martin Mildenberger, Medslugs (2022)	1999	1	1
Pellaro, Reggio Calabria, Italy	Gianni Neto, Medslugs (2022)	2000	1	1
Manzanillo, off MINAE, Costa Rica	Mario Calderon, Instituto Nacional de Biodiversidad - Mollusca, GBIF (2022)	2000	4	6
Beirut Harbor, Lebanon	Crocetta et al. (2013)	2000	6	2
Selaata, Lebanon	Crocetta et al. (2013)	2000	10	10
Piran, Marine Biology Station, Slovenia	Lipej et al. (2008) in Zenetos *et al.* (2016)	2001	1	1
Praia do Jabaquara, Ilhabela, São Paulo, Brasil	SINBIOTA Marine Data, OBIS (2022)	2001	4	24
S of Ilha do Tamanduá, Caraguatatuba, São Paulo, Brasil	SINBIOTA Marine Data, OBIS (2022)	2001	4	26
Ubatuba, São Paulo, Brasil	SINBIOTA Marine Data, OBIS (2022)	2002	3	21
Angourie Point, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)	2002	3	25
Cedar Key, Florida, USA	Florida Museum of Natural History - Invertebrate Zoology, GBIF (2022)	2002	10	8
Piran, Marine Biology Station, Slovenia	Lipej et al. (2008) in Zenetos *et al.* (2016)	2003	1	1
Cudjoe Key, Florida, USA	Florida Museum of Natural History - Invertebrate Zoology, GBIF (2022)	2004	3	18
Fannie Bay, Darwin, NT, Australia	Museum and Art Gallery of the Northern Territory - Malacology Collection GBIF (2022)	2004	9	12
North Field Island, Kakadu National Park, NT, Australia	Museum and Art Gallery of the Northern Territory - Malacology Collection GBIF (2022)	2004	11	23
Sistiana, Trieste, Italy	Borut Mavrić in Zenetos et al. (2016)	2006	1	1
Portorož (Seča), Slovenia	Lipej *et al.* (2008) in Zenetos et al. (2016)	2006	1	1
Magnetic Island, Townsville, QLD, Australia	Australian Museum Malacology Collection, OBIS (2022)	2006	2	28
Matanzas River, Marineland, Florida, USA	Jose Nunez, iNaturalist - Observations, GBIF (2022)	2006	11	9
Vrsar Harbor, Croatia	Andrej Jaklin in Zenetos *et al.* (2016)	2007	1	1
Miramare, Trieste, Italy	Crocetta et al. (2009); Crocetta (2011) in Zenetos *et al.* (2016)	2007	1	1
off Sečovlie, Slovenia	Lipej *et al.* (2008) in Zenetos *et al.* (2016)	2007	1	1
Piran Harbor, Slovenia	Lipej *et al.* (2008) in Zenetos *et al.* (2016)	2007	1	1
Strunjan, Slovenia	Lipej *et al.* (2008) in Zenetos *et al.* (2016)	2007	1	1
Isola della Certosa, Laguna di Venezia, Italy	Mizzan and Vianello (2009) in Zenetos *et al.* (2016)	2007	1	1
Cesenatico, Emilia-Romagna, Italy	Rinaldi (2007; 2008; 2012) in Zenetos *et al.* (2016)	2007	1	1
Cesenatico, Emilia-Romagna, Italy	Tisselli and Mazziotti (2009) in Zenetos *et al.* (2016)	2007	1	1
Strunjan, Slovenia	Turk and Furlan (2011) in Zenetos *et al.* (2016)	2007	1	1
Casuarina Beach, Darwin, NT, Australia	Museum and Art Gallery of the Northern Territory - Malacology Collection GBIF (2022)	2007	6	30
Strunjan, Slovenia	Lipej et al. (2008) in Zenetos *et al.* (2016)	2008	1	1
Marina di Ravenna, Italy	Tisselli and Mazziotti (2009) in Zenetos *et al.* (2016)	2008	1	1
Western False Bay, South Africa	Invert E Base (2022)	2008	1	6
Verde Island Passage, Philippines	Invert E Base (2022)	2008	3	21
Ciénaga de Progreso, Chuburná, Yucatán, México	Deneb Ortigosa, iNaturalist - Observations, GBIF (2022)	2008	4	17
Wellington Point, QLD, Austràlia	Queensland Museum Molluscs - Marine records, OBIS (2022)	2008	7	30
Fannie Bay, Darwin, NT, Australia	Museum and Art Gallery of the Northern Territory - Malacology Collection GBIF (2022)	2008	9	6
Moorea, French Polynesia	University of Florida Museum of Natural History, Invertebrate Zoology Collection, OBIS (2022)	2008	10	12
Moorea, French Polynesia	University of Florida Museum of Natural History, Invertebrate Zoology Collection, OBIS (2022)	2008	10	17
Moorea, French Polynesia	University of Florida Museum of Natural History, Invertebrate Zoology Collection, OBIS (2022)	2008	11	4
Boka Kotorska Bay (Sv. Nedelja), Montenegro	Mačić and Kljajić (2012) in Zenetos *et al.* (2016)	2009	1	1
Boka Kotorska Bay (near Bijela), Montenegro	Zenetos *et al.* (2011) in Zenetos *et al.* (2016)	2009	1	1
Cook's Bay, Moorea, French Polynesia	Cory Pittman, Florida Museum of Natural History - Invertebrate Zoology, GBIF (2022)	2009	11	21
I Filtri, Trieste, Italy	Crocetta *et al.* (2009); Crocetta (2011) in Zenetos *et al.* (2016)	2010	1	1

Punta Olmi, Muggia, Italy	Crocetta *et al.* (2009); Crocetta (2011) in Zenetos *et al.* (2016)	2010	1	1
Portorož (Seča), Slovenia	L. Lipej in Zenetos *et al.* (2016)	2010	1	1
Donsol, Sorsogon, Philippines	Terry Gosliner, iNaturalist Observations, GBIF (2022)	2010	2	12
Moorea, French Polynesia	University of Florida Museum of Natural History, Invertebrate Zoology Collection, OBIS (2022)	2010	11	11
Boka Kotorska Bay (Zelenika), Montenegro	Branislav Lazarevic In Zenetos *et al.* (2016)	2011	1	1
Ankaran, Slovenia	L. Lipej in Zenetos *et al.* (2016)	2011	1	1
Portorož (Seča), Slovenia	L. Lipej in Zenetos *et al.* (2016)	2011	1	1
Škocjanski zatok, Slovenia	L. Lipej in Zenetos *et al.* (2016)	2011	1	1
Piran Harbor, Slovenia	L. Lipej in Zenetos *et al.* (2016)	2012	1	1
Portorož (Seča), Slovenia	L. Lipej in Zenetos *et al.* (2016)	2012	1	1
Roquetas de Mar, Almería, Spain	Ibáñez-Yuste *et al.* (2012)	2012	2	21
Darwin Sailing Club, Fannie Bay, Darwin, NT, Australia	Museum and Art Gallery of the Northern Territory - Malacology Collection GBIF (2022)	2012	5	30
Boka Kotorska Bay (Dobrota), Montenegro	Mačić (2013) in Zenetos *et al.* (2016)	2013	1	1
Boka Kotorska Bay (Verige), Montenegro	Mačić (2013) in Zenetos *et al.* (2016)	2013	1	1
Burrill Lake, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)	2013	5	16
Port, La Ràpita, Tarragona, Spain	Guillem Mas, GROC (2022)	2013	10	6
Pottsville Beach, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)	2014	3	2
Kingscliff, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)	2014	3	3
Anilao Pier, Philippines	Carissa Shipman, California Academy of Sciences - Invertebrate Zoology, GBIF (2022)	2014	5	6
Verde Island Passage coast, off Lago de Oro Hotel, Philippines	Daisuke Uyeno, California Academy of Sciences - Invertebrate Zoology, GBIF (2022)	2014	5	13
Stari Trogir, Sevid, Croatia	Jakov Prkić, OPK (2022)	2014	11	15
Navarre Beach, Navarre, Florida, USA	Chuck Sexton, iNaturalist - Observations, GBIF (2022)	2015	6	27
Mare Grande, Taranto, Italy	Gianfranco Alemanno, OPK (2022)	2015	9	1
Central Térmica, Cubelles, Barcelona, Spain	Pablo Ruiz, GROC (2022)	2015	9	10
Port, La Ràpita, Tarragona, Spain	Xavier Salvador, GROC (2022)	2015	9	24
Fusaro Lagoon, Bacoli, Naples, Italy	Guido Villani, European Sea Slugs Reports (2022)	2015	10	1
Platja de Casablanca, La Ràpita, Tarragona, Spain	Neus Sanmartí, OPK (2022)	2015	11	25
Itea, Korinthiakos Gulf, Greece	Nassos Drosopoulos, Underwater Photography in Greece (2022)	2015	12	1
Henderson Bay, Northland, New Zealand	Tangatawhenua, iNaturalist Observations, GBIF (2022)	2015	12	15
Henderson Bay, Northland, New Zealand	Tangatawhenua, iNaturalist Observations, GBIF (2022)	2016	1	24
Kašuni, Split, Croatia	Jakov Prkić, OPK (2022)	2016	3	1
Kašuni, Split, Croatia	Jakov Prkić, OPK (2022)	2016	3	4
Kašuni, Split, Croatia	Jakov Prkić, OPK (2022)	2016	4	3
Spiaggia di San Vito, Taranto, Italy	Giacinto Ribezzo, Mare Nostrum Wildlife (2022)	2016	4	24
Girne, Kyrenia, Cyprus	Alper Karabacak in Lipej *et al.* (2018)	2016	8	16
Moll de Les Salines, La Ràpita, Tarragona, Spain	Josep Pepio, GROC (2022)	2016	9	17
Forum bathing area, Barcelona, Spain	Parera *et al.* (2020)	2017	11	23
Coves de Cala Masset, Sant Feliu de Guíxols, Girona, Spain	Xavier Salvador, GROC (2022)	2017	11	25
Forum bathing area, Barcelona, Spain	Parera *et al.* (2020)	2017	11	25
Forum bathing area, Barcelona, Spain	Parera *et al.* (2020)	2017	12	5
Forum bathing area, Barcelona, Spain	Parera *et al.* (2020)	2017	12	23
Forum bathing area, Barcelona, Spain	Parera *et al.* (2020)	2018	2	3
Forum bathing area, Barcelona, Spain	Parera *et al.* (2020)	2018	4	27
Forum bathing area, Barcelona, Spain	Parera *et al.* (2020)	2018	5	16
Forum bathing area, Barcelona, Spain	Parera *et al.* (2020)	2018	6	20
Forum bathing area, Barcelona, Spain	Parera *et al.* (2020)	2018	8	21
Forum bathing area, Barcelona, Spain	Parera *et al.* (2020)	2018	9	15
Forum bathing area, Barcelona, Spain	Parera *et al.* (2020)	2019	11	20

Platja de Calafat, L'Ametlla de Mar, Tarragona, Spain	Plancton divulgacio i serveis marins, GROC (2022)	2020	10	10
Angourie Point, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)			
Rose Bay, NSW, Austràlia	Australian Museum Malacology Collection, OBIS (2022)			
Goodwood Island, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)			
Eden, NSW, Australia	Australian Museum Malacology Collection, OBIS (2022)			
N of Tizimin, Yucatán, Mexico	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
Río Lagartos, Yucatán, Mexico	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
Ciudad Madero, Tamaulipas, Mexico	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
NW of Key West, Florida, USA	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
E of Tampico, Mexico	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
N of Sandino, Cuba	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
NE of Coatzacoalcos, Mexico	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
Padre Island National Seashore, Texas, USA	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
Tonalá, Veracruz, Mexico	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
Lake Lorraine, Florida, USA	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
S of Hulburt Field, Florida, USA	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
W of Sarasota, Florida, USA	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
SE of Corpus Christi, Texas, USA	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
Cortez, Florida, USA	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
Hackberry Beach, Louisiana, USA	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
S of Louisiana, USA	Biodiversity of the Gulf of Mexico Database, OBIS (2022)			
Krusadai Island, India	IndOBIS (2022)			
Sandbaai, South Africa	Iziko South African Museum - Mollusc Collection, OBIS (2022)			
Thermaic Gulf, Triglia, Greece	OBIS (2022)			
Toroneos Kolpos, Greece	OBIS (2022)			
Wollongong City Beach, NSW, Australia	Museums Victoria - Marine Invertebrates Collection GBIF (2022)			
E of Bilagiri, Nigeria	Nigerian Institute for Oceanography and Marine Research, OBIS (2022)			
Chios Island, Greece	Barash and Danin (1986) in Koutsoubas and Cinelli (1997)			
Mytilini Island, Greece	Barash and Danin (1986) in Koutsoubas and Cinelli (1997)			
Salamina Island, Greece	Barash and Danin (1986) in Koutsoubas and Cinelli (1997)			
Thermailkos Gulf, Greece	Koutsoubas and Voultsiadou-Koukoura (1991) in Koutsoubas and Cinelli (1997)			
Thermailkos Gulf, Greece	Koutsoubas, 1992 in Koutsoubas and Cinelli (1997)			
Angourie Point, NSW, Australia	Australian Museum Malacology Collection, GBIF (2022)			
Amuay, Falcón, Veneçuela	Academy of Natural Sciences of Philadelphia, Malacology, GBIF (2022)			
Lafayette ct, Florida, USA	Academy of Natural Sciences of Philadelphia, Malacology, GBIF (2022)			
Boca Ciega Bay, Tampa, United States	Academy of Natural Sciences of Philadelphia, Malacology, GBIF (2022)			
Swartkop Estuary, Port Elizabeth, South Africa	Academy of Natural Sciences of Philadelphia, Malacology, GBIF (2022)			
Tomioka, Kyushu, Japan	Academy of Natural Sciences of Philadelphia, Malacology, GBIF (2022)			
Gallico Marina, Reggio Calabria, Italy	Crocetta *et al.* (2009)			
Reggio Calabria Airport, Italy	Crocetta *et al.* (2009)			
Reggio Calabria Harbour, Candeloro Reggio Calabria, Italy	Crocetta *et al.* (2009)			
Toroneos Kolpos, Greece	Department of Zoology, Aristote Zoological Museum, GBIF (2022)			
Thermaic Gulf, Triglia, Grècia	Department of Zoology, Aristote Zoological Museum, GBIF (2022)			
Capo S. Vito, Taranto, Italy	Furfaro *et al.* (2020)			
Marina Mancaversa, Lecce, Italy	Furfaro *et al.* (2020)			
Santa Maria di Leuca, Lecce, Italy	Furfaro *et al.* (2020)			
Mar Piccolo, Taranto, Italy	Furfaro *et al.* (2020)			
Torre Pedrera, Rimini, Italy	Biologia Marina (2022)			
Idrelac, Pašman Island, Croatia	Jakov Prkić, OPK (2022)			
Lake Worth Lagoon, West Palm Beach, Florida, USA	JaxShells (2022)			
Izola, Slovenia	Lipej et al. (2008)			
Krusadai Island, India	IndOBIS (2022)			
S'Arenal de Llucmajor, Palma de Mallorca, Spain	Oliver and Terrasa (2004)			

Plettenberg Bay, South Africa	South Africa Museum Cape, GBIF (2022)
Klein River Lagoon Hermanus, South Africa	U C T Ecological Survey, South Africa Museum Cape, GBIF (2022)
Richards Bay Cape Province, South Africa	U C T Ecological Survey, South Africa Museum Cape, GBIF (2022)
St Lucia Estuary, South Africa	U C T Ecological Survey, South Africa Museum Cape, GBIF (2022)
Knysna, South Africa	Weber, M.W.C., Zoological Museum Amsterdam, GBIF (2022)

2.5. Results

2.5.1. *Phylogenetic tree analysis and species delimitation*

A total of 49 658-bp long sequences of the COI gene were used, after combining records from GenBank with our sequences. The tree showed two well-defined clades with a high support (Bs=99): *B. ocellifera* from the Indo-Pacific sea and *B. leachii*. *B. leachii* is divided into two main clades. The first clade was solely composed of *B. leachii* from the Indo-Pacific and South Africa (Bs=81). The second clade, with low support (Bs=49) recovered all the *B. leachii* specimens from the Atlanto-Mediterranean region, including the sequences newly obtained in this study (Figure 1). The results of the ASAP analysis yielded four different hypothetical groups: two outgroups (*A. bullata* and *A. californica*), *B. ocellifera* from the Philippines and the last group with all *B. leachii* specimens (Figure 1).

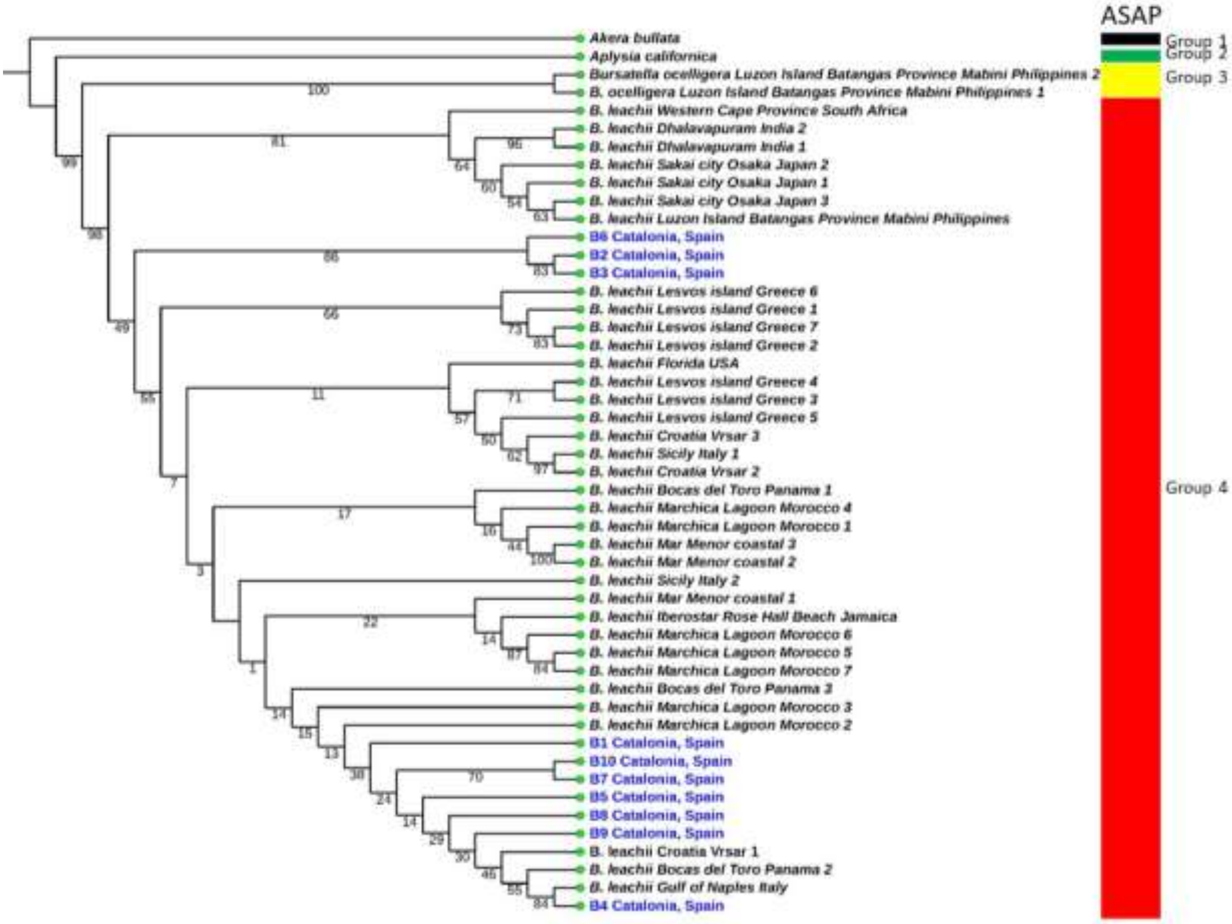

Figure 1. Phylogenetic tree for COI gene under maximum likelihood analysis by RAxML. The numbers at the nodes represent ML bootstraps. The names in blue are the specimens we sampled; names in black are GenBank sequences. The colored bars represent the results of the ASAP analysis.

2.5.2. *Haplotype network*

The haplotype network recovered several haplotypes. With the most common haplotypes found in specimens of *B. leachii* from Italy and Greece (Europe: Mediterranean), the coasts of the Mar Menor (Europe: Mediterranean), Lagoon Marchica in Morocco (North Africa: Eastern Atlantic and the Mediterranean), Jamaica and Panama (Western Atlantic: Caribbean Sea) and specimens collected by us as B1, B4, B5, B7, B9 and B10 (Europe: Mediterranean Coasts of Catalonia); haplogroup was *B. leachii* from the islands of Lesvos in Greece (Europe: Mediterranean); another combined with *B. leachii* from the island of Lesvos in Greece with Sicily in Italy and Vrsar in Croatia (Europe: Mediterranean); another haplogroup was the *B. leachii* from India and Japan (Indo-Pacific), ending with a haplogroup formed by specimens collected by us as B2, B3 and B6 (Europe: Mediterranean). In addition, the clade of *B. leachii* has a haplotype that differs from the haplotype of *B. leachii* from the coasts of Mar Menor, Murcia, Spain (Europe: Mediterranean), West Cape Province of South Africa (South Africa: Atlantic), Lagoon Marchica de Morocco (North Africa: Eastern Atlantic and Mediterranean) and some specimens collected by us as B2, B3 and B6 (Europe: Mediterranean Coasts of Catalonia); small mutations are also observed in specimens of B. leachii from Lesvos Island in Greece (Europe: Mediterranean), one from Lagoon Marchica in Morocco (North Africa: Eastern Atlantic and Mediterranean), another from Florida in the United States (Western Atlantic: Caribbean Sea) and a specimen collected by us the B8 (Europe: Mediterranean Coasts of Catalonia) (Figure 2).

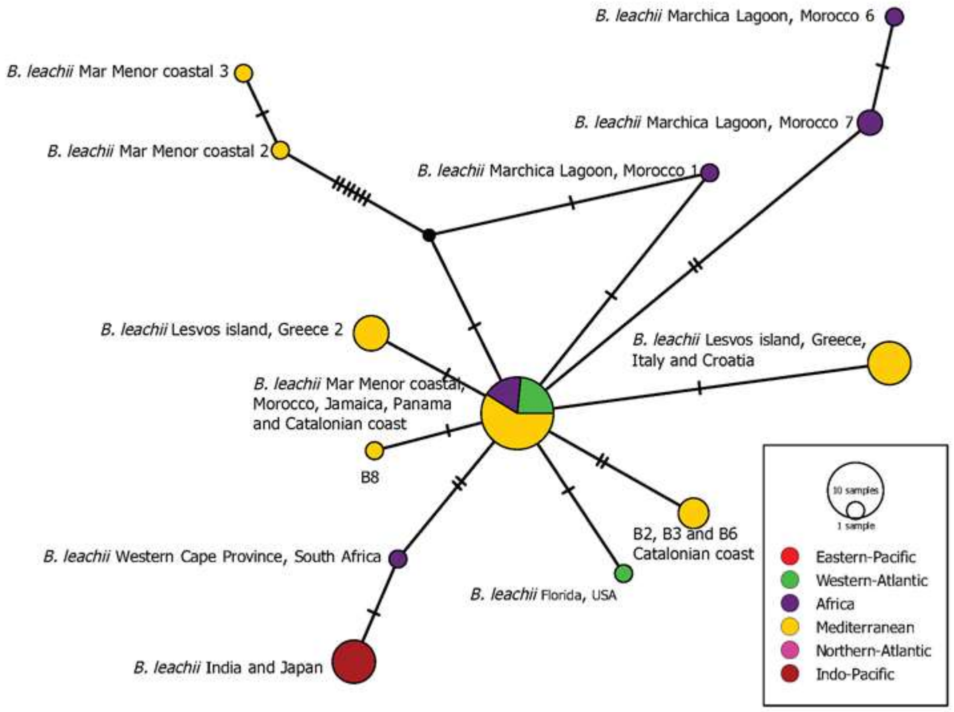

Figure 2. Haplotype networks based on COI sequence data, the geographic region of the specimen is in color. The relative size of the circles is proportional to the number of sequences of the same haplotype.

2.5.3. ***Morphological results***

The size of Catalan specimens is between 100-150 mm, although specimens up to 25 cm have been observed in the Adriatic (J. Prkić, personal communication). Specimens with black to grayish coloration, with the body decorated with round dark blotches that have a colored spot, usually bright blue, in the middle (Figure 3). The body surface is covered with elongated and uneven branched extensions that give the body its typical appearance similar to algae all over body to blend into environment. Rhinophores and tentacles of the same color as the body. A pair of fleshy parapodia cover the gills, and the head bears two long olfactory rhinophores and two fleshy oral tentacles on each side of the mouth; the adults lack a shell since the juveniles, when they reach 3 mm in length, detach from it. The parapodia does not let it swim like other sea hares because they are fused together, leaving only a slit in the center of the dorsum.

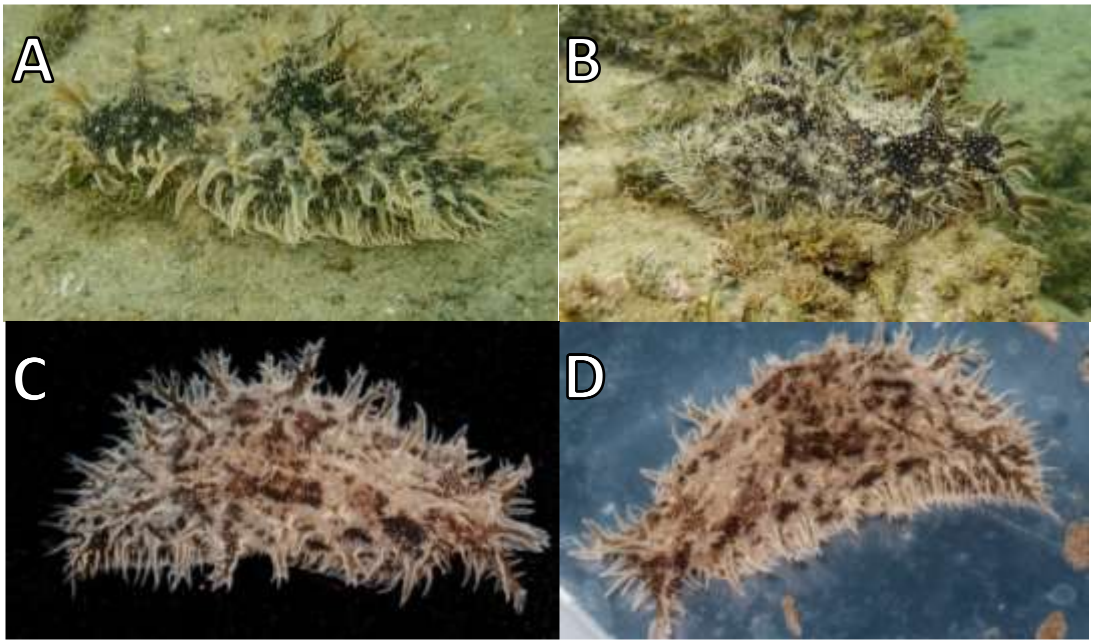

Figure 3. Specimens of *Bursatella leachii*, A and B from the bathing area of El Forum, Barcelona; C and D from the Ebro Delta.

2.5.4. ***Radular and jaw structure***

The radular formula of a 130 mm specimen collected alive at the bathing area of Fórum, Barcelona, Spain was 40x35-6-1-6-35. Radula Taenioglossate, the central or rachidial teeth with a geometric shape similar to a trapezoid on the top has a robust hair-shaped denticule with a cusp of four small denticles on both sides, they have a dentate main cusp and flanking cusps, basal projection with a concave shape and marginal crest, this tooth measures 84.72 μm long, 43.58 μm long, and 80.84 μm long (Figure 4A); the lateral teeth have a sickle-like cusp with three to four well-defined large denticles, between them there is a small space. Also, there is an apex, main cusp, inner flanking cusp, and outer flanking cusp, with outer margin, inner margin and the stem very well defined, they measure about 189.70 μm long and 7.89 μm wide (Figure 4B); the marginal teeth have a banana-shaped cusp and do not have denticles, but their outer margin, inner margin, and stem are very well defined, measuring approximately 200 µm long and 7.89 µm wide (Figure 4C). The elements of the mandible are made up of tiny rods that are curved, smooth, and with a round cusp apex (Figure 4D).

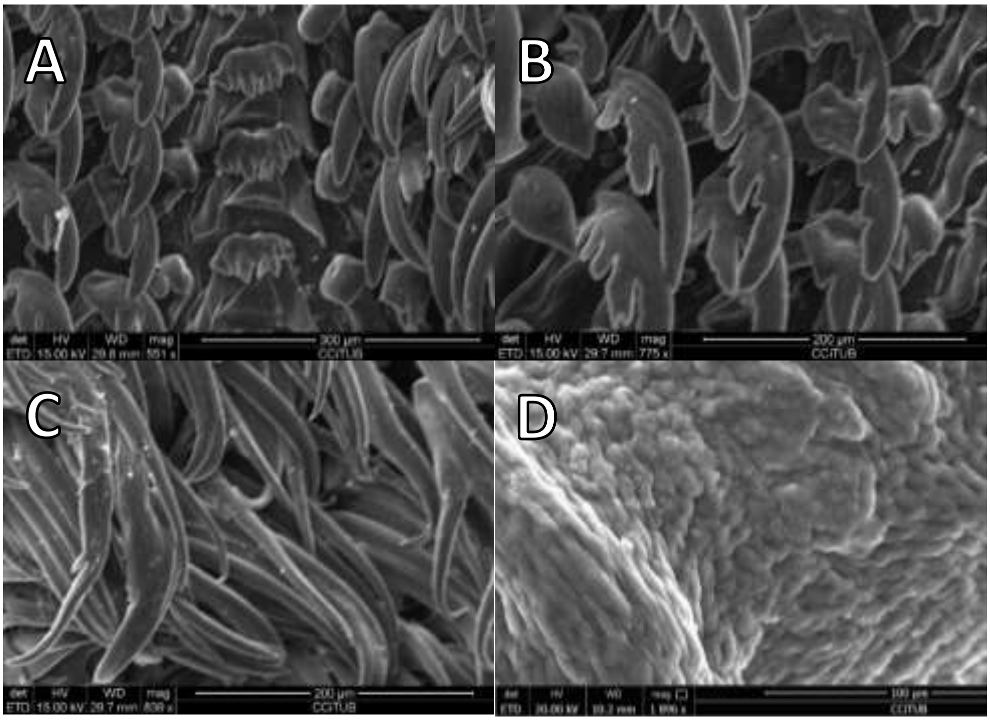

Figure 4. Scanning electron micrographs of radular teeth and jaws of samples of *Bursatella leachii* from the Fórum, Barcelona, Spain. A. Rachidian and first lateral teeth, B. Lateral teeth, C. Marginal teeth, and D. Elements of the jaw.

2.5.5. ***Biology***

B. leachii prefers shallow waters with almost no currents, which makes it very common in ports and lagoons. It is well associated with algae that grow on soft bottoms such as *Caulerpa prolifera* and *Cymodocea nodosa*, the aquatic plant *Zostera noltrii*, although it feeds on cyanobacteria such as *Lyngbya majuscula*, diatoms and macrophytes such as *Ectocarpus* and *Enteromorpha*. In the laboratory aquarium it has been possible to observe and film the feeding behavior over the *Dictyota dichotoma* algae: the animals rhythmically place their mouths on the algae without chopping it to possibly ingest the epiphytic flora of diatoms and other microscopic algae. Thanks to what they eat, the animals can accumulate secondary metabolites of lyngbyatoxin, a group that has an antimicrobial and cytotoxic effect, which accumulate in the glands of their skin; according to Capper *et al.* (2005) use it to protect themselves from any predator. Its behavior is described by Ramos *et al.* (1995), on the coast of Puerto Rico where they detail that they like to congregate at night and walk alone during the day. Paige (1988) has cited up to more than 600 individuals of *B. leachii* per square meter. This behavior of aggregation of individuals has also been observed in our paper within Forum bathing area, Barcelona, Spain, on a ramp to launch boats into the water at a depth of 1 m.

When they reproduce they gather in small groups of 4 to 5 individuals forming a little train in which some serve as males and at the same time as female; after fertilization, the encapsulated eggs are aligned in the form of a cord with one to 20 eggs inside each capsule and a variable coloration of orange, brown, yellow to green or pink, measuring approximately 87 microns in diameter (Paige 1988).

2.6. Discussion

The ragged sea hare *Bursatella leachii* is a species that has been widely known since the beginning of the 19th century. Since then and due to its chromatic variability and its wide geographical dispersion, numerous species and subspecies have been described in practically all the tropical and subtropical zones of the Pacific, Indian and Atlantic, all of them but *B. ocelligera* and *B. hirsuta*, are currently considered synonyms of *B. leachii.*

After analyzing the results of both species delimitation (ASAP) and haplotype networks; we realize that everything is reduced to species of a group of *B. leachii* from a combination of the American Atlantic, Africa and the Mediterranean since they share morphological characteristics and genotypic sequences. This agrees in part with the article by Bazzicaluppo *et al.* (2018) who indicate that the Atlantic and Mediterranean specimens share the most common haplotypes, which shows that the Atlantic Ocean is not a barrier to the dispersal of the species from the Atlantic western coasts. Thanks to environmental changes and human activities, there are species such as *B. leachii* that can travel long distances and manage to establish themselves in favorable regions of the Mediterranean, where they can settle and compete with local species, producing a great impact on Mediterranean marine ecosystems (Bianchi & Morri 2003; Raitsos *et al.* 2010).

In addition to the transport of foreign species in the waters of the ballast tanks of large ships in larval form or in resistance spores, another circumstance that allows species to migrate from one place to another would be climate change. The warm waters of the Mediterranean are being altered by global warming allowing the permeability of species that can cross the great natural barrier of the Atlantic and disperse in the Mediterranean helped by the weakening of the cold current of the Canary Islands and the Saharan upwelling (Vermeij 2012). These cold currents and upwelling are thought to have been for a long time the main factor that has constituted a barrier and prevented the arrival of tropical and subtropical species from the Atlantic and African coasts to the Mediterranean through the Straits of Gibraltar (Patarnello *et al.* 2007); we believe this should have facilitated the expansion of this species to the Mediterranean due to the coincidences of the haplotypes that we have found of the populations of West Africa and the American Atlantic, with those of the Mediterranean. Specimens of *B. leachii* from Catalonia share haplotypes with specimens from both shores of the Atlantic and with others from the

Mediterranean Sea, but not with those from the Indo-Pacific, which confirms the hypothesis that they entered the Mediterranean Sea through the Strait of Gibraltar.

On the other hand, the natural characteristics of *B. leachii* allows it to colonize territories other than those usual, even when it does not have adequate food, because it adapts to unfavorable conditions in terms of the amount of food available (Clarke 2006), a highly favorable trait for a species that can adapt to other regions (Blackburn *et al.* 2009). Another very important aspect is that their larvae can be kept for more than three months, immediately after hatching, because their life cycle is short: adults mature very rapidly in a matter of a few months (Paige 1988).

Although there are biotic and abiotic factors, such as demographic and environmental stochasticity that affect the adaptation of invasive species (Lockwood *et al.* 2007), in the case of Atlantic invaders such as *B. leachii* have sufficient phenotypic plasticity (the ability to cope with a variety of environmental conditions) to survive, mate, produce offspring, and succeed in new habitats such as the Mediterranean without using evolutionary adjustments (Bernardi *et al.* 2010), an aspect that makes us deduce that the existence of species such as *B. leachii* make the natural barrier of the Atlantic Ocean permeable, crossing into the Mediterranean.

2.7. Conclusions

This is a species that seems to be expanding along the Catalonian coasts; the first record of *B. leachii* on the Catalonian coast (NE Spain) was recorded by Weitzmann *et al.* (2007) in the Ebro Delta, where it has been able to adapt very well due to its high incidence in the area. There are subsequent reports of its presence in the cages of the Vilanova i la Geltrú fish farms (Barcelona) in 2011, in the Fòrum bathing area (Barcelona) in 2012, in Cubelles (Barcelona) in 2015 (Ballesteros & Weitzmann 2016) and in the small natural brackish ponds of Creixell - Gorg beach (Tarragona) in 2020 (Carlos San Vicente, pers. comm.); but so far it has not been found in the colder waters of the North of Catalonia, such as those of the Costa Brava.

The molecular data obtained from our specimens from NE Spain, compared with other sequences of specimens from different areas, indicate that they share haplotypes with specimens that live in the Atlantic but not with specimens that live in the Indo-Pacific. This agrees with the data provided by Bazzicalupo *et al.* (2020) and would confirm the hypothesis that the Mediterranean specimens come more from a migration from the Atlantic through the Strait of Gibraltar than from a Lessepsian migration of specimens from the Red Sea.

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2.9. References

Ballesteros M. & Weitzmann B. 2016. La liebre de mar *Bursatella leachii* continúa su expansión en las costas catalanas. *Noticiario SEM*, 65:23-24.

Barash A. & Danin Z. 1986. Further additions to the knowledge of Indo-Pacific Mollusca in the Mediterranean Sea. *Spixiana*, 9: 117–141

Bazzicalupo E., Crocetta F., Estores-Pacheco K., Golestani H., Bazairi H., Giacobbe S., Jaklin A., Poursanidis D., Chandran D.B., Cervera J.L. & Valdés Á. 2018. Population genetics of *Bursatella leachii* (De Blainville, 1817) and implications for the origin of the Mediterranean population. *Helgoland Marine Research*, 72:19.

Bazzicalupo E., Crocetta F., Gosliner T., Berteaux-Lecellier V., Camacho-García Y., Sneha B. & Valdés Á. 2020. Molecular and morphological systematics of *Bursatella leachii* de Blainville, 1817 and Stylocheilus striatus Quoy & Gaimard 1832 reveal cryptic diversity in pantropically distributed taxa (Mollusca: Gastropoda: Heterobranchia). *Invertebrate Systematics*, 34: 535–568.

Bernardi G., Golani D. & Azzuro E. 2010. The genetics of Lessepsian bioinvasions. In: Golani, D., Appelbaum-Golani, B. (Eds.), Fish Invasions of the Mediterranean Sea: Change and Renewal, p. 71 (Sofia, Moscow).

Bianchi C.N. & Morri C. 2003. Global sea warming and "tropicalization" of the Mediterranean Sea: biogeographic and ecological aspects. *Biogeogaphical. Journal of Integrated Biogeogr*aphy, 24:319–27.

Biologia Marina. 2022. Available at http://www.biologiamarina.org/wp/bursatella/ (accessed 20 April 2022)

Blackburn T.M., Cassey P. & Lockwood J.L. 2009. The role of species traits in the establishment of success of exotic birds. *Global Change Biol*ogy, 15(12):2852–60.

Capper A., Tibbetts I.R., O'Neil J.M. & Shaw G.R. 2005. The fate of *Lyngbya majuscula* toxins in three potential consumers. *Journal of Chemical Ecology*, 31:1595-1606.

Cesari P. 1990. La malacofauna della Laguna Veneta - 2. I gasteropodi Bullomorfi, Aplisiomorfi, Sacoglossi, Pleurobrancomorfi e Nudibranchi. *Bollettino del Museo Civico di Storia Naturale di Venezia*, 39: 21−43.

Cesari P. 1994. *I Molluschi della Laguna di Venezia.* Arsenale Editrice, Venezia, Italy, 190 pp

Cesari P., Mizzan L. & Motta E. 1986. Rinvenimento di *Bursatella leachii leachii* Blainville, 1817 in Laguna di Venezia. Prima segnalazione adriatica (Gastropoda Opistobranchia). *Lavori Sociata Veneziana Scientia Naturali*, 11: 5-16.

Clarke C.L. 2006. The population dynamics and feeding preferences of *Bursatella leachii* (Opisthobranchia: Anaspidea) in northeast Queensland, Australia. *Records of the Western Australian Museum, Suppl.*, 69:11–21.

Clement, M., Snell, Q., Walke, P., Posada, D. & Crandall, K. 2002. *TCS: Estimating Gene Genealogies.* Proceedings 16th International Parallel Distributed Processing Symposium, pp. 184

Córdoba D. & Ballesteros M. 2019. *La liebre de mar Bursatella leachii Blainville 1817, un invasor en las costas catalanas,* en VIMAR. Vida Marina, published on 31/01/2019 in https://vidamarina.info/?p=828, accessed 13 march 2022.

Crocetta F. 2011. Marine alien mollusca in Italy, a review. *Journal of the Marine Biological Association of the United Kingdom*, 2012, 92(6), 1357–1365

Crocetta F., Renda W. & Vazzana A. 2009. Alien mollusca along Calabrian shores of the Messina Strait area and a review of their distribution in the Italian seas. *Bolletino Malacologico*, 45: 15-30.

Crocetta F., Zibrowius H., Bitar G., Templado J. & Oliverio M. 2013. Biogeographical homogeneity in the eastern Mediterranean Sea - I: the opisthobranchs (Mollusca: Gastropoda) from Lebanon. *Mediterranean Marine Science*, 14(2): 403-408

Cunha C.M. & Simone L.R.L. 2019. Morphological re-description of *Aplysia depilans* (Gastropoda: Anaspidea): new insights into the anatomy of the anaspideans. *Journal of the Marine Biological Association of the United Kingdom*, 99(3): 595–610. https://doi.org/10.1017/S0025315418000528 (accessed 20 April 2022)

De Min R. & Vio E. 1998. Molluschi esotici nell'Alto Adriatico. *Annales 13 (compendio)*: 43–54

Despalatović M., Grubelić I., Nikolić V., Dragičević B., Dulčić J., Žuljević A., Cvitković I. & Antolić B. 2008. *Allochthonous warm water species in the benthic communities and ichthyofauna of the eastern part of the Adriatic Sea.* In: Briand F (ed), Climate warming and related changes in Mediterranean marine biota. CIESM Workshop Monographs N° 35, Monaco, pp 51−58

Drummond A.J., Ashton B., Buxton S., Cheung M., Cooper A., Heled J., Kearse M., Moir R., Stones-Havas S., Sturrock S., Thierer T. & Wilson A. 2010. *Geneious* v5.1. URL http://www.geneious.com.

European Sea Slugs Reports. 2022. Available at https://www.facebook.com/groups/OpisthobranchReports (accessed 20 April 2022)

Furfaro G., Vitale F., Licchelli C. & Mariottini P. 2020. Two Seas for One Great Diversity: Checklist of the Marine Heterobranchia (Mollusca; Gastropoda) from the Salento Peninsula (South-East Italy). *Diversity*, 12: 171.

GBIF. 2022. GBIF Home Page. Available from: https://www.gbif.org/species/9680062 (accessed 20 April 2022)

GROC. 2022. Available at https://opistobranquis.org/ca/guia/5 (accessed 20 April 2022)

Hillis D.M. & Bull J.J. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analyses. *Systematic Biology*, 42:182–192.

Ibáñez-Yuste A.J., Garrido-Díaz A., Espinosa-Torre F. & Terrón-Sigler A. 2012. Primera cita del molusco exótico *Bursatella leachii* de Blainville, 1817 (Mollusca: opistobranchia) en el litoral mediterráneo andaluz. *Chronica Naturae*, 2, 25-31.

IndOBIS. 2022. (Indian Ocean Node of Ocean Biodiversity Information System) Available at https://obis.org/node/1a3b0f1a-4474-4d73-9ee1-d28f92a83996 (accessed 19 april 2022)

Invert E Base. 2022. Available at https://www.invertebase.org/portal/taxa/index.php?tid=14826 (accessed 20 April 2022)

Jaklin A. & Vio E. 1989. *Bursatella leachii* Gastropoda Opisthobranchia in the Adriatic Sea. *Journal of Molluscan Studies*. 55(3): 419–420

JaxShells. 2022. Available at https://www.jaxshells.org/pete6018a.htm (accessed 20 April 2022)

Katsanevakis S., Zenetos A., Belchior C. and Cardoso A.C. 2013. Invading European seas: assessing pathways of introduction of marine aliens. *Ocean and Coastal Management*, 76:64–74.

Koutsoubas D. 1992. *Contribution to the study of the gastropod molluscs of the continental shelf of the North Aegean Sea*. PhD thesis, Biology Department, Aristotelion University of Thessaloniki, Greece, 585 pp

Koutsoubas, D. & Voultsiadou-Koukoura, E. 1991. The occurrence of *Rapana venosa* (Valenciennes, 1846) (Gastropoda, Thaididae) in the Aegean Sea. *Bollettino Malacologico*, 26(10-12): 201-204

Koutsoubas D. & Cinelli F. 1997. Indo-Pacific origin gastropod species in the Aegean Sea. *Melibe fimbriata* Alder & Hancock, 1864 a new invader. *Bollettino Malacologico* 32: 1–6

Lanfear R., Frandsen P.B., Wright A.M., Senfeld T. & Brett Calcott B. 2017. PartitionFinder 2: New Methods for Selecting Partitioned Models of Evolution for Molecular and Morphological Phylogenetic Analyses. *Molecular Biology and Evolution*, 34(3):772–773.

Leigh J.W. & Bryant D. 2015. PopART: full-feature software for haplotype network construction. *Methods in Ecology and Evolution*, 6:1110–1116.

Lipej L., Dobrajc Ž., Mavrič B., Šamu S. & Alajbegovič S. 2008. Opisthobranch mollusks (Mollusca: Gastropoda) from Slovenian Coastal waters (Northern Adriatic). Annales - *Series Historia Naturalis*, 18: 213–226

Lipej L., Acevedo I., Akel E., Anastasopoulou A., Angelidis A., Azzurro E., Castriota L., Çelik M., Cilenti L., Crocetta F., Deidun A., Dogrammatzi A., Falautano M., Fernández-Álvarez F., Gennaio R., Insacco G., Katsanevakis S., Langeneck J., Lombardo B., Mancinelli G., Mytilineou C., Papa L., Pitacco V., Pontes M., Poursanidis D., Prato E., Rizkalla S., Rodríguez-Flores P., Stamouli C., Tempesti J., Tiralongo F., Tirnettα S., Tsirintanis K., Turan C., Yaglioglu D., Zaminos G. & Zava B. 2018. New Mediterranean Biodiversity Records (March 2017). *Mediterranean Marine Science* 18(1): 179-201. http://dx.doi.org/10.12681/mms.2068

Lockwood J.L., Hoopes M.F. and Marchetti M.F. 2007. *Invasion Ecology*. Blackwell Publishing, Malden, p. 304.

Mačić V. and Kljajić Z. 2012. Pregled unešeneih vrsta u crnogorskom podmorju. *Vode*, 2012: 255–260

Mačić V. 2013. Contribution to the knowledge of *Bursatella leachii* De Blainville, 1817. Distribution and reproduction in the Boka Kotorska Bay (Montenegro). *Studia Marina*, 26: 119–128

Mare Nostrum Wildlife. 2022. Available at https://www.facebook.com/groups/meditphoto (accessed 20 April 2022)

Medslugs. 2022. Available from: http://www.medslugs.de/E/Med/Bursatella_leachii/Selection.htm

Mizzan L. 1999. Le specie alloctone del macrozoobenthos della Laguna di Venezia: il punto della situazione. *Bollettino del Museo Civico di Storia Naturale di Venezia*, 49: 145–177

Mizzan L. & Vianello C. 2009. Bursatella leachi – segnalazione di specie esotica infrequente nella laguna di Venezia. *Bollettino del Museo Civico di Storia Naturale di Venezia*, 59: 170

Molnar J.L.., Gamboa RL., Revenga C. & Spalding M.D. 2008. Assessing the global threat of invasive species to marine biodiversity. *Froniers in Ecology and Environ*ment, 6(9):485-492.

Nunes A.L., Katsanevkis S., Zenetos A. & Cardoso A.C. 2014. Gateways to alien invasions in the European seas. *Aquatic Invasions*, 9(2):133-144.

O'Donoghue C.H. and White KM. 1940. A collection of marine molluscs, mainly opisthobranchs, from Palestine. *Proceedings of the Malacological Society of London*, 24 (3):92-96.

OBIS. 2022. Ocean Biodiversity Information System. Intergovernmental Oceanographic Commission of UNESCO. https://obis.org/taxon/138759 (accessed 20 April 2022)

Oliver J.A. and Terrasa J. 2004. Primera cita de *Bursatella leachi* (de Blainville, 1817) (Mollusca, Opistobranchia) a Mallorca. *Bolletí de la Societatd'Història Natural de les Balears*, 47: 37-42

OPK. 2022. Available at https://opistobranquis.info/en/NNgfg (accessed 20 April 2022)

Paige J.A. 1988. Biology, metamorphosis and postlarval development of *Bursatella leachii plei* Rang (Gastropoda: Opisthobranchia). *Boletín de Ciencias del Mar*, 42:65-75.

Parera, A., Pontes, M., Salvador, X., & Ballesteros, M. 2020. Sea slugs (Mollusca, Gastropoda, Heterobranchia): the other inhabitants of the city of Barcelona (Spain). *Butlletí de la Institució Catalana d'Història Natural*, 84: 75-100.

Patarnello T., Volckaert F.A.M.J. & Castilho R. 2007. Pillar of Hercules: is the Atlantic Mediterranean transition a phylo-geographical break? *Molecular Ecology*, 16:4426–44.

Puillandre N., Brouillet S. and Achaz G. 2021. ASAP: assemble species by automatic partitioning. *Molecular Ecology Resources*, 21:609–620.

Raitsos D.E., Beaugrand G., Georgopoulos D., Zenetos A., Pancucci-Papadopoulou A.M., Theocharis A. & Papathanassiou E. 2010. Global climate change amplifies the entry of tropical species into the Eastern Mediterranean Sea. *Limnology and Oceanography*, 55(4):1478–84.

Ramos L.J., López R.J.L. & Miller M.W. 1995. Behavior patterns of the aplysiid gastropod *Bursatella leachii* in its natural habitat and in the laboratory. *Neurobiol. of Learning and Memory*, 63:246-259.

Rilov G. and Galil. B. 2009. Marine Bioinvasions in the Mediterranean Sea-History, distribution and Ecology. En: Rilov G, Crooks JA (eds.). *Biological Invasions in Marine Ecosystem*, capítulo 31:549-575.

Rinaldi A. 2007. Con la siccità migliora lo stato dell'Adriatico. *ARPA Rivista*, 4: 40–41

Rinaldi A. 2008. *Atlante della fauna e della flora nel sistema marino costiero dell'Emilia-Romagna*. Ed. La Mandragora, Imola, Italy, 408 pp

Rinaldi A. 2012. *Atlante della fauna e flora marina dell'Adriatico nord-occidentale*. Editrice La Mandragora, Imola, Italy, 642 pp

Selfati M., El Ouamari N., Crocetta F., Mesfioui A., Boissery P. & Bazairi H. 2017. Closing the circle in the Mediterranean Sea: *Bursatella leachii* Blainville, 1817 (Mollusca: Gastropoda: Anaspidea) has reached Morocco. *BioInvasions Records*, 6 (2): 129-134.

Stamatakis A. 2014. *RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies*. Oxford University Press.

Streftaris N., Zenetos A. & Papathanassiou E. 2005. Globalisation in marine ecosystems: the story of non-indigenous marine species acroos European seas. *Oceanography and Marine Biology, Annual Review*, 43:419-453.

Sylvester F., Kalaci O., Leung B., Lacoursie`re-Roussel A., Murray C.C., Choi F.M., Bravo M.A., Therriault T.W. & MacIsaac H.J. 2011. Hull fouling as an invasión vector: can simple models explain a complex problem? *Journal of Applied Ecology*, 48:415-423.

Tisselli M. and Mazziotti C. 2009. Distribuzione di *Bursatella leachii* De Blainville, 1817 lungo le coste italiane e segnalazioni dettagliate per le coste dell'Emilia-Romagna. *Notiziario S.I.M.* 27: 20–23

Turk T. & Furlan B. 2011. New records of Indo-Pacific and Atlantic mollusc species (Opisthobranchia) in the eastern Mediterranean and Adriatic Sea. *Annales - Series Historia Naturalis*, 21: 5–10

Underwater Photography in Greece. 2022. Available at https://www.facebook.com/groups/331466433724867 (accessed 20 April 2022)

Vaccarella R. 1986. Precisazioni sul ritrovamento di *Phyllidia pulitzeri* Pruvot-Fol e *Bursatella leachi* savignyana (Audouin) in Puglia. *Bollettino Malacologico*, 22: 91–92

Valdés A., Alexander J., Crocetta F., Yokeş M.B., Giacobbe S., Poursanidis D., Zenetos A., Cervera J.L., Caballer M., Galil B.S. & Schembri P.J. 2013. The origin and dispersal pathway of the spotted sea hare *Aplysia dactylomela* (Mollusca: Opisthobranchia) in the Mediterranean Sea. *Aquatic Invasions*, 8 (4):427–36.

Valdés A., Breslau E., Padula V., Schrödl M., Camacho-García Y., Malaquias M.A.E., Alexander J., Bottomley M., Vital X.G., Hooker Y. & Gosliner T.M. 2017. Molecular and morphological systematics of *Dolabrifera* Gray, 1847 (Mollusca: Gastropoda: Heterobranchia: Aplysiomorpha). *Zoological Journal of the Linnean Society*, 184:31–65. https://doi.org/10.1093/zoolinnean/zlx099 (accessed 20 April 2022)

Vermeij G.J. 2012. The tropical history and future of the Mediterranean biota and the West African enigma. *Journal of Biogeography*, 39:31–41.

Vio E. & De Min R. 1996. Contributo alla conoscenza dei Molluschi marini del Golfo di Trieste. *Atti del Museo Civico di Storia Naturale di Trieste*, 47: 173–233

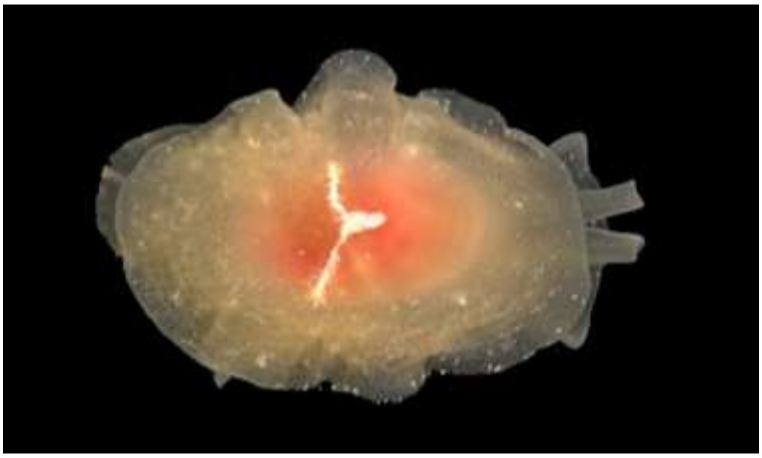
Weitzmann B., García M. & Ballesteros E. 2007. Primera cita de la llebre de mar *Bursatella leachi* (de Blainville, 1817) a la costa mediterrània peninsular. *Butlletí de la Institució Catalana d´Història Natural* 75:153-158.

Zenetos, A., Gofas, S., Russo, G. & Templado, J. 2004. *CIESM Atlas of Exotic Species in the Mediterranean* Vol. 3 Molluscs. (F. Briand, Ed) CIESM, Mónaco, 376 pp.

Zenetos A., Katsanevakis S., Beqiraj S., Mačić V., Poursanidis, D. & Kashta L. 2011. *Rapid assessment survey of marine alien species in the Albanian and Montenegrin coast.* Technical report. RAC/SPA, N° 37/38/39/2010: 54 pp

Zenetos A., Mačić V., Jaklin A., Lipej L., Poursanidis D., Cattaneo-Vietti R., Beqiraj S., Betti F., Poloniato D., Kashta L., Katsanevakis S. and Crocetta F. 2016. Adriatic 'opisthobranchs' (Gastropoda, Heterobranchia): shedding light on biodiversity issues. *Marine Ecology*, 37:1239–1255, https://doi.org/10.1111/maec.12306

CHAPTER III. Molecular analysis and population monitoring of *Berthella stellata* (Risso, 1826), (Mollusca: Gastropoda: Heterobranchia) from the Catalonian coasts.



Molecular analysis and population monitoring of *Berthella stellata* (Risso, 1826) (Mollusca: Gastropoda: Heterobranchia) from the Catalonian coasts (NE Spain).

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3.1. Abstract

Berthella stellata is a species of Pleurobranchidae characterized by a Y-shaped white patch on the dorsum, distributed in the Mediterranean and Eastern Atlantic. In this paper we have compiled records of this species on the Catalonian coast (NE Spain) and studied a permanent population of *B. stellata* over time in the town of Es Caials (Costa Brava, NE Spain). Live specimens were collected and photographed and details of their morphology, radula, and jaws, as well as molecular data were studied to compare them with other specimens from different parts of the range. Our results indicate that the specimens of population of *B. stellata* from Es Caials it has a great chromatic variability and shares both morphology and molecular aspects with specimens from the northeastern Atlantic and Mediterranean of Europe.

3.2. Keywords: *Berthella stellata*, molecular, specimens, population, Catalonian, Mediterranean

3.3. Introduction

The Pleuroibranchida *Berthella stellata* (Risso 1826) was identified for the first time in the Mediterranean (Risso, 1826; Thompson, 1981); it has also been recorded in the Indo-Pacific tropics to South Africa as *Berthella tupala* Er. Marcus, 1957 (Gosliner 1987), in the Sudanese Red Sea as *Berthella stellata albocrossata* (Heller & Thompson, 1983), in Australia as *Berthella postremana* (Burn 1962) and *Berthella pellucida* (Pease, 1860), such as *B. pellucida* in New Caledonia and Hawaii (Pease 1860; Risbec 1928; Burn 1962; Baba 1969; Thompson, 1970; Kay 1979; Willan 1984; Carlson and Hoff 2003; Wägele *et al.* 2006; Cobb 2008; Nakano 2018; Gosliner *et al.* 2018).

The Mediterranean Sea is extremely important to work on zoogeographical studies of populations of species such as *B. stellata*, because it is connected to the Atlantic Ocean by the Strait of Gibraltar, its apparent isolation, geological, climatic, and ecological alterations and high salinity throughout the year (Cattaneo-Vietti & Thompson 1989).

Berthella stellata is a species of sea slug characterized by having a white patch on the dorsum, variable background coloration, but normally brown, an internal shell, rolled rhinophores, and a flat frontal veil (Ballesteros *et al.* 2021). According to Thompson and Colman (1984) this white spot prevents teleost predators from the danger posed by eating a *B. slellata* because they can discharge inorganic acid allomones with a pH of 1-2.

Gosliner and Bertsch (1988) considered that *B. stellata* had a wide geographical spread in different oceanic regions, but the molecular data made in the work of Ghanimi *et al.* (2020) revealed that this species forms a complex of six cryptic species and that the name *B. stellata* is restricted to the Mediterranean and the eastern Atlantic.

The main objective of this work is to study the population of *B. stellata* in the locality of Es Caials (Costa Brava, Catalonia, NE Spain) and comparing it with other specimens of the same species from the northeastern Atlantic and Mediterranean regions of Europe. For doing this we have used morphological aspects, where we analyze the evolution of the population during two decades, the chromatic variability of the specimens and details of their biology. We also combined it with molecular analysis, using two mitochondrial genes (COI and 16S) and one nuclear gene (H3); in order to compare whether these populations of *B. stellata* are the same, both in the Northeast Atlantic and in the Mediterranean of Europe, with those found by us on the Catalonian coast of Es Caials.

3.4. Materials and methods

3.4.1 *Study area*

The evolution of the permanent population of *B. stellata* in Es Caials (Costa Brava, NE Spain) has been intermittently studied from 2001 to 2021 through qualitative samplings of about 3 h duration each. This locality is characterized by having a very shallow rocky beach formed by metamorphic schists with numerous stones under which a very diverse invertebrate community settle. The depth of the sampled area varies between 0.5 and 1.5 m (Figure 1). The upper surface of the stones located more superficially does not have algal settlement since they can frequently remain out of the water in times of high atmospheric pressure (called "secas" in the area). From 0.5 m the stones are covered with algae such as *Ulva* sp., *Dictyota dichotoma* Lamouroux 1809*, Ellisolandia elongata* Ellis & Solander 1786*, Padina pavonica* Thivy 1960*, Cystoseira* sp., *Halopteris* sp. and *Laurencia pinnatifida* Lamouroux 1813. From a depth of 2 m there is a meadow of *Posidonia oceanica* Delile 1813 with a high foliar density.

Figure 1. Location of Es Caials, Costa Brava, Girona, Spain and characteristics of the studied stone beach.

On the underside of the stones occurs an dense population of *B. stellata* accompanied by encrusting sponges (*Terpios fugax* Duchassaing & Michelotti 1864*, Halichondria panicea* (Pallas 1766), *Myxilla rosacea* (Lieberkühn 1859)*, Haliclona fistulosa* (Bowerbank 1866), *Tethya aurantium* (Pallas 1766)); actiniarians (*Anemonia viridis* (Forsskål 1775), *Exaiptasia diaphana* (Rapp 1829)); turbellarians as *Thysanozoon brocchii* (Risso 1818); colonial tunicates (*Botryllus schllosseri* (Pallas 1766), *Lissoclinum perforatum* (Giard 1872)*, Didemnum* sp.); sea stars (*Coscinasterias tenuispina* (Lamarck 1816), *Asterina gibbosa* (Pennant 1777)); sea urchins (*Paracentrotus lividus* (Lamarck 1816)*, Arbacia lixula* (Linnaeus 1758)); crustaceans (*Porcellana plathycheles* (Pennant 1777), *Pisidia longicornis* (Linnaeus 1767), *Eriphia verrucosa* (Forskål 1775), *Xantho poressa* (Olivi 1792), *Palaemon elegans* Rathke 1836, *Paguroidea* sp.); polyplacophorans molluscs such as *Rhysoplax olivaceus* (Spengler 1797), *Lepidopleurus cajetanus* (Poli 1791) and *Acanthochitona* sp.; bivalve molluscs (*Chama gryphoides* Linnaeus 1758*, Cardita calyculata* (Linnaeus 1758)); gastropods such as *Phorcus turbinatus* (Born 1778), *Columbella rustica* (Linnaeus 1758), *Aplus dorbigny* (Payraudeau 1826)*, Muricopsis cristata* (Brocchi 1814), *Gibula* sp., *Cerithium vulgatum* Bruguière 1792*, Vermetus triquetrus* Bivona-Bernardi 1832; other sea slugs such as *Dendrodoris limbata* (Cuvier 1804), *Doris verrucosa* Linnaeus 1758*, Tayuva lilacina* (Gould 1852), *Geitodoris planata* (Alder & Hancock 1846) and *Spurilla neapolitana* (Delle Chiaje 1841). This locality is also a place of copulation and spawning of numerous specimens of the sea hare *Aplysia punctata* (Cuvier 1803).

3.4.2. *Taxon sampling*

Berthella stellata specimens coded as Be and *Berthella* sp. called Bs were collected from Es Caials, Girona, NE Spain (Table 1). The specimens were collected while freediving at 0.5–1.5 m depth. One sequence of

B. pellucida from Maui, Hawaiian and *Berthella andromeda* Ghanimi, Schrödl, Goddard, Ballesteros, Gosliner & Valdés 2020 from Mexico was obtained from Genbank and used as an outgroup. To complete the dataset, we downloaded from Genbank all the available sequences of the species of the species *B. stellata* from different countries of Europe (Table 1).

Table 1. Information on all the specimens used in this study, including the specie, location, voucher (collection code) and the COI, 16S and H3 GenBank accession number.

Especie	Localidad	Voucher	COI	16S	H3
Berthella stellata	Es Caials, Girona, Spain	Be1	OK076928	OK067403	-------------
Berthella stellata	Es Caials, Girona, Spain	Be2	OK076927	-------------	-------------
Berthella stellata	Es Caials, Girona, Spain	Be3	OK076926	-------------	-------------
Berthella stellata	Es Caials, Girona, Spain	Be4	OK076925	OK067402	-------------
Berthella stellata	Es Caials, Girona, Spain	Be5	OK076924	OK067401	-------------
Berthella stellata	Es Caials, Girona, Spain	Be6	OK076923	-------------	-------------
Berthella stellata	Es Caials, Girona, Spain	Be7	OK076922	-------------	-------------
Berthella stellata	Es Caials, Girona, Spain	Be8	OK076921	-------------	OK073555
Berthella stellata	Es Caials, Girona, Spain	Be9	OK076920	OK067400	OK073554
Berthella stellata	Es Caials, Girona, Spain	Be10	OK076919	OK067399	OK073553
Berthella stellata	Es Caials, Girona, Spain	Be11	OK076918	OK067398	OK073552
Berthella stellata	Es Caials, Girona, Spain	Be12	OK076917	OK067397	OK073551
Berthella stellata	Es Caials, Girona, Spain	Be13	OK076916	OK067396	OK073550
Berthella stellata	Es Caials, Girona, Spain	Be14	OK076915	-------------	OK073549
Berthella stellata	Es Caials, Girona, Spain	Be15	OK076914	OK067395	OK073548
Berthella stellata	Es Caials, Girona, Spain	Be16	OK076913	-------------	OK073547
Berthella sp.	Es Caials, Girona, Spain	Bs1	OK076912	OK067394	OK073546
Berthella sp.	Es Caials, Girona, Spain	Bs2	OK076911	OK067393	OK073545
Berthella sp.	Es Caials, Girona, Spain	Bs3	OK076910	OK067392	OK073544
Berthella sp.	Es Caials, Girona, Spain	Bs4	OK076909	OK067391	OK073543
B. andromeda	Mazatlán, Mexico (1)	LACM 3654	MK542746	MK542708	MK542774
B. andromeda	Mazatlán, Mexico (2)	CPIC 01418	------------	MK542709	MK542775
B. andromeda	El Tomatal, Baja California, Mexico	CASIZ 182217A	------------	MK542710	MK542776
B. pellucida	Maui, Hawaiian Is. (1)	CPIC 01714	MK542752	MK542716	MK542783
B. pellucida	Maui, Hawaiian Is. (2)	CPIC 01714	MK542753	MK542717	MK542784
B. pellucida	Maui, Hawaiian Is. (3)	CPIC 01689	MK542754	MK542718	MK542785
B. stellata	Porto, Portugal	CPIC 01391	MK542755	MK542719	MK542786
B. stellata	Elba Is., Italy (1)	ZSM 20013043	MK542756	MK542720	MK542787
B. stellata	Elba Is., Italy (2)	ZSM 20013041	MK542757	MK542721	MK542788
B. stellata	Trapani, Sicily, Italy (1)	ZSM 20110680	MK542758	MK542722	------------
B. stellata	Trapani, Sicily, Italy (2)	ZSM 20110680	MK542759	MK542723	------------
B. stellata	Es Caials, Catalonia, Spain (1)	CPIC 02105	MK542760	MK542724	MK542789
B. stellata	Es Caials, Catalonia, Spain (2)	CPIC 02106	MK542761	MK542725	MK542790
B. stellata	St James, Jamaica	CPIC 00655	KM521691	KM521594	KM521621
B. stellata	Isla Canal de Afuera, Panama	LACM 153343	KM521692	------------	KM521622
B. stellata	Muros de Nalón, Asturias, Spain	CPIC 00445	KM521693	MK542726	KM521623
B. stellata	Italy	-----------------------	FJ917488	FJ917430	------------

3.4.3. ***Morphological analysis***

Dorsal incisions were made on specimens to study the internal anatomy under an Olympus SZ-PT binocular microscope; the buccal bulb, the radula, and jaws were extracted to study their characteristics under the scanning electron microscope. The buccal mass was immersed in 10% potassium hydroxide (KOH) for three hours to dissolve the tissue and separate the radula and jaws, which were then rinsed with distilled water. Radula and jaws were air-dried and mounted on a metallic stub with an adhesive layer and sputter coated with a carbon layer. Subsequently, the mounted samples were analyzed and photographed with a Quanta 200 model scanning electron microscope at the Technical Scientific Service (CCiTUB) of the University of Barcelona.

3.4.4. ***Molecular procedures***

Specimens were collected live in the field, immediately transferred to absolute ethanol and stored at -20 ºC for the subsequent DNA extraction. Total genomic DNA was extracted from foot tissue of each specimen using the REDExtract-N-Amp™ TissuePCR Kit Protocol from Sigma-Aldrich, following the manufacturer's protocol.

Partial fragments of two mitochondrial genes and one nuclear gene were sequenced: COI (cytochrome c oxidase subunit I), 16S (ribosomal RNA) and histone H3. The primers used for amplification are listed in Table 2. The LCO1490/HCO2198 was the preferred combination, while Nancy was used as a replacement for HCO2198.

Table 2. Primers used for each gene

Gene	Primers Name	Direction	Secuencia	Reference
COI	LCO1490	Forward	5'-GGTCAACAAATCATAAAGATATTGG-3'	Folmer *et al.* 1994
COI	HCO2198	Reverse	5'-TAAACTTCAGGGTGACCAAAAAATCA-3'	Folmer *et al.* 1994
COI	Nancy	Reverse	5'-CCCGGTAAAATTAAAATATAAACTTC-3'	Simon *et al* 1994
16S	16Sar	Forward	5'-CGCCTGTTTATCAAAAACAT-3'	Palumbi *et al.* 1996
16S	16Sbr	Reverse	5'-CCGGTYTGAACTCAGATCAYGT-3'	Palumbi *et al.* 1996
H3	H3F	Forward	5'-ATGGCTCGTACCAAGCAGACVGC-3'	Bernhard 1999
H3	H3R	Reverse	5'-CTTCTGGCGAGTTGCATATCCT-3'	Bernhard 1999

The polymerase chain reaction (PCR) was performed using 5µl 5x MyTaq Reaction Buffer (BIOLINE), 0,4 µl primers forward and reverse (10 µM), 0.2 µl MyTaq Red DNA Polymerase (BIOLINE), 4 µl of diluted DNA and ultrapure distilled water up to a total reaction volume of 20 µl. PCR conditions were as follows: for COI 5 min at 94°C followed by 35 cycles of denaturation at 95°C for 30 s, annealing temperature range of 45°C for 35 s, 72°C for 45 s and final extension at 72°C for 5 min; for Histone H3 5 min at 95°C followed by 35 cycles of denaturation at 95°C for 30 s, annealing at 48ºC for 35 s and extension at 72°C for 45 s and final extension at 72°C for 10 min; for 16s 5 min at 95°C followed by 35 cycles of denaturation 94°C for 35 s, annealing at 45°C for 35 s and extension at 72°C for 45 s. Final extension at 72°C for 5 min.

Fragments were visualized by agarose gel electrophoresis at a concentration of 1% (w/v) in 1X TBE buffer (0.89 M Tris, 0.89 M boric acid, 0.02 M EDTA) (Panreac AppliChem, Barcelona, Spain) at 110 V for 45 min. PCR products were sequenced in both directions using one of the respective amplification primers at Macrogen services (www.macrogen.com). The chromatograms were assembled and edited with Geneious Prime v. 2021.1.1. (Drummond *et al.* 2010).

3.4.5. ***Phylogenetic analysis***

Different matrices were built for downstream phylogenetic analyses: the COI, 16S and H3 data matrix contained all the available *Berthella stellata* sequences; the concatenated mitochondrial matrix with COI and 16S sequences; and the concatenated matrix with mitochondrial (COI + 16S) and nuclear (H3) sequences.

Phylogenetic analyses were conducted under Maximum likelihood (ML). The best partition scheme and evolutionary model for each partition was selected with Partition Finder v2.1.1 (Lanfear *et al.* 2017). ML analyses were performed with RAxML 8.0 (Stamatakis 2014) with 10000 replicates, random initial trees, and estimated parameters evolutionary models. Branches with bootstrap values above 70% were considered supported (Hillis & Bull 1993). The resulting trees were visualized with iToL (https://itol.embl.de/itol.cgi).

3.4.6. *Genetic p-distances and Species delimitation under the ASAP algorithm*

The MEGA X software (Kumar *et al.* 2018) was used to estimate uncorrected pairwise (p) distances within and between species using the Kimura 2-parameter model (1980). The Assemble Species by Automatic Partitioning (ASAP) species delimitation analysis (Puillandre *et al.* 2021) was used to help delimiting species using the three evolutionary models available (Simple Distance, Kimura (K80) and Jukes-Cantor (JC69)). Each analysis was run independently using default settings.

3.4.7. *Biological data*

The specimens were photographed live both in the field and in the laboratory to observe the different color patterns. In some instances, specimens were left in small aquaria with seawater to induce them to lay eggs. The characteristics of the community where the specimens were found were noted, as well as the possible food sources and predators. In total, all the observation data corresponding to approximately 100 sampling hours, including the number of specimens, the substrate where they were found, the copulations between specimens and spawning, were recorded.

3.5. Results

3.5.1. *Phylogenetic tree analysis*

The COI, 16S mitochondrial data array and the concatenated H3 data array included, respectively, 1113 bases and 1441 bases with 34 sequences. Maximum likelihood analysis of the arrays resulted in tree-like topologies (Figure 2, Figure 8, Figure 9, and Figure 10). The *Berthella stellata* from the Mediterranean, those from the Northeast Atlantic and the specimens collected in Es Caials, Catalonia, NE Spain (Be and Bs) are a monophyletic group (Figure 2, group 1, red bar) with an equal high-supporting Bootstrap to 100 (Figure 2).

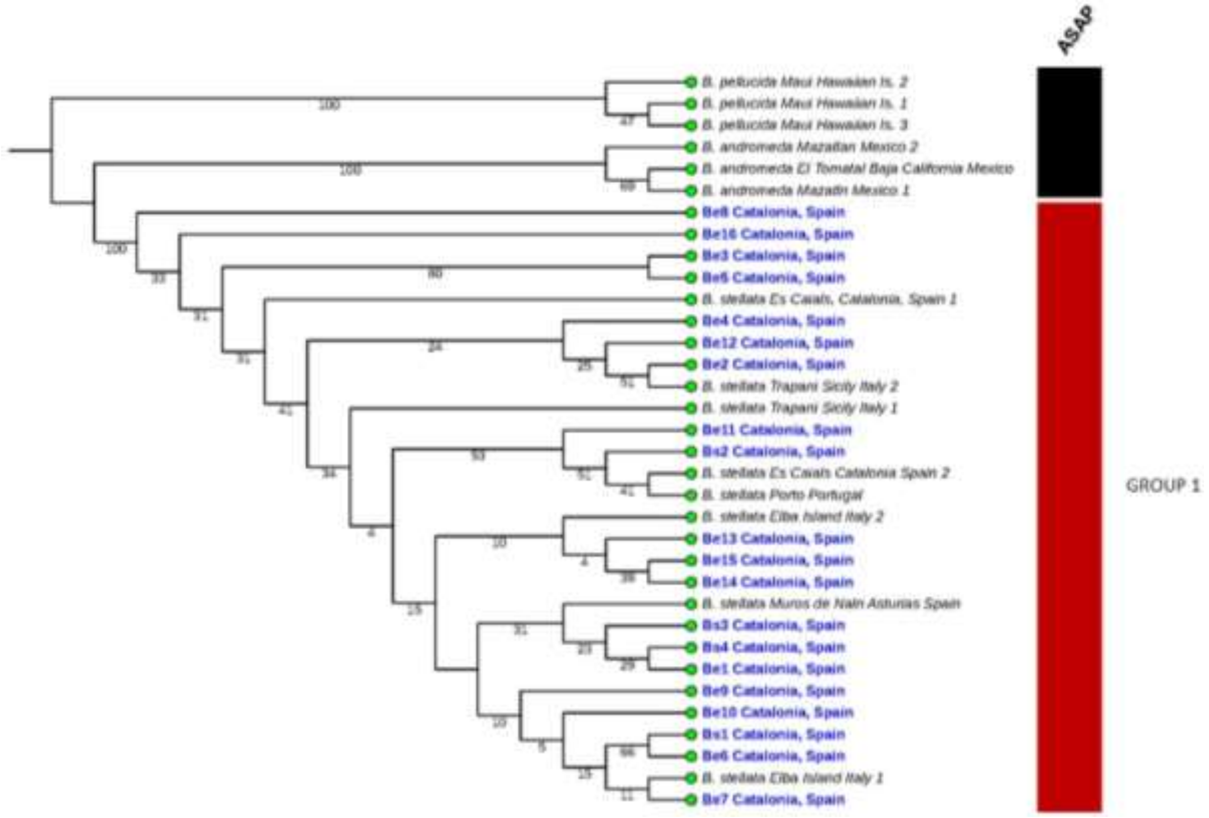

Figure 2. Combined results of Maximum Likelihood (ML) and species delimitation analysis. Phylogenetic tree of concatenated genes (COI, 16S and H3) of *Berthella stellata* under maximum likelihood analysis by RAxML. The numbers at the nodes represent ML bootstraps. The names in blue are the specimens we sampled; names in black are GenBank sequences. The colored bars represent the results of the ASAP analysis.

3.5.2. *Genetic distances and Species delimitation under the ASAP algorithm*

The p-genetic distances between the Es Caials (Be and Bs) specimens studied in this work and those of other *Berthella stellata* have been calculated using molecular data obtained from Genbank. These data allow us to verify that the specimens of *B. stellata* (Be) and *Berthella* sp. (Bs) along with those from the Mediterranean and the Northeast Atlantic, represent the same species since, the minimum p-genetic distance for COI between Be and Bs specimens is 0% and the maximum is 2.4%; among specimens of Be, Bs and those of *B. stellata* from other Mediterranean sites, the minimum is 0% and the maximum is 2%; and the minimum p-genetic distance with the other specimens from the Northeast Atlantic is 0.03% and the maximum is 2.1%.The intra- and interspecific genetic distances (p-genetic distance) for the *Berthella stellata* are shown in Table 3. The results of the analysis with ASAP yielded one "groups" (red bar) there are 28 specimens from the Mediterranean Sea identified as *B. stellata*: *B. stellata* from Portugal; from Trapani, Sicily, and Elba Island, Italy; from Es Caials, Catalonia, NE Spain (Be and Bs, all collected by us) (Figure 2).

Table 3. Comparison of the intraspecific and interspecific genetic p-distance of *Berthella stellata*

Specimens	Be1	Be2	Be3	Be4	Be5	Be6	Be7	Be8	Be9	Be10	Be11	Be12	Be13	Bs1	Bs2	Bs3	Bs4
Be1	0	0.018	0.020	0.018	0.020	0.016	0.010	0.021	0.014	0.013	0.010	0.021	0.015	0.016	0.024	0.016	0.019
Be2	0.018	0	0.001	0	0.002	0.005	0.008	0.002	0.004	0.004	0.003	0.003	0.004	0.005	0.009	0.004	0.004
Be3	0.020	0.001	0	0.01	0.001	0.006	0.010	0.001	0.005	0.006	0.004	0.004	0.006	0.006	0.011	0.006	0.006
Be4	0.018	0	0.001	0	0.002	0.005	0.008	0.002	0.004	0.004	0.003	0.003	0.004	0.005	0.009	0.004	0.004
Be5	0.020	0.002	0.001	0.002	0	0.007	0.010	0	0.006	0.006	0.005	0.005	0.006	0.007	0.011	0.006	0.006
Be6	0.016	0.005	0.006	00.5	0.007	0	0.006	0.007	0.002	0.002	0.004	0.008	0.002	0	0.011	0.003	0.005
Be7	0.010	0.008	0.010	0.008	0.010	0.006	0	0.011	0.004	0.003	0.008	0.011	0.005	0.006	0.014	0.006	0.009
Be8	0.021	0.002	0.001	0.002	0	0.007	0.011	0	0.006	0.007	0.006	0.006	0.007	0.008	0.012	0.007	0.007
Be9	0.014	0.004	0.005	0.004	0.006	0.002	0.004	0.006	0	0	0.003	0.007	0	0.002	0.010	0.002	0.004
Be10	0.013	0.004	0.006	0.004	0.006	0.002	0.003	0.007	0	0	0.004	0.007	0.001	0.002	0.010	0.002	0.005
Be11	0.018	0.003	0.004	0.003	0.006	0.004	0.008	0.006	0.003	0.004	0	0.006	0.004	0.004	0.006	0.004	0.004
Be12	0.021	0.003	0.004	0.003	0.005	0.008	0.011	0.006	0.007	0.007	0.006	0	0.007	0.008	0.012	0.007	0.007
Be13	0.015	0.004	0.006	0.004	0.006	0.002	0.005	0.007	0	0.001	0.004	0.007	0	0.002	0.010	0.002	0.005
Be14	0.015	0.004	0.006	0.004	0.006	0.002	0.005	0.007	0	0.001	0.004	0.007	0	0.002	0.010	0.002	0.005
Be15	0.015	0.003	0.004	0.003	0.005	0.001	0.005	0.006	0	0.001	0.003	0.006	0.001	0.002	0.009	0.001	0.004
Be16	0.020	0.001	0	0.001	0.001	0.006	0.009	0.001	0.005	0.006	0.004	0.004	0.006	0.006	0.010	0.006	0.006
Bs1	0.016	0.005	0.006	0.005	0.007	0	0.006	0.008	0.002	0.002	0.004	0.008	0.002	0	0.011	0.003	0.005
Bs2	0.024	0.009	0.011	0.009	0.011	0.011	0.014	0.012	0.010	0.010	0.006	0.012	0.010	0.011	0	0.010	0.010
Bs3	0.016	0.004	0.006	0.004	0.006	0.003	0.006	0.007	0.002	0.002	0.004	0.007	0.002	0.003	0.010	0	0.005
Bs4	0.019	0.004	0.006	0.004	0.006	0.005	0.009	0.007	0.004	0.005	0.004	0.007	0.005	0.005	0.010	0.005	0
B. stellata Es Caials, Catalonia, Spain	0.020	0.001	0	0.001	0.001	0.006	0.010	0.001	0.005	0.006	0.004	0.004	0.006	0.006	0.011	0.006	0.006
B. stellata Muros de Nalón, Asturias, Spain	0.016	0.004	0.006	0.004	0.006	0.003	0.006	0.007	0.002	0.002	0.004	0.007	0.002	0.003	0.010	0	0.005
B. stellata Porto, Portugal	0.021	0.006	0.007	0.006	0.008	0.007	0.011	0.009	0.006	0.007	0.003	0.009	0.007	0.008	0.006	0.007	0.007
B. stellata Trapani, Sicily, Italy	0.017	0.001	0.003	0.001	0.003	0.003	0.006	0.004	0.002	0.003	0.001	0.004	0.002	0.003	0.007	0.003	0.003
B. stellata Elba Island Italy	0.010	0.004	0.005	0.004	0.006	0.001	0.005	0.007	0	0.001	0.003	0.007	0.001	0.001	0.010	0.002	0.004

3.5.3. *Morphological results*

Specimens can reach up to 30 mm in length. There is a certain variability between the specimens studied. Some specimens are translucent-white, others light and dark brown (Figure 3), with a white Y-shaped spot on the dorsum that varies in shape until it disappears in adults, and others with numerous white spots all over body and without the white Y-shaped spot on the dorsum; the smaller specimens can be white, yellow or red; rhinophores, oral veil, gill and tentacles of same coloration of body, rhinophores and tentacles short and thick (Figure 4), bipinnate gill with 16 laminations in 10 mm specimen; oval shell with semi-transparent inner shell; our live specimens have a size between 8-30 mm and the preserved ones between 6-12 mm.

Figure 3. Different colors of *Berthella stellata* specimens under the same stone in Es Caials.

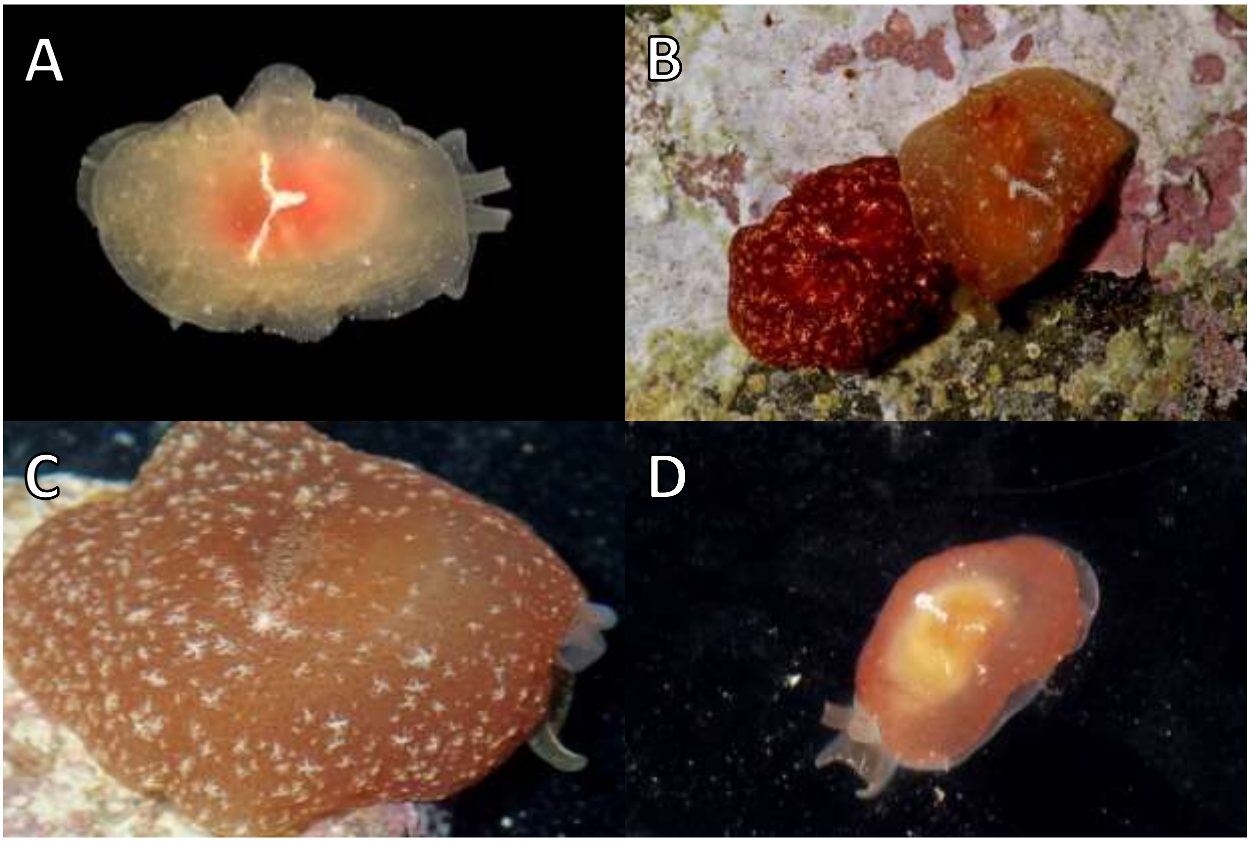

Figure 4. Specimens of *Berthella stellata* from A and D from the Costa Brava; B and C from Es Caials, Girona, Spain

3.5.4. Radular and jaw structure

The radular formula of a 15 mm living specimen, collected in Es Caials, Girona, was 56 x 50-0-50. The type of radula is ptenoglossate, the radular teeth are hook-shaped and attached to the radular membrane by a broad base; the innermost teeth are smaller and have a short cusp, as the teeth are more lateral they become larger and with a longer hooked cusp; the outermost teeth of each row are elongated with the end somewhat curved (Figure 5A). The elements of the jaws have a central cusp with 4-5 denticles on each side (Figure 5B). The shell is oval and internal, very fragile and semi-transparent.

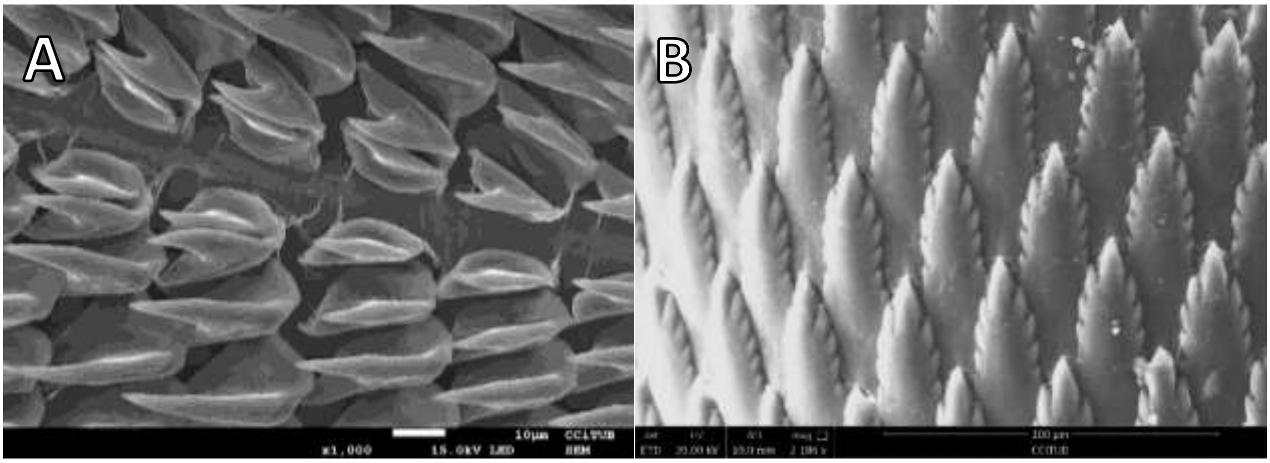

Figure 5. Scanning electron micrographs of radular teeth and jaw of *Berthella stellata* samples from Es Caials, Girona, Spain. A. mediolateral and internal teeth, B. elements of the jaw.

3.5.5. Biology

Berthella stellata is relatively frequent on the Catalonian coasts (NE Spain), living under stones or other submerged objects in shallow water. In Table 4 all the localities in which the species has been cited in the Mediterranean Sea and nearby Atlantic are listed. The locality of Es Caials is special because it has some ideal characteristics for the persistence of a population year after year: a stable environment protected from wave action, shallow depth, abundant in stones that it uses for its protection and in numerous colonies of colonial tunicates; feeds on sponges and sea squirts. Although specimens can be found throughout the year, it is in the months of May and June when they are more abundant in Es Caials (Figure 6), with up to 10-12 specimens closely together under the same stone, at about 30-50 cm depth. During this time the individuals copulate and lay egg masses under the stones in the form of a gelatinous and semi-transparent spiral ribbon of about 2 whorls with white eggs (Figure 7).

According to a personal communication from Enric Madrenas, another locality of the Catalonian coast where *B. stellata* is well established and has a permanent population is La Punta del Romaní, in L'Escala (see Table 4). In this locality, the specimens are found under stones on the coast, about 30 m long and up to 8 m deep. Under the stones there is a significant amount of sponges, bryozoans, platyhelminths, ascidians, etc. Two to three individuals of *B. stellata* can appear under a stone and have been observed spawning in the months of July, August and December.

Table 4. Georeferenced records of *Berthella stellata* in the Mediterranean and near Atlantic based on the OPK database. The records that do not have a collection date have been placed at the end of the table. Notes: OPK: OPK Opistobranquis, the site to watch and learn about Mediterranean and the Iberian sea slugs. GROC: Research Group of Catalan Opisthobranchs. CAT: records of specimens on the Catalonian coasts. UB: University of Barcelona.

Locality	**Observer**	**Date (D/M/Y)**
Greece	Aegean macrobenthic fauna	07/02/1937
Cabo de Palos, Murcia, Spain	Templado, 1982	07/01/1981
Playa Santa Mª del Mar, Cádiz, Spain	Cervera & Garcia, 1986	08/01/1984
Qalet Marku, Maghtab, Malta Is.	Constantine Mifsud (in Medslugs)	06/26/1993
Capo Ceraso, Olbia, Sardegna, Italy	Mauro Doneddu (in Medslugs)	06/01/1994
Porto Legnaiuolo, Porto Istana, Sardegna, Italy	Mauro Doneddu (in Medslugs)	07/01/1994
Capo Ceraso, Olbia, Sardegna, Italy	Mauro Doneddu (in Medslugs)	04/01/1995
Calahonda, Granada, Spain	Sánchez Tocino, 2001	01/01/1996
Cerro Gordo, Granada, Spain	Sánchez Tocino, 2001	01/01/1996
Castell de Ferro, Granada, Spain	Sánchez Tocino, 2001	01/01/1996
Calahonda, Granada, Spain	Sánchez Tocino, 2001	11/01/1999
Cerro Gordo, Granada, Spain	Sánchez Tocino, 2001	11/01/1999
Castell de Ferro, Granada, Spain	Sánchez Tocino, 2001	11/01/1999
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	06/23/2001
Galenzana, Elba, Italy	P. Durán (in Ghanimi *et al.*, 2020)	06/30/2001
La Foradada, Portbou, CAT, Spain	Miquel Pontes, M@re Nostrum	10/13/2001
Sagres, Portugal	Fauna Ibérica, Museo Nacional Ciencias Naturales	07/10/2002
Uc Adalar, Antalya, Turkey	Adnan Buyuk, Sea Slug Forum	01/13/2003
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	02/17/2003
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	05/20/2004
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	05/13/2005
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	05/18/2005
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	05/24/2007
Faial, Azores Is.	Malaquias et al. (2009)	08/19/2007
Muros de Nalón, Asturias, Spain	Angel Valdés (in Ghanimi *et al.*, 2020)	08/28/2010
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	06/02/2011
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	06/22/2011
Bastione, Sicily, Italy	Vinicius Padula (in Ghanimi *et al.*, 2020)	10/21/2011
Portinho da Arrábida, Setúbal, Portugal	João Pedro Silva	01/23/2012
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	05/23/2013
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	05/28/2013
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	05/29/2013
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	06/12/2013
Morro de Vedell, Palamós, CAT, Spain	Enric Madrenas, OPK	01/03/2014
Morro de Vedell, Palamós, CAT, Spain	Enric Madrenas, OPK	01/25/2014
Port de València, Valencia, Spain	Joan Josep Soto Àngel, GROC	05/23/2014
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	05/27/2014
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	06/09/2014
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	06/09/2014
Es Caials, Cadaqués, CAT, Spain	Enric Madrenas, OPK	06/15/2014
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/28/2014
Cala d´Aiguafreda, Begur, CAT, Spain	Enric Madrenas, OPK	03/13/2015
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	05/26/2015
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	05/26/2015
Platja de Sant Antoni, Portlligat, CAT, Spain	Enric Madrenas, OPK	07/03/2015
Platja de Sant Antoni, Portlligat, CAT, Spain	Enric Madrenas, OPK	07/03/2015
Platja de Sant Antoni, Portlligat, CAT, Spain	Miquel Pontes, M@re Nostrum	07/03/2015
Cala d´Aiguafreda, Begur, CAT, Spain	Enric Madrenas, OPK	07/05/2015
Praia de Gondarém, Porto, Portugal	Angel Valdés (in Ghanimi *et al.*, 2020)	07/13/2015
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	07/21/2015
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	07/21/2015
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	07/22/2015
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	07/22/2015
Es Caials, Cadaqués, CAT, Spain	Enric Madrenas, OPK	07/24/2015
Es Caials, Cadaqués, CAT, Spain	Enric Madrenas, OPK	07/24/2015

Cala Margarida, Palamós, CAT, Spain	Enric Madrenas, OPK	07/28/2015
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	08/04/2015
Es Caials, Cadaqués, CAT, Spain	Enric Madrenas, OPK	08/04/2015
Es Caials, Cadaqués, CAT, Spain	Enric Madrenas, OPK	08/04/2015
Es Caials, Cadaqués, CAT, Spain	Enric Madrenas, OPK	08/04/2015
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	08/08/2015
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	08/08/2015
Coves Cala Maset, Sant Feliu de Guíxols, CAT, Spain	Xavier Salvador, GROC	08/09/2015
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	08/13/2015
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	08/13/2015
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	08/21/2015
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	08/21/2015
Morro de Vedell, Palamós, CAT, Spain	Xavier Salvador, GROC	08/22/2015
Morro de Vedell, Palamós, CAT, Spain	Xavier Salvador, GROC	08/22/2015
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	08/26/2015
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	08/26/2015
Punta d´en Bosch, Sant Feliu de Guíxols, CAT, Spain	Xavier Salvador, GROC	08/29/2015
Punta d´en Bosch, Sant Feliu de Guíxols, CAT, Spain	Xavier Salvador, GROC	08/29/2015
Punta d´en Bosch, Sant Feliu de Guíxols, CAT, Spain	Xavier Salvador, GROC	09/03/2015
Morro de Vedell, Palamós, CAT, Spain	Xavier Salvador, GROC	09/05/2015
Cala Aigua-xelida, Palafrugell, CAT, Spain	Xavier Salvador, GROC	09/05/2015
Llafranc, CAT, Spain	Xavier Salvador, GROC	09/09/2015
Cala Ventosa, Sant Feliu de Guíxols, CAT, Spain	Xavier Salvador, GROC	09/15/2015
Platja de Sant Antoni, Portlligat, CAT Spain	Enric Madrenas, OPK	12/07/2015
Morro de Vedell, Palamós, CAT, Spain	Enric Madrenas, OPK	04/08/2016
Adriatic Sea	Gianni Colucci, Facebook	04/16/2016
Maremorto lagoon, Bacoli, Naples, Italy	Guido Villani, Opisthobranch Reports (Facebook)	04/19/2016
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	05/24/2016
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	05/24/2016
La Fosca, Palamós, CAT, Spain	Manuel Ballesteros, UB, OPK	05/26/2016
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	06/08/2016
La Fosca, Palamós, CAT, Spain	Enric Madrenas, OPK	06/10/2016
Lošinj, Croatia	Biostation Losinj	06/23/2016
Es Caials, Cadaqués, CAT, Spain	5ª Marató GROC 2016	06/25/2016
Es Caials, Cadaqués, CAT, Spain	Bernat Garrigós, GROC	06/25/2016
Es Caials, Cadaqués, CAT, Spain	Francisdco Javier Lindo, GROC	07/06/2016
Es Caials, Cadaqués, CAT, Spain	Enric Madrenas, OPK	07/14/2016
Punta d´en Bosch, Sant Feliu de Guíxols, CAT, Spain	Xavier Salvador, GROC	07/25/2016
Far de S'Arnella, Port de la Selva, CAT, Spain	Enric Madrenas, OPK	07/29/2016
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	07/30/2016
Cala Castell, Palamós, CAT, Spain	Xavier Salvador, GROC	08/01/2016
S´Arenella, Cadaqués, CAT, Spain	Carles Galiá, UB	05/17/2017
Es Caials, Cadaqués, CAT, Spain	Carles Galiá, UB	05/17/2017
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	06/14/2017
Punta del Romaní, L'Escala, CAT, Spain	Miquel Pontes, M@re Nostrum, OPK	07/08/2017
Cala Margarida, Palamós, CAT, Spain	Enric Madrenas, OPK	07/25/2017
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	08/03/2017
Llafranc, CAT, Spain	Xavier Salvador, GROC	08/09/2017
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	08/12/2017
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	08/18/2017
Punta del Romaní, L'Escala, CAT, Spain	Xavier Salvador, GROC	08/30/2017
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	09/05/2017
Coves Cala Maset, Sant Feliu de Guíxols, CAT, Spain	Xavier Salvador, GROC	09/14/2017
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	09/21/2017
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	10/13/2017
Coves Cala Maset, Sant Feliu de Guíxols, CAT, Spain	Xavier Salvador, GROC	10/16/2017
Coves Cala Maset, Sant Feliu de Guíxols, CAT, Spain	Xavier Salvador, GROC	10/24/2017
Es Caials, Cadaqués, CAT, Spain	Guillem Mas, GROC	11/12/2017
Piscines del Forum, Barcelona, CAT, Spain	Xavier Salvador (in Parera *et al*., 2020)	11/23/2017
Piscines del Forum, Barcelona, CAT, Spain	Xavier Salvador (in Parera *et al*., 2020)	11/25/2017
Piscines del Forum, Barcelona, CAT, Spain	Xavier Salvador (in Parera *et al*., 2020)	12/23/2017
Piscines del Forum, Barcelona, CAT, Spain	Xavier Salvador (in Parera *et al*., 2020)	02/03/2018

Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	02/16/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	02/17/2018
Cala d´Aiguafreda, Begur, CAT, Spain	Enric Madrenas, OPK	03/28/2018
Far de S'Arnella, Port de la Selva, CAT, Spain	Enric Madrenas, OPK	04/21/2018
Piscines del Forum, Barcelona, CAT, Spain	Xavier Salvador (in Parera *et al*., 2020)	04/27/2018
Piscines del Forum, Barcelona, CAT, Spain	Manuel Ballesteros (in Parera *et al*., 2020)	05/16/2018
Piscines del Forum, Barcelona, CAT, Spain	Xavier Salvador (in Parera *et al*., 2020)	05/18/2018
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	05/23/2018
Cala d´Aiguafreda, Begur, CAT, Spain	Xavier Salvador, GROC	05/25/2018
Cala d´Aiguafreda, Begur, CAT, Spain	Enric Madrenas, OPK	05/27/2018
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	06/05/2018
Piscines del Forum, Barcelona, CAT, Spain	Enric Madrenas, OPK	06/20/2018
Badia dels Alfacs, Ebro Delta, CAT, Spain	Manuel Ballesteros, UB, OPK	06/21/2018
Es Caials, Cadaqués, CAT, Spain	Enric Madrenas, OPK	06/23/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/13/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/15/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/16/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/19/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/23/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/26/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/27/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/28/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/30/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/31/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	08/01/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	08/03/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	08/04/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	08/07/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	08/08/2018
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	08/09/2018
Cala d´Aiguafreda, Begur, CAT, Spain	Enric Madrenas, OPK	12/30/2018
Piscines del Forum, Barcelona, CAT, Spain	Xavier Salvador (in Parera *et al*., 2020)	02/02/2019
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	03/10/2019
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	03/16/2019
Piscines del Forum, Barcelona, CAT, Spain	Marc Peralta (in Parera *et al*., 2020)	04/27/2019
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	05/22/2019
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/01/2019
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	06/05/2019
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/17/2019
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/23/2019
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/08/2019
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/12/2019
Es Caials, Cadaqués, CAT, Spain	Enric Madrenas, OPK	08/12/2019
Cala Margarida, Palamós, CAT, Spain	Enric Madrenas, OPK	09/12/2019
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	09/16/2019
Piscines del Forum, Barcelona, CAT, Spain	Xavier Salvador (in Parera *et al*., 2020)	11/20/2019
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/18/2020
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/28/2020
Racó d'en Bofill, Cadaqués, CAT, Spain	Anja Mares, GROC	06/30/2020
Es Caials, Cadaqués, CAT, Spain	Enric Madrenas, OPK	07/03/2020
Es Caials, Cadaqués, CAT, Spain	Enric Madrenas, OPK	07/16/2020
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	08/19/2020
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	09/01/2020
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	09/03/2020
Cala Margarida, Palamós, CAT, Spain	Enric Madrenas, OPK	11/04/2020
Cala Montgó, L'Escala, CAT, Spain	Enric Madrenas, OPK	12/16/2020
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	12/29/2020
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	02/10/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	03/25/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	03/30/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	04/09/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	04/10/2021

Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	04/26/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	04/29/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	04/30/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	05/04/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	05/05/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	05/07/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	05/12/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	05/20/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	05/24/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	05/27/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	05/31/2021
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	06/02/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/04/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/08/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/11/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/15/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/16/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/20/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/22/2021
Punta del Romaní, L’Escala, CAT, Spain	Enric Madrenas, OPK	06/23/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/24/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/25/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	06/27/2021
Es Caials, Cadaqués, CAT, Spain	Enric Madrenas, OPK	07/03/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/19/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/28/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/30/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	07/31/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	08/06/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	08/07/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	08/10/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	08/12/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	08/13/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	08/14/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	08/15/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	09/25/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	10/30/2021
Cala d´Aiguafreda, Begur, CAT, Spain	Enric Madrenas, OPK	12/08/2021
Punta del Romaní, L'Escala, CAT, Spain	Enric Madrenas, OPK	12/17/2021
Es Caials, Cadaqués, CAT, Spain	Manuel Ballesteros, UB, OPK	06/23/2021
Los Escullos, Almería	Ballesteros *et al*., 1986	
Menorca Is.	Ballesteros *et al*., 1986	
Canary Is.	Malaquias & Calado, 1997	
Canary Is.	Ortea *et al.,* 2001	
Platja de Sant Antoni, Portlligat CAT, Spain	Domènech *et al.,* 2002	
Canary Is.	Wirtz & Debelius, 2003	
Azores Is.	Wirtz & Debelius, 2003	
Península ibérica	Cervera *et al*., 2004	
Marina de Arrecife, Lanzarote, Spain	Bacallado *et al*., 2008	
Izola, Slovenia	Lipej *et al*., 2008	
Turkish coasts	Ozturk *et al.,* 2014	
Otranto, Lecce, Italy (Adriatic Sea)	Furfaro *et al*., 2020	
Torre Inserraglio, Lecce, Italy (Ionian Sea)	Furfaro *et al*., 2020	
Omiš, Croatia	Jakov Prkić (unpublished obs.)	
Split, Croatia	Jakov Prkić (unpublished obs.)	
Marina, Croatia	Jakov Prkić (unpublished obs.)	
Murter Island, Croatia	Jakov Prkić (unpublished obs.)	
Biograd, Croatia	Jakov Prkić (unpublished obs.)	
Turanj, Croatia	Jakov Prkić (unpublished obs.)	
Zadar, Croatia	Jakov Prkić (unpublished obs.)	
Ugljan Island, Croatia	Jakov Prkić (unpublished obs.)	
Privlaka, Croatia	Jakov Prkić (unpublished obs.)	

Vir Island, Croatia	Jakov Prkić (unpublished obs.)
Pag Island, Croatia	Jakov Prkić (unpublished obs.)
Madeira Is.	Malaquias (unpublished data).
Rimini, Italy	http://www.biologiamarina.org/wp/bertella-stellata/
Greece	Mediterranean Ocean Biogeographic Information System

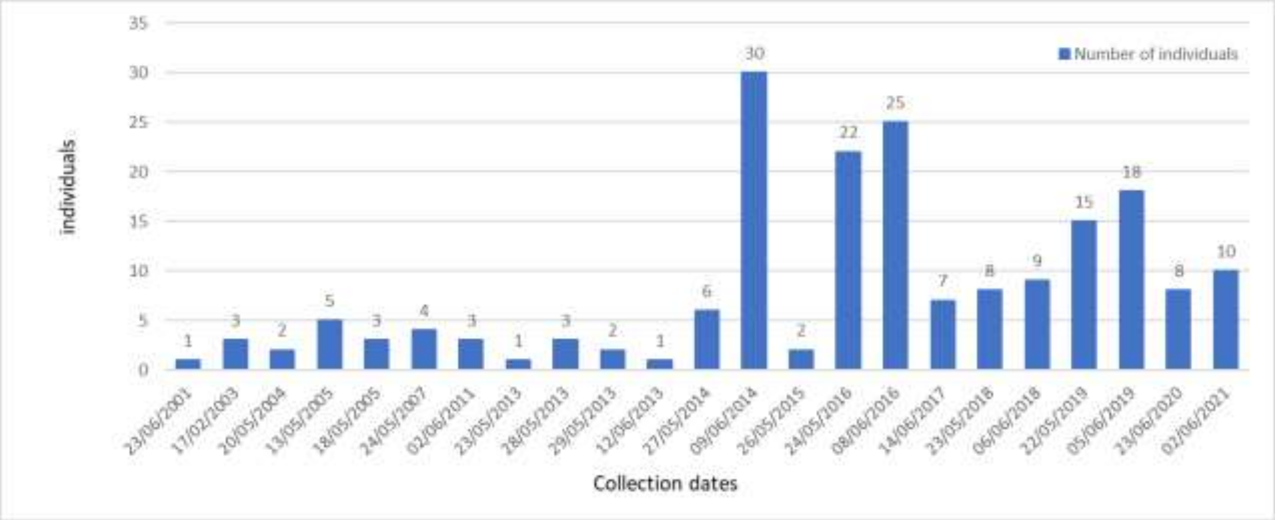

Figure 6. Qualitative sampling of *Berthella stellata* specimens collected in Es Caials, Girona, Spain by dates.

Figure 7. Gelatinous spiral eggs ribbon of *Berthella stellata* from Es Caials, Girona, Spain.

3.6. Discussion

Populations of marine heterobranchs are often highly variable, making it very difficult to study them over time (Clark 1975; Doménech *et al.* 2002). As Miller (1962) indicates, most species of marine heterobranchs are so scarce in number of individuals and appear so sporadically that numerical studies cannot be carried out to determine their life cycle. However, some works have been published on the lifecycles and ecology of some species. Miller (1962) analyzed the annual cycle of several intertidal species on the Isle of Man for a little over two years (*Elysia viridis* (Montagu 1804), *Limapontia senestra* (Quatrefages 1844), *Limapontia capitata* (Müller 1774), *Doris pseudoargus* Rapp 1827, *Polycera quadrilineata* (Müller 1776), *Acanthodoris pilosa* (Abildgaard 1789), *Onchidoris bilamellata* (Linnaeus 1767), *Onchidoris muricata* (Müller 1776), *Atalodoris pusilla* (Alder & Hancock 1845), *Goniodoris nodosa* (Montagu 1808), *Doto coronata* (Gmelin 1791) and *Hero formosa* (Lovén 1844)), providing for the first time ecological data on their life cycle. Potts (1970) studied the ecology of the nudibranch *Onchidoris fusca* (Müller 1776) (now considered synonym of *O. bilamellata*) and Todd (1979) that of *O. bilamellata*, while Aerts (1994) studied the seasonal distribution of nudibranchs on the south coast of Netherlands. On the Californian coast, Nybbaken (1978) conducted a study of the abundance, diversity and temporal variability over 40 months of an intertidal community of nudibranchs limited in space (250 m^2). More recently some studies have been carried out that delve into the variability of these populations of marine heterobranchs over time (Doménech *et al.* 2002; Hermosillo-González, 2003; Bertsch 2008; Malaquias 2014; Goodheart *et al.* 2016; Goddard *et al.* 2020; Nimbs *et al.* 2020; Papu *et al.* 2020; Goddard *et al.* 2021; Toma *et al.* 2022).

In the Mediterranean, populations of marine heterobranch species with abundant individuals that can be studied over time are rare. For example, aeolids such as *Flabellina affinis* (Gmelin 1791), *Paraflabellina ischitana* (Hirano & T. E. Thompson 1990*)* and *Cratena peregrina* (Gmelin 1791) living on colonies of the hydrozoan of the genera *Eudendrium* Ehrenberg, 1834 are known, although there are no published data on its population biology or competition for food. A population of the dorid nudibranch *Dendrodoris temarana* Pruvot-Fol, 1953 has recently been studied during an annual cycle in a locality on the Catalonian coast (NE Spain) (unpublished and personal communication from M. Ballesteros). For these reasons, the data provided in this paper on the population of *B. stellata* in Es Caials are important. Although with fluctuations in the abundance of individuals, the population of this locality is stable over multiple years, being able to verify that it is a place where individuals copulate and lay their eggs. We have verified the great chromatic variability of the species, with light specimens, others brown with scattered white spots and others with the typical Y-shaped white spot.

According to Gosliner & Bertsch (1988), simple morphological characteristics such as body coloration, shell shape, radular teeth, jaw parts, and reproductive appearance were considered intraspecific elements to be taken into account to designate a species; for them all the specimens of different populations with similar external morphologies were of the same species; premise that molecular analyzes deny because we have seen that specimens of the same coloration can be of different species and others that have various colorations belong to the same population and therefore are of the same species.

Three different colorations were found in the morphological aspects of the populations of *B. stellata* (Be and Bs) from Es Caials; according to the results of our molecular analyzes of species delimitation and the phylogenetic trees they are the same species; this indicates that using a molecular and morphological approach together can help improve the determination of populations of Heterobranchia sea slug species; for Ghanimii *et al.* (2020), both used together, are a very important tool in the identification of heterobranch species..

Finally, in this paper we see that the Mediterranean populations of *B. stellata* from Es Caials and those from Italy share both morphological and molecular aspects with populations from the European northeastern Atlantic region such as Portugal.

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3.8. Supplementary material

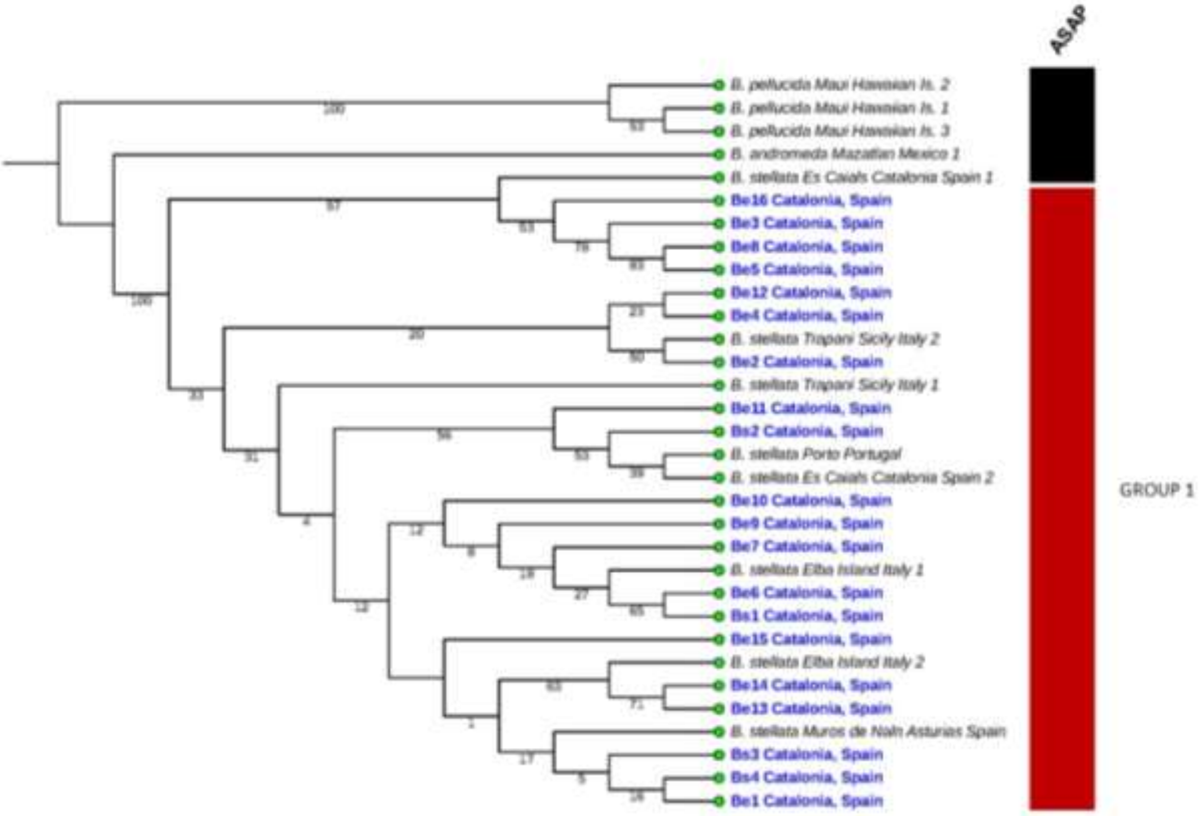

Figure 8. Combined results of Maximum Likelihood (ML) and species delimitation analysis. Phylogenetic tree of gene COI of *Berthella stellata* under maximum likelihood analysis by RAxML. The numbers at the nodes represent ML bootstraps. The names in blue are the specimens we sampled; names in black are GenBank sequences. The colored bars represent the results of the ASAP analysis.

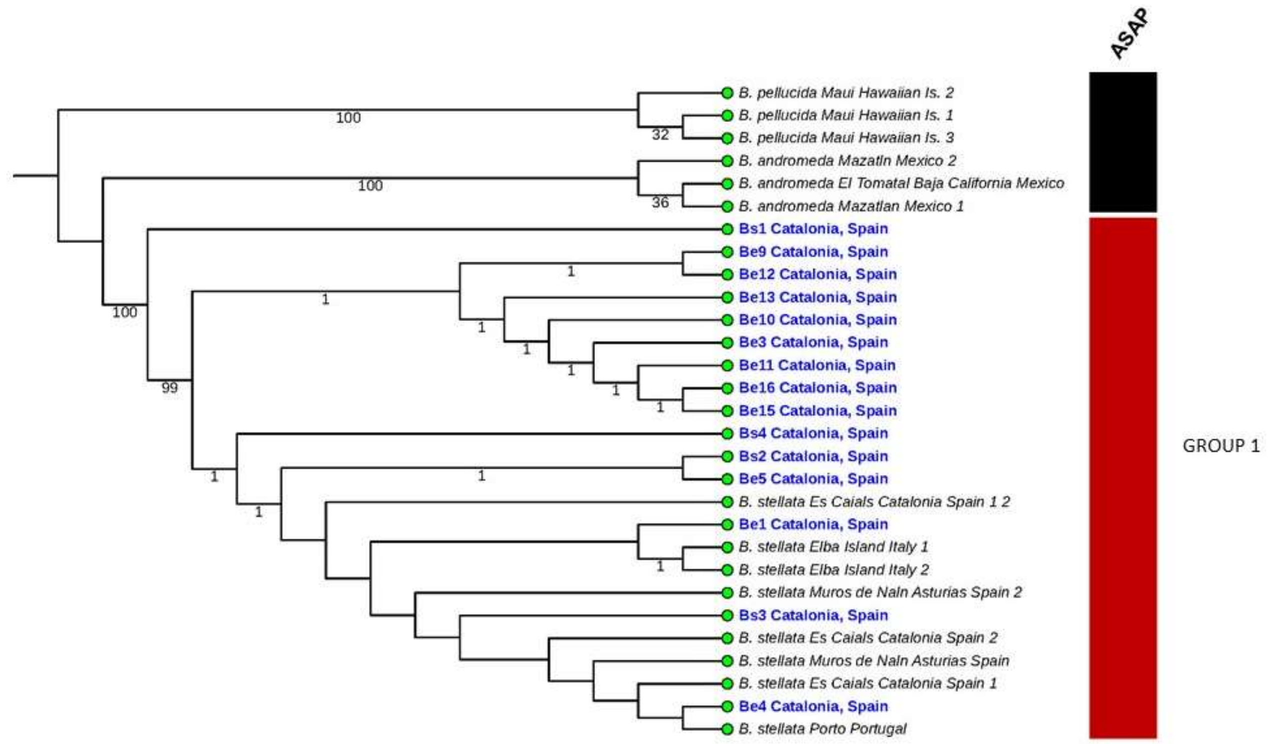

Figure 9. Combined results of Maximum Likelihood (ML) and species delimitation analysis. Phylogenetic tree of gene 16S of *Berthella stellata* under maximum likelihood analysis by RAxML. The numbers at the nodes represent ML bootstraps. The names in blue are the specimens we sampled; names in black are GenBank sequences. The colored bars represent the results of the ASAP analysis.

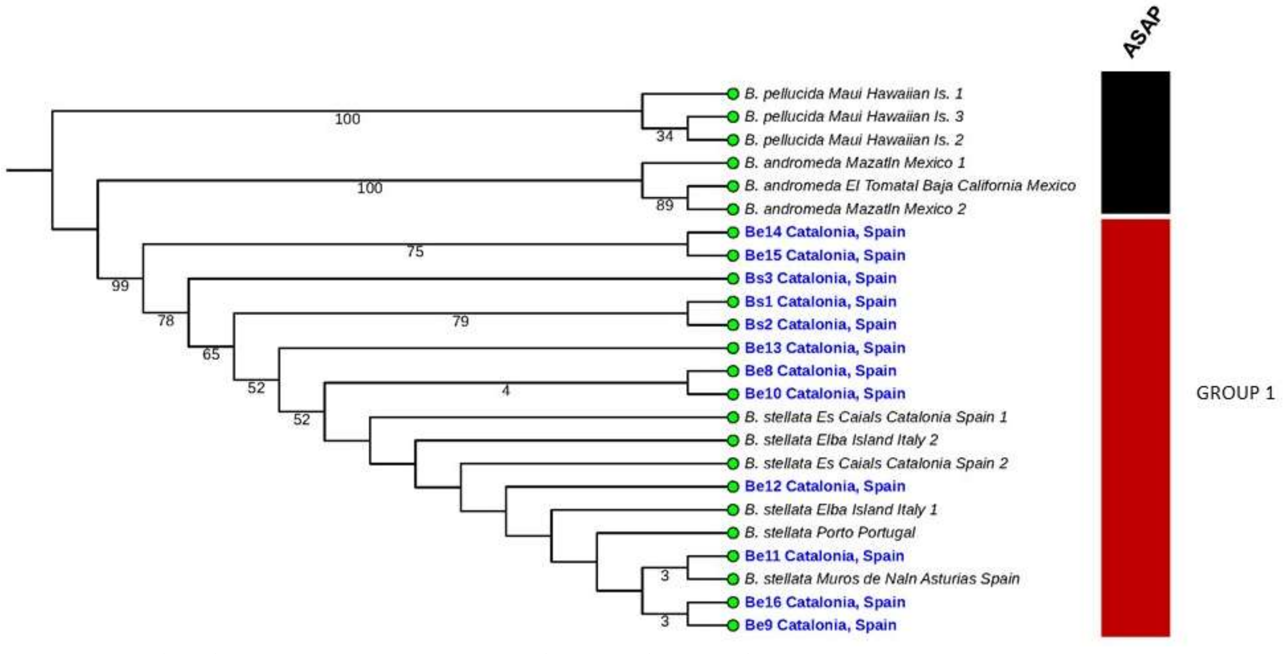

Figure 10. Combined results of Maximum Likelihood (ML) and species delimitation analysis. Phylogenetic tree of gene H3 of *Berthella stellata* under maximum likelihood analysis by RAxML. The numbers at the nodes represent ML bootstraps. The names in blue are the specimens we sampled; names in black are GenBank sequences. The colored bars represent the results of the ASAP analysis.

3.9. References

Aerts L.A.M. 1994. Seasonal distribution of nudibranchs in the southern delta area, S.W. Netherlands. *Journal of Molluscan Studies*, 60: 129-139.

Baba K. 1969. List of the Pleurobranchidae and the Pleurobranchaeidae from Japan. *Collect Breed,* 31:190–191.

Bacallado J.J., Ortea J., Moro L., Martín Barrios F.J., Cruz Simó T. & Mesa Hernández R. 2008. *Inventario de los moluscos de la marina de Arrecife, Lanzarote*. Canarias Conservación. 1–32.

Ballesteros, M., Barrajón A., Luque A., Moreno D., Talavera P. & Templado J. 1986. Contribución al conocimiento de los Moluscos Gasterópodos marinos de Almería. *Iberus*, 6: 39-57.

Ballesteros M., Madrenas E. & Pontes M. 2021. *Berthella stellata* in OPK-Opistobranquis. Published: 15/05/2012, Accesed: 10/03/2021 (https://opistobranquis.info/es/guia/pleurobranchida/berthella-stellata/).

Bernhard D. 1999. Several highly divergent histone H3 genes are present in the hypotrichous ciliate *Stylonychia lemnae*. *FEMS Microbiology Letters*, 175: 45-50.

Bertsch H. 2008. "*Ten-Year Baseline Study of Annual Variation in the Opisthobranch (Mollusca: Gastropoda) Populations at Bahia de los Angeles, Baja California, Mexico*", en Gustavo D. Danemann y Exequiel Ezcurra (eds.), Bahía de los Ángeles: Recursos naturales y comunidad. Línea Base. México, semarnat/Pronatura Noroeste/sdnhm/Instituto Nacional de Ecología, pp. 319-338.

Burn R. 1962. On the new pleurobranch subfamily Berthellinae (Mollusca: Gastropoda); a revision and new classification of the species of New South Wales and Victoria. *Memories of the National Mueum of Victoria*, 25: 129–148.

Carlson C.L. & Hoff P.J. 2003. The opisthobranchs of the Mariana Islands. *Micronesica*, 35: 271–293.

Cattaneo-Vietti R. & Thompson T.E. 1989. Mediterranean opisthobranch molluscs: A zoogeographic approach. *Bollettino Malacologico*, 25(5-8): 183–204.

Cervera, J. L., and J. C. García-Gómez. 1986. Moluscos opistobranquios del litoral occidental andaluz: nuevas aportaciones faunísticas. *Iberus*, 6 (2): 201-207.

Cervera, J. L., G. Calado, C. Gavaia, M. A. E. Malaquías, J. Templado, M. Ballesteros, J. C. García-Gómez, and C. Megina. 2004. An annotated and updated checklist of the opisthobranchs (Mollusca: Gastropoda) from Spain and Portugal (including islands and archipelagos). *Boletín Instituto Español de Oceanografía*, 20 (1-4): 1-111.

Clark K.B. 1975. Nudibranch life cycles in the Northwest Atlantic and their relationship to the ecology of fouling communities. *Helgoländer wissenschaftliche Meeresuntersuchungen*, 27: 28−69. DOI: https://doi.org/10.1007/BF01611686

Cobb G.C. 2008. *Berthella stellata* found south Queensland. Sea Slug Forum, Australian Museum, Sydney http://wwwseaslugforumnet/find/22063

Domènech A., Avila, C. & Ballesteros, M. 2002. Spatial and Temporal variability of the Opisthobranch molluscs of Port Lligat Bay (Catalonia, NE Spain). *Journal of Molluscan Studies*, 68:29-37.

Drummond A.J., Ashton B., Buxton S., Cheung M., Cooper A., Heled J., Kearse M., Moir R., Stones-Havas S., Sturrock S., Thierer T. & Wilson A. 2010. Geneious v5.1. URL http:// www.geneious.com.

Folmer O., Black M., Hoeh W., Lutz R. & Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3(5):294-9.

Furfaro, G., F. Vitale, C. Licchelli, and P. Mariottini. 2020. Two Seas for One Great Diversity: Checklist of the Marine Heterobranchia (Mollusca; Gastropoda) from the Salento Peninsula (South-East Italy). *Diversity*. 12: 171.

Ghanimi H., Schrödl M., Goddard J., Ballesteros M. Gosliner T., Buske Y. & Valdés Á. 2020. Stargazing under the sea: molecular and morphological data reveal a constellation of species in the *Berthella stellata* (Risso, 1826) species complex (Mollusca, Heterobranchia, Pleurobranchidae). *Marine Biodiversity*, 50: 11. https://doi.org/10.1007/s12526-019-01027-w

Goddard J., Goddard, W. & Goddard Z.2020. Benthic Heterobranch Sea Slugs (Gastropoda: Heterobranchia) from Santa Barbara County, California I. Review of the literature, and Naples Point, 2002–2019. *Proceedings of the California Academy of Sciences*, 66(10): 275–298.

Goddard J., Goddard Z. & Goddard, W. 2021. Benthic Heterobranch Sea Slugs (Gastropoda: Heterobranchia) from Santa Barbara County, California. II. Tar Pits Reef, Carpinteria, 2008-2020. *Occasional papers of the California Academy of Sciences*, 67. 1-20.

Goodheart J., Ellingson, R., Vital X., Galvão Filho H., McCarthy J., Medrano S., Bhave V., García-Méndez K., Jiménez L., López G., Hoover C., Awbrey J., De Jesus J., Gowacki W., Krug P. & Valdés Á. 2016. Identification guide to the heterobranch sea slugs (Mollusca: Gastropoda) from Bocas del Toro, Panama. *Marine Biodiversity Records*, 9:56 DOI 10.1186/s41200-016-0048-z

Gosliner T.M. 1987. *Nudibranchs of Southern Africa. A guide to opisthobranch molluscs of Southern Africa*. Sea Challengers, Monterey, California.

Gosliner T.M. & Bertsch H. 1988. A Review of the Genus *Berthella* (Opisthobranchia: Notaspidea) from the Pacific Coast of North America. *Veliger*, 31(1/2): 46-67.

Gosliner T.M., Valdés A. & Behrens D.W. 2018. *Nudibranch and sea slug identification: Indo-Pacific*, 2nd edn. New World Publications, Jacksonville.

Grup de Recerca d'Opistobranquis de Catalunya (GROC). 2021. https://opistobranquis.org/es/guia/19.

Heller J. & Thompson T.E. 1983. Opisthobranch molluscs of the Sudanese Red Sea. *Zool. J. Linnean Soc.*, 78: 317–348. https://doi.org/10.1111/j.1096-3642.1975.tb02263.x

Hermosillo-González A. 2003. New distributional records of opisthobranch mollusks for Bahía de Banderas, México (Tropical Eastern Pacific). *The Festivus*, 35:21–28.

Hillis D.M. & Bull J.J. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analyses. *Systematic Biology*, 42: 182–192.

Kay E.A. 1979. Hawaiian marine shells. Reef and shore fauna of Hawaii, Section 4: Mollusca. *Bernice P. Bishop Museum, Special Publications,* 64: 1–653.

Kimura M. 1980. A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16: 111–20.

Kumar S., Stecher G. & Tamura K. 2016 MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, 33: 1870–1874.

Lanfear R., Frandsen P.B., Wright A.M., Senfeld T. & Brett Calcott B. 2017. PartitionFinder 2: New Methods for Selecting Partitioned Models of Evolution for Molecular and Morphological Phylogenetic Analyses. *Molecular Biology and Evolution*, 34(3): 772–773.

Lipej L., Dobraic Z., Mavric B., Samu S. & Alajbegovic S. 2008. Opisthobranchs molluscs (Mollusca: Gastropoda) from Slovenian coastal waters (Northern Adiatic). *Annales Serie historia natural*, 18 (2): 213-221.

Malaquias M.A. & Calado G.J.P. 1997. The malacological fauna of Salvage Islands - 1. Opisthobranch Molluscs. *Boletim do Museo Muicipal de Funchal*, 49(281): 149-170.

Malaquias M., Calado G., Padula V., Villani G. & Cervera J.L. 2009. Molluscan diversity in the North Atlantic Ocean: new records of opisthobranch gastropods from the Archipelago of the Azores. *Marine Biodiversity*, 2: e38.

Malaquias M.A.E. 2014. New data on the heterobranch gastropods ('opisthobranchs') for the Bahamas (tropical western Atlantic Ocean). *Marine Biodiversity Records*, 7: e27.

Miller M.C. 1962. Annual cycles of some Manx nudibranchs, with a discussion of the problem of migration. *Journal of Animal Ecology*, 31: 545–569.

Nakano R. 2018. *Field guide to sea slugs and nudibranchs of Japan*. Shosoichi Publishing, Tokyo.

Nimbs M., Hutton I., Davis T., Larkin M. & Smith S. 2020. The heterobranch sea slugs of Lord Howe Island, NSW, Australia (Mollusca: Gastropoda). *Proceedings of the Royal Society of Victoria*, 132(1) 12 – 41.

Nybakken J. 1978. Abundance, diversity and temporal variability in a California intertidal nudibranch assemblage. *Marine Biology*, 45: 129–146.

Ortea J.A., Moro L., Bacallado J.J. & Herrera R. 2001. Catálogo actualizado de los moluscos opistobranquios de las islas Canarias. *Revista de la Academia Canaria de Ciencias*, XII(3-4): 105-134.

Ozturk B., Dogan A., Bitlis-Bakir B. & Salman A. 2014. Marine Molluscs of the Turkish Coasts: An Updated Checklist. *Tübitak, Turkish Journal of Zoology*, 38.

Palumbi S.R., Martin A.P., Romano S.L., McMillan W.O., Stice L. & Grabowski G. 1991. *The Simple Fool's Guide to PCR.* Dept. of Zoology, University of Hawaii, Honolulu.

Papu A., Undap N., Martinez N.A., Segre M.R., Datang I.G., Kuada R.R., Perin M., Yonow N. & Wägele H. 2020. First Study on Marine Heterobranchia (Gastropoda, Mollusca) in Bangka Archipelago, North Sulawesi, Indonesia. *Diversity*, 12(2):52. https://doi.org/10.3390/d12020052

Parera A., Pontes M., Salvador, X. & Ballesteros M. 2020. Sea slugs (Mollusca, Gastropoda, Heterobranchia): the other inhabitants of the city of Barcelona (Spain). *Butlletí de la Institució Catalana d'Història Natural*, 84: 75-100.

Pease W.H. 1860. Descriptions of new species of Mollusca from Sandwich Islands. *Procedings of the Zoological Society of London*, 28:18–37.

Potts G.W. 1970. The ecology of *Onchidoris fusca* (Nudibranchia). *Journal of the marine biological Association of the U. K.*, 50: 269-292.

Puillandre N., Brouillet S. & Achaz G. 2021. ASAP: assemble species by automatic partitioning. *Molecular Ecology Resources*, 21: 609–620.

Risbec J. 1928. Étude anatomique des gastéropodes Tectibranches de la presqu'île de Nouméa, avec description de cinq espèces nouvelles. *Archives du Museum d'Histoire Naturelle*, 3:37–68.

Risso A. 1826. *Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes.* Volume 4. F.-J. Levrault, Paris.

Sánchez Tocino, L. 2001. *Berthella stellata* accessed through: Opistobranquios de la Costa de Granada on 2014-12-14. (http://www.ugr.es/~lstocino/berthella_stellata.htm).

Simon C., Frati F. & Beckenbach A. 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequencesand a compilation of conserved PCR primers. *Annals of the Entomological Society of America*, 87: 651–701.

Stamatakis, A. 2014. RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. *Bioinformatics*, 30(9): 1312–1313.

Templado J. 1982. Datos sobre los opistobranquios del Cabo de Palos (Murcia). *Bollettino Malacologico*, 18 (9-12): 247-254.

Thompson T.E. 1970. Eastern Australian Pleurobranchomorpha (Gastropoda. Opisthobranchia). *Journal of Zoology*, 60: 173–198. https://doi.org/10.1111/j.1469-7998.1970.tb02902.x

Thompson T.E. 1981. Taxonomy of three misunderstood opisthobranchs from the northern Adriatic Sea. *J. Molluscan. Stud.*, 47: 73–79. https://doi.org/10.1093/oxfordjournals.mollus.a065559

Thompson T.E. & Colman J.G. 1984. Histology of acid glands in Pleurobranchomorpha. *Journal of Molluscan Studies,* 50(1): 65-67.

Todd C.D. 1979. The population ecology of *Onchidoris bilamellata* (L.) (Gastropoda: Nudibranchia). *Journal of Experimental Marine Biology and Ecology*, 41: 213-255.

Toma M., Betti F., Bavestrello G., Cattaneo-Vietti R., Canese S., Cau A., Andaloro F., Greco S.& Bo M. 2022. Diversity and abundance of heterobranchs (Mollusca, Gastropoda) from the mesophotic and bathyal zone of the Mediterranean Sea. *The European Zoological Journal*, 89:1, 167-189, DOI: 10.1080/24750263.2022.2033859

Wägele H., Burghardt I., Anthes N., Evertsen J., Klussmann-Kolb A. & Brodie G. 2006. Species diversity of opisthobranch molluscs on Lizard Island, Great Barrier Reef, Australia. *Records of the Western Australian Museum, Supp*lement, 9: 33–59.

Willan R.C. 1984. The Pleurobranchidae (Opisthobranchia: Notaspidea) of the Marshall Islands, central-west Pacific Ocean. *Veliger*, 27: 37–53.

Wirtz, P., and Debelius, H. 2003. *Mediterranean and Atlantic invertebrate guide*. ConchBooks, Hackenheim, Germany.

CHAPTER IV. Changing feeding habits and ontogenetic dimorphism in juvenile and adult *Aplysia punctata* (Cuvier, 1803) (Mollusca, Gastropoda, Heterobranchia) in the Mediterranean.

Changing feeding habits and ontogenetic dimorphism in juvenile and adult *Aplysia punctata* (Cuvier, 1803) (Mollusca, Gastropoda, Heterobranchia) in the Mediterranean.

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4.1. Abstract

Specimens of *Aplysia punctata* inhabiting the Catalonian coasts (NE Spain, Western Mediterranean Sea) display two different color patterns, which have been thought to represent two distinct species. However, molecular analyses conducted by other authors and confirmed herein show that there are no genetic differences between individuals of the two-color morphs. At the same time, these color morphs display distinct life history traits, including different size, mating behavior, and egg mass and larvae coloration. In this paper, it is hypothesized that distinct diets are responsible of these differences. The results of this study confirm that small red specimens of *A. punctata* feed on red algae, primarily *Sphaerococcus coronopifolius* and *Plocamium cartilagineum*; pigments from these algae give small specimens of *A. punctata* a very similar morphological appearance to adults of the *Aplysia parvula* species complex. In contrast, adult specimens of *A. punctata* feed preferentially on green algae of the specie *Ulva lactuca*. This change in feeding behavior is probably related to defensive strategies involving camouflage. Además, las masas de huevos adquieren un color entre rosado y rojizo que se retiene en la fase larvaria de APA.

4.2. Keywords: *Aplysia punctata*, Catalonian, dietary preference, dimorphism, coloration

4.3. Introduction

The adoption of molecular phylogenetic methods has resulted in significant classification and taxonomic changes among diverse groups of living organisms (Field *et al.* 1988), confirming the limitations of morphological data for phylogenetic reconstruction (Doyle 1992; Knowlton 2000). Some examples involve species previously considered to have wide geographic distributions (Andrews *et al.* 2014; Gaither *et al.* 2016) or organisms with reduced morphological diversification (Fukami *et al.* 2004). Cooke *et al.* (2014), Kienberger *et al.* (2016), Lindsay & Valdés (2016) indicated that molecular analyses have been very useful to clarify the classification of sea slugs, in cases where several species with similar morphology could not be discerned by traditional methods, and were formerly considered to be single widespread species. According to different authors (Ornelas-Gatdula *et al.* 2012; Carmona *et al.* 2014; Uribe *et al.* 2018; Valdés *et al.* 2017) molecular analyses have confirmed that most species with large geographical ranges across different ocean basins are in fact pseudo-cryptic or cryptic species complexes of closely related taxa, and provide hypotheses on the mechanisms of evolution resulting in their current distribution.

Species of the genus *Aplysia* Linnaeus 1767, known as sea hares (Heterobranchia, Anaspidea), live in the intertidal or upper subtidal zones where they feed on different species of algae, mate, and lay their eggs masses (Ribero *et al.* 1998). According to Bouchet and Gofas (2022) there are around 45 species of *Aplysia* worldwide and many other species considered nomina dubia or taxa inquirenda. Species of Aplysia live in temperate or tropical waters, no species has been able to colonize the cold waters of the Arctic or the Antarctic oceans. Medina and Walsh (2000) carried out the first phylogenetic analysis of the Anaspidea based on mitochondrial DNA, while Medina *et al.* (2001) carried out a preliminary phylogeny on the genus Aplysia in which they include *Aplysia parvula* Mörch 1863, and *Aplysia punctata* (Cuvier 1803) as distinct species.

The identification of species of *Aplysia* based on morphological traits is problematic as some species are highly variable in external coloration (Medina and Walsh 2000). An example is *A. punctata*, a very common species in the Mediterranean Sea that displays high levels of chromatic diversity. Ballesteros and Templado (1987) missidentified small specimens of *A. punctata* as *A. parvula*, because of their reduced size and reddish coloration similar to that of *A. parvula*. Ballesteros and Templado (1987) also carried out a morphological study of these small *Aplysia*, analyzing their radular structure and providing data on their biology and reproduction. Since the paper of Ballesteros and Templado (1987) small specimens of *A. punctata* with a length of 5-20 mm are cited under the name of *A. parvula* in the western Mediterranean (see Martín *et al.* 1990; Sánchez Tocino 2001; Domènech *et al.* 2002; Cervera *et al.* 2004; Ballesteros 2007; Templado and Villanueva 2010; Ballesteros *et al.* 2016; Gofas *et al.* 2017), although we found in this paper, a brown coloration with white spots similar to adult specimens of *A. punctata* in juveniles of 20-25 mm and a green coloration with white spots in adults of 25-100 mm (Figure 1). However, Golestani *et al.* (2019), using molecular data, found that there is no evidence of the presence of *A. parvula* in the Mediterranean Sea and that all specimens showing the *A. parvula* phenotype are *A. punctata* or possible hybrids. Ballesteros *et al.* (2021) provided additional information on these small red *A. punctata* specimens with numerous photographs illustrating details of their coloration and morphology, as well as how this species changes coloration at different stages of its life cycle.

Figure 1. Comparison between the "typical" small reddish APJ specimens (above) with a length between 5-20 mm (cited as *Aplysia parvula* in the Mediterranean), with juvenile *Aplysia punctata* in the intermediate process to pass to the adult phase with a length between 20-25 mm (lower left) and APA adult specimens with a length between 25-100 mm (lower right).

However, the boundaries in external morphology between the two-color morphs still needs to be clarified, as well as the reasons why the feeding strategy of individuals changes as their size increases. In this paper we attempt to address these questions by examining changes in feeding behavior during different stages of the life cycle of *A. punctata*, as well as the reproductive period, mating behavior, egg mass coloration and other traits based on natural populations and individuals collected for observation in the laboratory. Moreover, molecular analyses were conducted to verify the identity of the specimens examined and confirm or refute the results by Golestani *et al.* (2019).

4.4. Materials and methods

4.4.1. *Morphological analysis*

In this paper the abbreviature APJ is used for the small red specimens previously cited as *A. parvula* and the abbreviature APA is used for larger animals typically identified as *A. punctata*. Live specimens of APJ and APA with their egg masses were photographed live in the field or in the laboratory, some were induced to ink by touching them, others were collected with their respective algae that serve as food and habitat to observe their behavior at the laboratory. A binocular Olympus SZ-PT dissecting microscope was used to study their internal anatomy; a dorsal incision was made on the anterior portion of the animal to dissect the distal anterior part of the digestive tract, which includes the buccal bulb, radula, and jaws; the buccal mass was immersed in a potassium hydroxide (KOH) solution (10%) for three hours to dissolve the organic tissues and then rinsed with distilled water. The radula was mounted on a metal stub with bio adhesive tabs, coated with a carbon layer, and examined under a FEI Quanta 200 scanning electron microscope (SEM).

4.4.2. *DNA extraction and amplification*

For the molecular analyses, 13 specimens of APJ and 13 of APA were collected by SCUBA diving or snorkeling in different locations on the Catalonian coast (NE Spain): Costa Brava (Cala Sant Antoni, Port Lligat, Es Caials, Bau Cap Falcó, Roses, Cala Aiguablava-Fornells, Cala Fosca), Mataró and Fòrum (Barcelona). Specimens were collected live in the field, immediately transferred to 99% ethanol and stored at -20°C for the subsequent DNA extraction. To complete the dataset, we retrieved all the available sequences of the *A. parvula* and *A. punctata* from Genbank, listed in Table 1. Four specimens of *Bursatella leachi* from Fòrum (Barcelona, Spain), Ebro Delta (Tarragona, Spain) were used to root the tree.

Table 1. Information on all the specimens used in this study for molecular phylogeny, including the specie, location, voucher (collection code) and the COI GenBank accession number.

Specie	Location	Voucher	COI	16S	H3	Reference
Bursatella leachii	Fôrum, Barcelona, Spain	B1	OK066363	--------------	--------------	present study
B. leachii	Fôrum, Barcelona, Spain	B2	OK066356	--------------	--------------	present study
B. leachii	Ebro Delta, Tarragona, Spain	B6	OK066355	--------------	--------------	present study
B. leachii	Ebro Delta, Tarragona, Spain	B7	OK066359	--------------	--------------	present study
APA	Roses (Costa Brava), Spain	Ap1	OK066334	OK066287	OK073542	present study
APA	Roses (Costa Brava), Spain	Ap2	OK066333	OK066286	OK073541	present study
APA	Fôrum, Barcelona, Spain	Ap3	--------------	OK066285	OK073540	present study
APA	Fôrum, Barcelona, spain	Ap4	--------------	OK066284	--------------	present study
APA	Fôrum, Barcelona, Spain	Ap5	--------------	--------------	OK073539	present study
APA	Cala Fosca (Costa Brava), Spain	Ap6	OK066332	OK066283	OK073538	present study
APA	Cala Fosca (Costa Brava), Spain	Ap7	OK066331	OK066282	OK073537	present study
APA	Es Caials (Costa Brava), Spain	Ap8	--------------	OK066281	OK073536	present study
APA	Cala Sant Antoni (Costa Brava), Spain	Ap9	OK066330	OK066280	OK073535	present study
APA	Fôrum, Barcelona, Spain	Ap10	--------------	OK066279	OK073534	present study
APA	Fôrum, Barcelona, Spain	Ap11	--------------	OK066278	OK073533	present study
APA	Rosas (Costa Brava), Spain	AR	OK066337	OK050558	OK073519	present study
APA	Rosas (Costa Brava), Spain	AR1	--------------	OK050559	OK073520	present study
APJ	Bau Cap Falco (Costa Brava), Spain	A1	OK066349	OK050571	--------------	present study
APJ	Bau Cap Falco (Costa Brava), Spain	A2	OK066348	OK050570	OK073532	present study
APJ	Cala Fosca (Costa Brava), Spain	A3	OK066336	OK050569	OK073531	present study
APJ	Cala Aiguablava-Fornells (Costa Brava), Spain	A4	OK066347	OK050568	OK073530	present study
APJ	Cala Aiguablava-Fornells (Costa Brava), Spain	A5	OK066340	OK050567	OK073529	present study
APJ	Mataró, Spain	A6	OK066339	OK050566	OK073528	present study
APJ	Mataró, Spain	A7	OK066346	--------------	OK073527	present study
APJ	Mataró, Spain	A8	OK066345	OK050565	OK073526	present study
APJ	Mataró, Spain	A9	OK066344	OK050564	OK073525	present study
APJ	Port lligat (Costa Brava), Spain	A10	OK066338	OK050563	OK073524	present study
APJ	Fôrum, Barcelona, Spain	A11	OK066343	OK050562	OK073523	present study

APJ	Fôrum, Barcelona, Spain	A12	OK066335	OK050561	OK073522	present study
APJ	Fôrum, Barcelona, Spain	A13	OK066342	OK050560	OK073521	present study
A. fasciata	Israel	---------------	AF343428	AF192298	--------------	Medina *et al*., 2005
A. fasciata	Sao Sebastiao, Sao Paulo, Brazil (1)	MZSP 103234	KM272290	KM272281	--------------	de Oliveira *et al*., 2014
A. fasciata	Sao Sebastiao, Sao Paulo, Brazil (2)	MZSP 103233	KM272291	KM272282	--------------	de Oliveira *et al*., 2014
A. fasciata	Sao Sebastiao, Sao Paulo, Brazil (3)	MZSP 103250	KM272292	KM272283	--------------	de Oliveira *et al*., 2014
A. fasciata	Sao Sebastiao, Sao Paulo, Brazil (4)	MZSP 103217	KM272295	--------------	--------------	de Oliveira *et al*., 2014
A. fasciata	Ponta da Praia, Santos, Sao Paulo, Brazil (1)	MZSP 109903	--------------	KM272284	--------------	de Oliveira *et al*., 2014
A. fasciata	Ponta da Praia, Santos, Sao Paulo, Brazil (2)	MZSP 113776	KM272293	KM272285	--------------	de Oliveira *et al*., 2014
A. fasciata	Ponta da Praia, Santos, Sao Paulo, Brazil (3)	MZSP 109975	--------------	KM272286	--------------	de Oliveira *et al*., 2014
A. fasciata	Ponta da Praia, Santos, Sao Paulo, Brazil (4)	MZSP 109978	--------------	KM272287	--------------	de Oliveira *et al*., 2014
A. fasciata	Ponta da Praia, Santos, Sao Paulo, Brazil (5)	MZSP 104038	KM272294	KM272288	--------------	de Oliveira *et al*., 2014
A. fasciata	Ponta da Praia, Santos, Sao Paulo, Brazil (6)	MZSP 113777	--------------	KM272289	--------------	de Oliveira *et al*., 2014
A. fasciata	Florida, USA	---------------	AF343426	AF192296	--------------	Medina *et al*., 2005
A. nigrocincta	Madang, Papua New Guinea (1)	CASIZ 191092	--------------	MK422792	--------------	Golestani *et al*., 2019
A. nigrocincta	Madang, Papua New Guinea (2)	CASIZ 191115	--------------	MK422793	MK422692	Golestani *et al*., 2019
A. nigrocincta	Espiritu Santo, Vanuatu	CASIZ 176792	MK422893	--------------	MK422693	Golestani *et al*., 2019
A. punctata	North Sea (1)	---------------	KR084671	--------------	--------------	Barco *et al*., 2016
A. punctata	North Sea (2)	---------------	KR084707	--------------	--------------	Barco *et al*., 2016
A. punctata	North Sea (3)	---------------	KR084714	--------------	--------------	Barco *et al*., 2016
A. punctata	North Sea (4)	---------------	KR084740	--------------	--------------	Barco *et al*., 2016
A. punctata	North Sea (5)	---------------	KR084809	--------------	--------------	Barco *et al*., 2016
A. punctata	North Sea (6)	---------------	KR084865	--------------	--------------	Barco *et al*., 2016
A. punctata	North Sea (7)	---------------	KR084890	--------------	--------------	Barco *et al*., 2016
A. punctata	North Sea (8)	---------------	KR084908	--------------	--------------	Barco *et al*., 2016
A. punctata	Norwegian archipelago	---------------	KT952472	--------------	--------------	Ware *et al*., 2015
A. punctata	Azores, Portugal (1)	CPIC 01363	MK422894	MK422795	MK422695	Golestani *et al*., 2019
A. punctata	Azores, Portugal (2)	CPIC 01364	MK422895	MK422796	MK422696	Golestani *et al*., 2019
A. punctata	Azores, Portugal (3)	CPIC 01366	MK422896	MK422798	MK422698	Golestani *et al*., 2019
A. punctata	Azores, Portugal (4)	CPIC 01365	--------------	MK422797	MK422697	Golestani *et al*., 2019
A. punctata	Azores, Portugal (5)	CPIC 01356	--------------	MK422794	MK422694	Golestani *et al*., 2019
A. punctata	Cadiz, Spain	CPIC 01359	MK422897	--------------	MK422699	Golestani *et al*., 2019
A. punctata	Santander, Spain	CPIC 01424	MK422898	MK422799	MK422700	Golestani *et al*., 2019
A. punctata	Pontevedra, NW Spain	---------------	AY345019	--------------	--------------	Grande *et al*., 2004
A. punctata	Brittany, France (1)	ZSM Mol 20180005	MK422899	MK422800	MK422701	Golestani *et al*., 2019
A. punctata	Brittany, France (2)	ZSM Mol 20180005	MK422900	MK422801	MK422702	Golestani *et al*., 2019
A. punctata	Brittany, France (3)	ZSM Mol 20180006	MK422901	MK422802	MK422703	Golestani *et al*., 2019
A. punctata	Banyuls sur Mer, France (1)	CPIC 01360	MK422902	MK422803	MK422704	Golestani *et al*., 2019
A. punctata	Banyuls sur Mer, France (2)	CPIC 01360	MK422903	MK422804	MK422705	Golestani *et al*., 2019
A. punctata	Banyuls sur Mer, France (3)	CPIC 01362	MK422904	MK422805	MK422706	Golestani *et al*., 2019
A. punctata	Giannutri Island, Italy (1)	---------------	MK422905	MK422806	--------------	Golestani *et al*., 2019
A. punctata	Giannutri Island, Italy (2)	---------------	MK422906	MK422807	MK422707	Golestani *et al*., 2019
A. punctata	Giannutri Island, Italy (3)	---------------	MK422907	MK422808	MK422708	Golestani *et al*., 2019
A. punctata	Giannutri Island, Italy (4)	CPIC 01422	MK422908	MK422809	MK422709	Golestani *et al*., 2019
A. punctata	Livorno, Italy (1)	---------------	MK422909	MK422810	MK422710	Golestani *et al*., 2019
A. punctata	Livorno, Italy (2)	---------------	MK422910	MK422811	--------------	Golestani *et al*., 2019
A. punctata	Capraia Island, Italy (1)	---------------	MK422911	MK422813	MK422712	Golestani *et al*., 2019
A. punctata	Capraia Island, Italy (2)	---------------	--------------	MK422812	MK422711	Golestani *et al*., 2019
A. punctata	Capraia Is., Italy (3)	CPIC 01423	--------------	MK422814	MK422713	Golestani *et al*., 2019
A. punctata	Gallipoli, Italy (1)	CPIC 01353	--------------	MK422815	MK422714	Golestani *et al*., 2019
A. punctata	Gallipoli, Italy (2)	CPIC 01358	--------------	MK422816	MK422716	Golestani *et al*., 2019
A. punctata	Gallipoli, Italy (3)	CPIC 01357	--------------	--------------	MK422715	Golestani *et al*., 2019
A. punctata	Levanto, Italy	CPIC 01421	MK422912	MK422817	MK422717	Golestani *et al*., 2019
A. punctata	Rhodes, Greece (1)	---------------	MK422913	MK422818	MK422718	Golestani *et al*., 2019

A. punctata	Rhodes, Greece (2)	---------------	MK422914	MK422819	MK422719	Golestani *et al.*, 2019
A. punctata	Rhodes, Greece (3)	---------------	MK422915	MK422820	MK422720	Golestani *et al.*, 2019
A. punctata	Rhodes, Greece (4)	---------------	MK422916	MK422821	MK422721	Golestani *et al.*, 2019
A. punctata	Rhodes, Greece (5)	---------------	MK422917	MK422822	MK422722	Golestani *et al.*, 2019
A. punctata	Rhodes, Greece (6)	---------------	MK422918	MK422823	MK422723	Golestani *et al.*, 2019
A. punctata	Heraklion, Crete, Greece	CPIC 01388	MK422919	MK422824	MK422724	Golestani *et al.*, 2019
A. punctata	Cape Kamenjak, Croatia (1)	ZSM Mol 20090003-1	MK422920	MK422825	MK422725	Golestani *et al.*, 2019
A. punctata	Cape Kamenjak, Croatia (2)	ZSM Mol 20090003-2	MK422921	MK422826	MK422726	Golestani *et al.*, 2019
A. punctata	Cape Kamenjak, Croatia (3)	ZSM Mol 20090003-3	MK422922	MK422827	MK422727	Golestani *et al.*, 2019
A. punctata	Cape Kamenjak, Croatia (4)	---------------	MK422923	MK422828	MK422728	Golestani *et al.*, 2019
A. punctata	Umago, Croatia	CPIC 01374	MK422913	MK422829	MK422729	Golestani *et al.*, 2019
A. punctata	Helgoland, North Sea	---------------	--------------	AF249253	--------------	Wollscheid-Lengeling *et al.*, 2001
A. punctata	Southwest Turkey (1)	---------------	MF784857	--------------	MK184485	Yokes, 2018
A. punctata	Southwest Turkey (2)	---------------	MF784858	--------------	MK184486	Yokes, 2018
A. punctata	Southwest Turkey (3)	---------------	MF784859	--------------	MK184487	Yokes, 2018
A. punctata	Southwest Turkey (4)	---------------	MF784860	--------------	MK184488	Yokes, 2018
A. punctata	Southwest Turkey (5)	---------------	MF784861	--------------	MK184490	Yokes, 2018
A. punctata	Southwest Turkey (6)	---------------	MF784862	--------------	MK184491	Yokes, 2018
A. punctata	Southwest Turkey (7)	---------------	MF784863	--------------	MK184492	Yokes, 2018
A. punctata	Southwest Turkey (8)	---------------	MF784864	--------------	MK184493	Yokes, 2018
A. punctata	Southwest Turkey (9)	---------------	--------------	--------------	MK184489	Yokes, 2018

Total genomic DNA was extracted from the foot of each specimen using the REDExtract-N-Amp™ TissuePCR Kit Protocol from Sigma-Aldrich and following the manufacturer's protocol. Partial fragments of two mitochondrial genes and one nuclear gene were sequenced: COI (cytochrome c oxidase subunit I), 16S (ribosomal RNA) and Histone H3. The primers used for amplification are listed in Table 2. The LCO1490/HCO2198 was the preferred combination, while Nancy was used as a replacement for HCO2198.

Table 2. Primers used for each gene

Gene	**Primers Name**	**Direction**	**Secuencia**	**Reference**
COI	LCO1490	Forward	5'-GGTCAACAAATCATAAAGATATTGG-3'	Folmer *et al.* 1994
COI	HCO2198	Reverse	5'-TAAACTTCAGGGTGACCAAAAAATCA-3'	Folmer *et al.* 1994
COI	Nancy	Reverse	5'-CCCGGTAAAATTAAAATATAAACTTC-3'	Simon *et al* 1994
16S	16Sar	Forward	5'-CGCCTGTTTATCAAAAACAT-3'	Palumbi *et al.* 1991
16S	16Sbr	Reverse	5'-CCGGTYTGAACTCAGATCAYGT-3'	Palumbi *et al.* 1991
H3	H3F	Forward	5'-ATGGCTCGTACCAAGCAGACVGC-3'	Bernhard 1999
H3	H3R	Reverse	5'-CTTCTGGCGAGTTGCATATCCT-3'	Bernhard 1999

The polymerase chain reaction (PCR) was performed using 5µl 5× MyTaq Reaction Buffer (BIOLINE), 0.4 µl primers forward and reverse (10 µM), 0.2 µl MyTaq Red DNA Polymerase (BIOLINE), 4 µl of diluted DNA and ultrapure distilled water up to a total reaction volume of 20 µl. COI was amplified as a follows: 5 min at 94°C followed by 35 cycles of denaturation at 94°C for 30 s, annealing temperature range of 42°C for 35 s, 72°C for 45 s and final extension at 72°C for 5 min; 16S and Histone H3 were amplified as a follows: 2 min at 94°C followed by 30 cycles of denaturation at 94°C for 30 s, annealing at 50°C for 35 s and extension at 68°C for 1 min and final extension at 68°C for 7 min.

Fragments were visualized by agarose gel electrophoresis at a concentration of 1% (w/v) in 1× TBE buffer (0.89 M Tris, 0.89 M boric acid, 0.02 M EDTA) (Panreac AppliChem, Barcelona, Spain) at 110 V for 45 min. PCR products were sequenced in both directions using one of the respective amplification primers at Macrogen services (www.macrogen.com). The chromatograms were assembled and edited in Geneious Prime v2021.1.1. (Drummond *et al.* 2010).

4.4.3. ***Phylogenetic analysis***

Different matrices were built for downstream phylogenetic analyses containing all the available *Aplysia fasciata* Poiret 1789, *Aplysia nigrocincta* E. von Martens 1880 and *A. punctata* sequences and four *Bursatella leachii* Blainville 1817 sequences from Catalonian coast, including: the individual COI, 16S and Histone H3 data matrices; the concatenated mitochondrial matrix with COI and 16S sequences; and the concatenated matrix with mitochondrial (COI + 16S) and nuclear (Histone H3) sequences.

Maximum likelihood (ML) and Bayesian inference analysis (BI) phylogenetic analyses were conducted using the best partition scheme and evolutionary model for each partition selected with Partition Finder v2.1.1. (Lanfear *et al.*, 2017). ML analyses were performed with RAxML 8.0 (Stamatakis 2014) with 10000 replicates, random initial trees, and estimated parameters evolutionary models. Branches with bootstrap values above 70% were considered supported (Hillis & Bull 1993). The first 10% of the generations were discarded as a burn-in for the analyses. Posterior probability node values (PP) higher than 0.9 were considered supported (Huelsenbeck & Rannala 2004). The resulting trees were visualized with iToL (https://itol.embl.de/itol.cgi).

4.4.4. ***Species delimitation under the ASAP algorithm and Haplotype network***

COI sequences were also used for species delimitation analyses with Assemble Species by Automatic Partitioning (ASAP; Puillandre *et al.* 2021). Jukes Cantor (JC69), Kimura (K80) and Simple Distance substitution models were tested. Finally, a haplotype network for the COI dataset was constructed using the TCS algorithm (Clement *et al.* 2000) implemented in the program PopArt 1.7 program v4.8.4 (Leigh & Bryant 2015).

4.4.5. ***Biological data***

Most of the observations of APJ and APA have been carried out in different locations on the Costa Brava (NE Spain) (Figure 2). Data on the biology of APJ and APA in the Catalonian coasts is based on long-term field observations by one of the authors (MB), compiled for more than 40 years. Moreover, records of specimens from other sources, mainly from members of the GROC (Grup de Recerca dels Opistobranquis de Catalunya) as well as photographs published on the internet have been examined. All data are provided in Table 3. Data collected include the color pattern of the specimen, date, locality. When possible, the number of specimens, the substrate, and any noteworthy behavior such as copulation and the presence of egg masses, were recorded both in the field observations or photographs. In total, all the observational data correspond to approximately 150 hours of scuba diving by different divers. Due to the small size and camouflage of APJ specimens, masses of frondose red algae such as *Sphaerococcus coronopifolius* Stackhouse 1797 and *Plocamium cartilagineum* (Linnaeus) P.S. Dixon 1967 were collected in different locations and the specimens were separated from the algae in the laboratory, by placing them in small-capacity aquaria. Some specimens of APJ and APA were induced to ink by touching them, others were collected with their respective algae that serve as food and habitat to observe their behavior in the laboratory. The feeding and reproductive behavior, the deposition of egg masses was observed in the laboratory.

Figure 2. Specimens capture locations of APJ and APA. In red the zone of the Costa Brava that is between 41°46'43" N and 3°1'44" E.

Table 3. Observations of APJ (as *A. parvula*) and APA on the Catalonian coast. Notes: the observations not reported by M. Ballesteros, M. Pontes and E. Madrenas correspond to members of the GROC (Grup de Recerca dels opistobranquis de Catalunya, https://opistobranquis.org/es/home) and are documented with photographs. CB= localities on the Costa Brava. * means observation not quantified in number of individuals. Blank substrate cells = no data.

Species	Observer	date	locality	other data	substrate
APJ	M. Ballesteros	27/02/1985	Punta de Santa Anna (Blanes, CB)	*	on *Codium* and *Halopteris*
APJ	M. Pontes	01/03/1985	Punta de Santa Anna (Blanes, CB)	*	
APJ	M. Pontes	27/05/1985	Pedra de Deu (Medes Is., CB)	*	
APJ	M. Pontes	27/05/1985	Punta de Santa Anna (Blanes, CB)	*	
APJ	M. Ballesteros	27/05/1985	Meda Gran (Illes Medes, CB)	*	on hidrarians and red algae
APJ	M. Ballesteros M. Pontes	07/06/1985	Mar Menuda (Tossa de Mar, CB)	*	
APJ	M. Pontes	09/03/1986	Mar Menuda (Tossa de Mar, CB)	*	
APJ	M. Ballesteros	12/05/1999	Cadaqués, CB	* copulate	
APJ	M. Ballesteros	22/05/2000	Roses, CB	*	

APJ	M. Pontes	01/02/2002	Illa Mateua (L. Escala, CB)	*	
APJ	M. Ballesteros	21/03/2002	Punta de Santa Anna (Blanes, CB)	*	
APJ.	M. Ballesteros	15/05/2002	Es Caials (Cadaqués, CB)	1	between red algae
APJ	M. Ballesteros	17/05/2002	L'Almadrava (Roses, CB)	2	between algae
APJ	M. Ballesteros	23/05/2002	Es Caials (Cadaqués, CB)	1	
APJ	M. Ballesteros	21/05/2003	Es Caials (Cadaqués, CB)	1	
APJ	M. Ballesteros	23/05/2003	Punta de la Creu (Roses, CB)	1	
APJ.	M. Ballesteros	14/05/2004	Cala dels Gats (Palamós, CB)	*	
APJ	M. Ballesteros	24/05/2004	Punta de Santa Anna (Blanes, CB)	*	
APJ	M. Ballesteros	16/05/2005	L'Almadrava (Roses, CB)	*	
APJ	M. Pontes	26/01/2008	Es Caials, CB	*	
APJ	M. Pontes	02/02/2008	Es Caials, CB	*	
APJ	J. Regás	02/03/2008	Illa Mateua (L´ Escala, CB)	*	
APJ	M. Pontes	03/05/2008	Es Caials, CB	*	
APJ	M. Ballesteros	19/05/2008	Bau Cap Falcó (Roses, CB)	*	
APJ	M. Ballesteros	18/05/2009	El Bisbe de Norfeu, CB	1	
APJ	M. Ballesteros	19/05/2010	Punta Falcó, CB	7	between algae
APJ	M. Pontes	20/02/2010	Es Caials, CB	*	
APJ.	M. Ballesteros	23/02/2010	Cala Sant Francesc (Blanes, CB)	*	on *Halopteris*
APJ	M. Ballesteros	23/02/2010	Cala Sant Francesc (Blanes, CB)	*	on *Sphaerococcus*
APJ	M. Pontes	06/03/2010	Es Caials, CB	*	
APJ	A. López-Arenas	06/03/2010	Mar Menuda (Tossa de Mar, CB)	*	
APJ	M. Pontes	17/04/2010	Cala Aiguafreda, CB	*	
APJ	GROC 2010	03/07/2010	Ferranelles (Illes Medes, CB)	*	
APJ	M. Pontes	22/01/2011	Es Caials, CB	*	
APJ	M. Pontes	16/04/2011	La Caleta (Palamós, CB)	*	
APJ	M. Ballesteros	23/05/2011	Mar Menuda (Tossa de Mar,)	*	on *Halopteris*
APJ	M. Pontes	28/05/2011	Es Caials (Cadaqués, CB)	*	
APJ	M. Pacareu	21/04/2012	Pota del Llop (Medes Is., CB)	*	
APJ	M. Ballesteros	21/05/2012	El Bisbe de Norfeu, CB	11	
APJ	M. Ballesteros	04/06/2012	Es Caials (Cadaqués, CB)	*	
APJ	M. Ballesteros	05/06/2012	Cap Norfeu (Roses, CB)	*	
APJ	M. Pontes	30/06/2012	El Port de la Selva, CB	*	
APJ	L. Toll	10/11/2012	Salpatxot (Medes Is., CB)	*	
APJ	E. Madrenas	18/01/2013	Punta del Romaní (L'Escala, CB)	*	
APJ	E. Madrenas	17/04/2013	Mataró	*	
APJ	M. Ballesteros	07/05/2013	Mar Menuda (Tossa de Mar, CB)	1	
APJ	E. Madrenas	19/05/2013	Punta del Romaní (L'Escala, CB)	*	
APJ	M. Ballesteros	23/05/2013	Els Caials (Cadaqués, CB)	*	on *Sphaerococcus*
APJ	M. Ballesteros	10/06/2013	Punta Falconera (Roses, CB)	1	
APJ	M. Ballesteros	11/06/2013	El Gat de Norfeu (Roses, CB)	1	
APJ	E. Madrenas	25/06/2013	Escollera Port (Tarragona)	3	on *Codium*
APJ	E. Madrenas	05/07/2013	Cala dels Gats (Palamós, CB)	*	
APJ	X. Salvador	10/12/2013	Palamós, CB	*	
APJ	X. Salvador	14/12/2013	Cala Bramant, CB	*	
APJ	X. Salvador	04/01/2014	Llançá, CB	*	
APJ	M. Pontes	22/02/2014	Cala Aiguafreda, CB	*	
APJ	M. Pontes	08/03/2014	Cala Aiguafreda, CB	*	
APJ	M. Pontes	18/04/2014	Cala Margarida, CB	*	
APJ	M. Pontes	26/04/2014	Cala Sa Tuna (Begur, CB)	*	
APJ	G. Morera	14/05/2014	La Caleta (Palamós, CB)	* copulate	on *Sphaerococcus*
APJ	M. Ballesteros	26/05/2014	Punta de la Creu (Roses, CB)	2	
APJ	M. Ballesteros	10/06/2014	Bau de Punta Falconera (Roses, CB)	15	on *Sphaerococcus*
APJ	M. Ballesteros	11/06/2014	Punta de la Creu (Roses, CB)	1	
APJ	X. Lindo	06/09/2014	Cala Margarida (Palamós, CB)	*	on *Flabellia*
APJ	M. Pontes	24/01/2015	Es Caials (Cadaqusés, CB)	*	
APJ	M. Pontes	28/02/2015	Es Caials (Cadaqués, CB)	*	
APJ	M. Pontes	14/03/2015	Es Caials (Cadaqués, CB)	*	
APJ	M. Pontes	16/05/2015	Es Caials (Cadaqués, CB)	*	
APJ	M. Ballesteros	25/05/2015	Bau de Punta Falconera (Roses, CB)	5	
APJ	M. Ballesteros	26/05/2015	Es Caials (Cadaqués, CB)	3	
APJ	M. Ballesteros	08/06/2015	La Trona (Roses, CB)	3	
APJ	M. Ballesteros	09/06/2015	Punta Falconera (Roses, CB)	7	
APJ	X. Salvador	14/07/2015	Les Sofreres (Sant Feliu de Guíxols, CB)	*	
APJ	G. Mas	12/09/2015	Sa Tuna, CB	*	
APJ	F. Asensio	29/11/2015	Es Caials (Cadaqués, CB)	*	
APJ	E. Madrenas	05/12/2015	Punta del Falaguer (Medes Is., CB)	*	

APJ	E. Madrenas	16/04/2016	Salpatxot (Medes Is., CB)	*	
APJ	M. Ballesteros	23/05/2016	Cap Falcó (Roses, CB)	1	
APJ	M. Pontes	14/01/2017	Es Caials (Cadaqués, CB)	*	
APJ	X. Salvador	02/03/2017	La Caleta (Palamós, CB)	*	
APJ	M. Casanovas	06/03/2017	Tossa de Mar, CB	*	on green algae
APJ	X. Salvador	15/04/2017	Llafranc, CB	*	on red algae
APJ	X. Salvador	18/04/2017	Cala Aiguaxelida, CB	*	on red algae
APJ	X. Salvador	08/05/2017	Cala Ventosa (Sant Feliu de Guíxols, CB)	*	on red algae
APJ	S. Fuertes	20/05/2017	El Guix (Medes Is., CB)	*	
APJ	X. Salvador	26/12/2017	Cala Montgó (L´Escala, CB)	*	on *Sphaerococcus*
APJ	X. Salvador	31/01/2018	Cala Aiguafreda, CB	*	
APJ	X. Salvador	08/03/2018	Cala Sa Tuna, CB	*	on *Ulva*
APJ	X. Salvador	24/04/2018	Punta del Romaní (L´Escala, CB)	*	on red algae
APJ	X. Salvador	27/04/2018	El Fòrum (Barcelona)	*	on red algae
APJ	G. Biscop	16/05/2018	Tascó Gros (Medes Is., CB)	*	on green algae
APJ	X. Salvador	25/05/2018	Cala Aiguafreda, CB	*	on red algae
APJ	M. Ballesteros	04/06/2018	Cap Falcó (Roses, CB)	2	on *Sphaerococcus*
APJ	M. Ballesteros	05/06/2018	La Trona (Roses, CB)	5	on *Sphaerococcus*
APJ	A. Mares	05/07/2018	Cala El Bofill (Cadaqués, CB)	*	
APJ	J. Fernández	08/08/2018	Platja del Pas (El Port de la Selva, CB)	*	
APJ	X. Lindo	09/02/2019	Cala Sa Tuna, CB	*	
APJ	X. Salvador	13/03/2019	Tamariu, CB	*	
APJ	M. Ballesteros	21/05/2019	El Bisbe (Roses, CB)	5	on *Sphaerococcus*
APJ	M. Ballesteros	27/05/2019	Bau Cap Falcó (Roses, CB)	4	on *Sphaerococcus*
APJ	M. Ballesteros	28/05/2019	Cala Sant Antoni (Cadaqués, CB)	4	on *Sphaerococcus*
APJ	M. Ballesteros	03/06/2019	Bau Cap Falcó (Roses, CB)	3	
APJ	X. Salvador	07/05/2020	Punta d´en Bosch (Sant Feliu de Guíxols, CB)	*	
APJ	X. Salvador	30/01/2021	Coves Cala Maset (Sant Feliu de Guíxols, CB)	*	
APJ	M. Ballesteros	25/05/2021	Bau Cap Falcó (Roses, CB)	13	
APA	M. Ballesteros	26/05/1977	Cubelles	61 + egg masses + copulate	under stones, on *Dictyota*
APA	M. Ballesteros	09/11/1978	Mar Menuda (Tossa de Mar, CB)	*	
APA	M. Ballesteros	14/03/1979	Punta de Santa Anna (Blanes, CB)	*	
APA	M. Ballesteros	25/05/1979	Cubelles	*	under stones
APA	M. Ballesteros	14/06/1979	Cubelles	*	under stones
APA	M. Ballesteros	25/11/1979	Cala Sant Francesc (Blanes, CB)	*	
APA	M. Ballesteros	10/04/1982	Cubelles	*	under stones
APA	M. Ballesteros	11/04/1982	Cubelles	*	under stones
APA	M. Ballesteros	22/05/1985	Cubelles	*	under stones
APA	M. Ballesteros	07/05/1986	Cubelles	*	under stones
APA	M. Ballesteros	01/05/1993	Roses, CB	*	
APA	M. Pontes	01/08/2000	Torre Valentina (Calonge, CB)	*	
APA	M. Ballesteros	06/05/2002	Cala Fosca (Palamós, CB)	*	
APA	M. Ballesteros	27/08/2003	Punta de Santa Anna (Blanes, CB)	*	
APA	M. Ballesteros	28/08/2003	Punta de Santa Anna (Blanes, CB)	*	
APA	M. Ballesteros	18/05/2005	Es Caials (Cadaqués, CB)	1	
APA	M. Pontes	08/04/2006	Es Caials (Cadaqués, CB)	*	
APA	E. Madrenas	20/02/2010	Sa Tuna (Begur, CB)	*	
APA	E. Madrenas	27/03/2010	La Caleta (Palamós, CB)	*	
APA	A. López-Arenas	29/03/2010	La Caleta (Palamós, CB)	*	
APA	GROC	03/07/2010	Ferranelles (Illes Medes, CB)	*	
APA	A. López-Arenas	25/02/2012	Cala Aiguafreda, CB	*	
APA	M. Ballesteros	22/05/2012	Es Caials (Cadaqués, CB)	1 juv.	under stones
APA	M. Ballesteros	01/06/2012	Cala Fosca (Palamós, CB)	*	
APA	M. Ballesteros	05/06/2012	Cap Norfeu (Roses, CB)	*	
APA	E. Madrenas	25/11/2012	Punta del Romaní (L'Escala, CB)	*	
APA	E. Madrenas	25/11/2012	Punta del Romaní (L'Escala, CB)	*	
APA	E. Madrenas	26/03/2013	La Caleta (Palamós, CB	*	
APA	E. Madrenas	31/03/2013	Aiguafreda (Begur, CB)	*	
APA	M. Ballesteros	28/05/2013	Cala Fosca (Palamós, CB)	3	under stones
APA	M. Ballesteros	29/05/2013	Cala Fosca (Palamós, CB)	3	under stones
APA	E. Madrenas	01/06/2013	Cala Margarida (Palamós, CB)	*	
APA	E. Madrenas	25/06/2013	Barcelona breakwater	*	
APA	M. Pontes	29/03/2014	Cala Sa Tuna (Begur, CB)	*	
APA	X. Salvador	11/04/2014	La Llosa (Palamós, CB)	*	
APA	G. Mas	02/08/014	Cala Margarida, CB	*	
APA	X. Salvador	10/04/2015	Cova d´Ariadna (Sa Riera, CB)	*	on algae

APA	E. Madrenas	18/04/2015	Tascons Petits (Medes Is., CB)	*	
APA	M. Ballesteros	26/05/2015	Es Caials (Cadaqués, CB)	3	under stones
APA	M. Ballesteros	27/05/2015	Cala Fosca (Palamós, CB)	*	under stones
APA	M. Ballesteros	01/07/2015	Cubelles	12	under stones
APA	M. Badía	28/07/2015	Sant Pol	*	
APA	M. Codina	01/05/2016	Cala Santa Anna, CB	*	
APA	M. Ballesteros	24/05/2016	Es Caials (Cadaqués, CB)	10 + copulate	under stones
APA	M. Ballesteros	25/05/2016	La Fosca (Palamós, CB)	11 + eggs masses	under stones
APA	M. Ballesteros	27/05/2016	La Fosca (Palamós, CB)	10	under stones
APA	M. Ballesteros	8/06/2016	Es Caials (Cadaqués, CB)	4 + copulate	under stones
APA	X. Salvador	18/04/2017	Cala Aiguaxelida, CB	*	on algae
APA	E. Madrenas	18/11/2017	Llosa del Falaguer (Medes Is., CB)	*	
APA	M. Bosch	29/12/2017	La Gavina (Sant Feliu de Guixols, CB)	*	
APA	X. Salvador	27/04/2018	El Fòrum (Barcelona)	*	
APA	A. Mares	16/05/2018	Cala El Bofill (Cadaqués, CB)	*	
APA	G. Alvarez	16/05/2018	El Forum (Barcelona)	*	
APA	M. Ballesteros	17/05/2018	El Forum (Barcelona)	> 150 + copulate	under stones
APA	M. Ballesteros	24/05/2018	La Fosca (Palamós, CB)	7	under stones
APA	X. Salvador	24/05/2018	Punta del Romaní (L´Escala, CB)	*	
APA	X. Salvador	25/05/2018	Cala Aiguafreda, CB	*	on red algae
APA	M. Ballesteros	04/06/2018	Cap Falcó (Roses, CB)	1	
APA	M. Ballesteros	06/06/2018	Es Caials (Cadaqués, CB)	5	
APA	M. Ballesteros	05/07/2018	El Fòrum (Barcelona)	7	under stones
APA	M. Ballesteros	12/07/2018	El Fòrum (Barcelona)	*	
APA	X. Salvador	09/03/2019	Cala Sa Tuna, CB	*	
APA	A. Parera	02/04/2019	El Fòrum (Barcelona)	*	
APA	M. Bosch	16/04/2019	Cala Aiguablava, CB	*	on algae
APA	A. Parera	13/05/2019	El Fòrum (Barcelona)	*	on red algae
APA	M. Ballesteros	22/05/2019	Es Caials (Cadaqués, CB)	1	under stones
APA	M. Ballesteros	24/05/2019	La Fosca (Palamós)	13 + egg masses	under stones
APA	M. Ballesteros	05/06/2019	Es Caials (Cadaqués, CB)	5	under stones
APA	A. Parera	15/06/2019	El Fòrum (Barcelona)	*	
APA	J. Vilanova	06/07/2019	Tamariu, CB	*	
APA	C. Escarré	13/07/2019	El Fòrum (Barcelona)	*	
APA	M. Ballesteros	18/07/2019	El Fòrum (Barcelona)	4	under stones
APA	X. Salvador	15/06/2020	Coves Cala Maset (Sant Feliu de Guíxols, CB)	*	on algae
APA	A. Mares	30/06/2020	Cala El Bofill (Cadaqués, CB)	*	on algae
APA	X. Salvador	12/07/2020	Cala Aiguafreda, CB	*	on algae
APA	M. Ballesteros	2/06/2021	Es Caials (Cadaqués, CB)	7 + egg masses	under stones
APA	E. Badosa	06/04/2021	Cala Aiguaxelida, CB	*	on algae
APA	J. M. Flamarich	09/08/2021	Es Caials (Cadaqués, CB)	*	on algae

4.5. Results

4.5.1. *Phylogenetic trees*

The mitochondrial data matrix and the concatenated COI, 16S and H3 data matrix included, respectively, 1113 bases and 1441 bases with 103 sequences. All the trees designed showed a topology with a similar or very similar behavior, giving us Bayesian analysis as maximum likelihood where clades were recovered; well defined as that of *A. fasciata* from the western Atlantic with Israel (Bs = 87), as well as another well-defined clade from *A. nigrocincta* from the Indo-Pacific (Bs = 97), another clade between *A. punctata* from the eastern Atlantic (only those from Azores, Portugal) and a specimen from southwest Turkey and a large clade where all the specimens collected by us on the Catalonian Mediterranean coasts (APJ and APA) nest, along with the vast majority of the *A. punctata* of the eastern Atlantic and the Mediterranean (Bs = 72) (Figure 3).

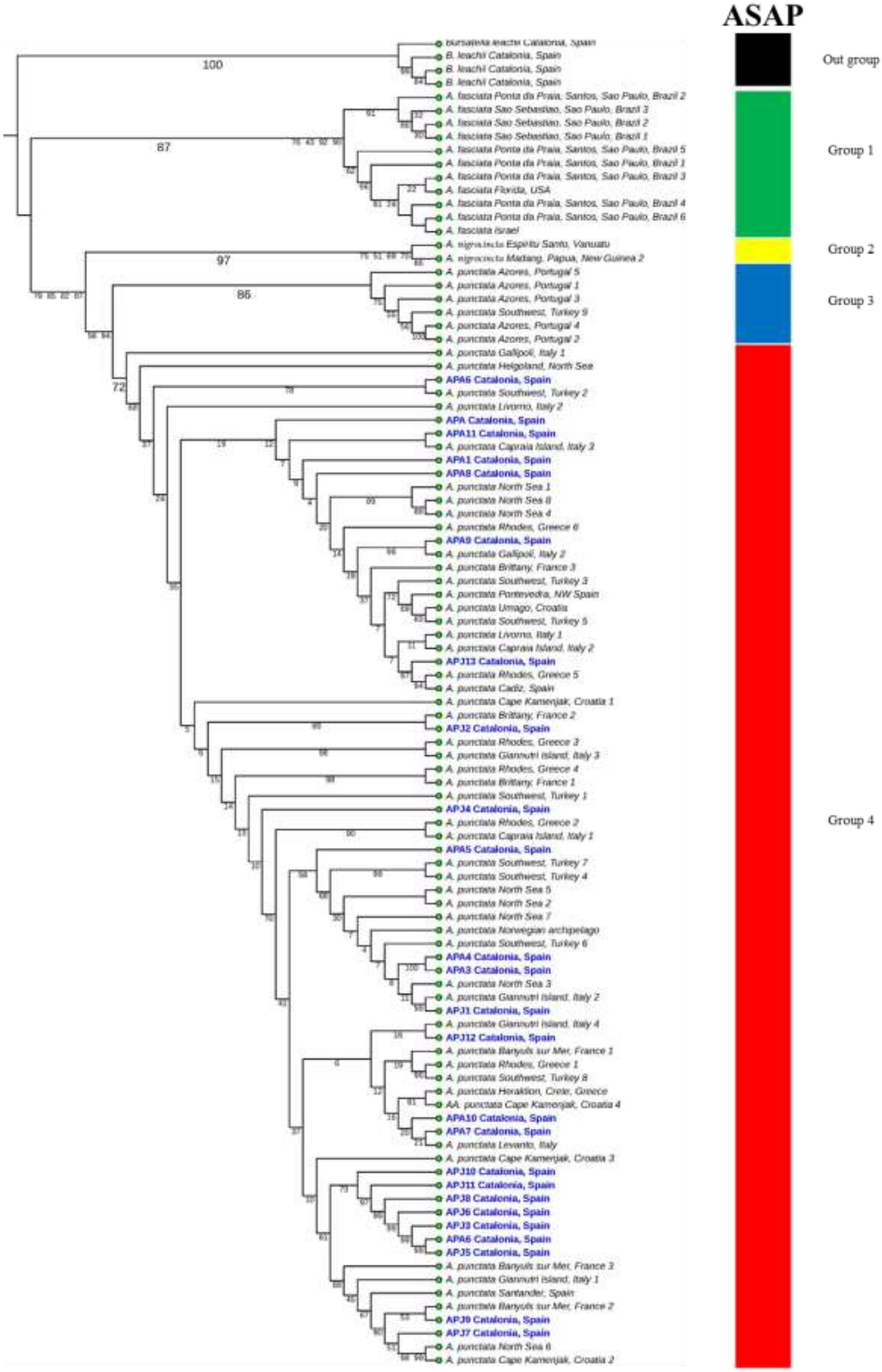

Figure 3. Phylogenetic tree from the obtained sequences and those of Genbak. Consensus tree topology of mtDNA haplotypes and ASAP species delineation colored clusters; the specimens placed by us (APJ and APA), are in blue.

4.5.2. *Species delimitation*

The species recovered in the ASAP species delimitation analysis correspond to well-supported clades that include four different hypothetical "groups" of which it stands out; group four: with all the APJ and the APA collected by us together with all the *A. punctata* of the Mediterranean and the great majority of the eastern Atlantic (represented with the red bar); the other groups are constituted as follows: group one with the *A. fasciata* from the western Atlantic and Israel (Green Bar), group two: the *A. nigrocincta* from the Indo-Pacific and finally group three: the *A. punctata* from the eastern Atlantic (only those of Azores, Portugal) together with a specimen from southwest Turkey (blue bar) (Figure 3).

4.5.3. *Haplotype network*

The COI data matrix included 668 bases in the species *A. punctata*. The haplotype network showed five different haplotypes, differentiated by several mutations from each other. The *A. punctata* clade has a haplotype that differs by many mutations from the *A. punctata* from eastern Atlantic (only those from Azores, Portugal), and one specimen of *A. punctata* from southwest Turkey; small mutations are also observed in specimens of *A. pu*nctata collected by us, together with specimens of the same species found both in the Mediterranean and Eastern Atlantic The haplotype network shows a clear geographic structure in specimens of *A. punctata* from the Mediterranean, those from the eastern Atlantic and all the specimens collected by us (APJ and APA) in two well-defined groups: APJ7 which includes the specimens collected by us on the Catalonian coasts such as APJ4, APJ5, APJ11, APJ12, APA2 and APA3; together with *A. punctata* from the Mediterranean of France, Italy, Turkey, Greece and Croatia; and other *A. punctata* from the eastern Atlantic, North Sea and the Norwegian archipelago; the other group is *A. punctata* from Livorno, Italy, which groups *A. punctata* from the Mediterranean of Spain, Greece and Turkey, with *A. punctata* from the eastern Atlantic of the North Sea and the APJ6 collected by us on the Catalonian coast (Figure 4).

4.5.4. *External morphology*

The smallest specimens (APJ), about 4-20 mm long, have a reddish-brown coloration due to a dense crosslinking of this color that delimits polygonal areas in the center, where there is usually an irregular white spot; also, we found some juveniles of length between 20-25 mm of brown coloration with white spots and morphology very similar to the adult specimens of *A. punctata* (Figure 1). There are also usually larger white spots scattered along the lateral walls of the body and parapodium, which may be grouped into larger whitish spots. When the animal is moving, the body is elongated and slender and the head is joined to the rest of the visceral mass by a long neck, which can be shrunk and stretched. To the right of the body, the spermatic sulcus is clearly visible, which runs from the anterior end of the parapodium to almost the base of the right cephalic tentacle. The cephalic tentacles are curled throughout and the rhinophores have a slit in their lateral area; both are the same color as the body except for its apical area, which is usually black. The black eyes are located in a slightly prominent whitish areas somewhat to the right and in front of the base of the rhinophores. The mantle has a wide oval foramen through which the shell can be seen. The parapodia are not very wide, they are slightly undulating and they are fused behind. The edge of each parapodium is black, sometimes interrupted by white spots and in some specimens a fine white marginal line is observed. The parapodia are joined in the posterior end, which prevents the animal from making swimming movements. On the dorsal inside of the parapodium there are usually white granulations that form a spot of this very apparent color and that also adorn the anal siphon. The gill is pink and semitransparent. The foot is pink except in the anterior and posterior areas whose margins are black. There may also be white granulations on the rest of the foot margin (Figure 5). The penis is spoon-shaped and pink and semi-transparent.

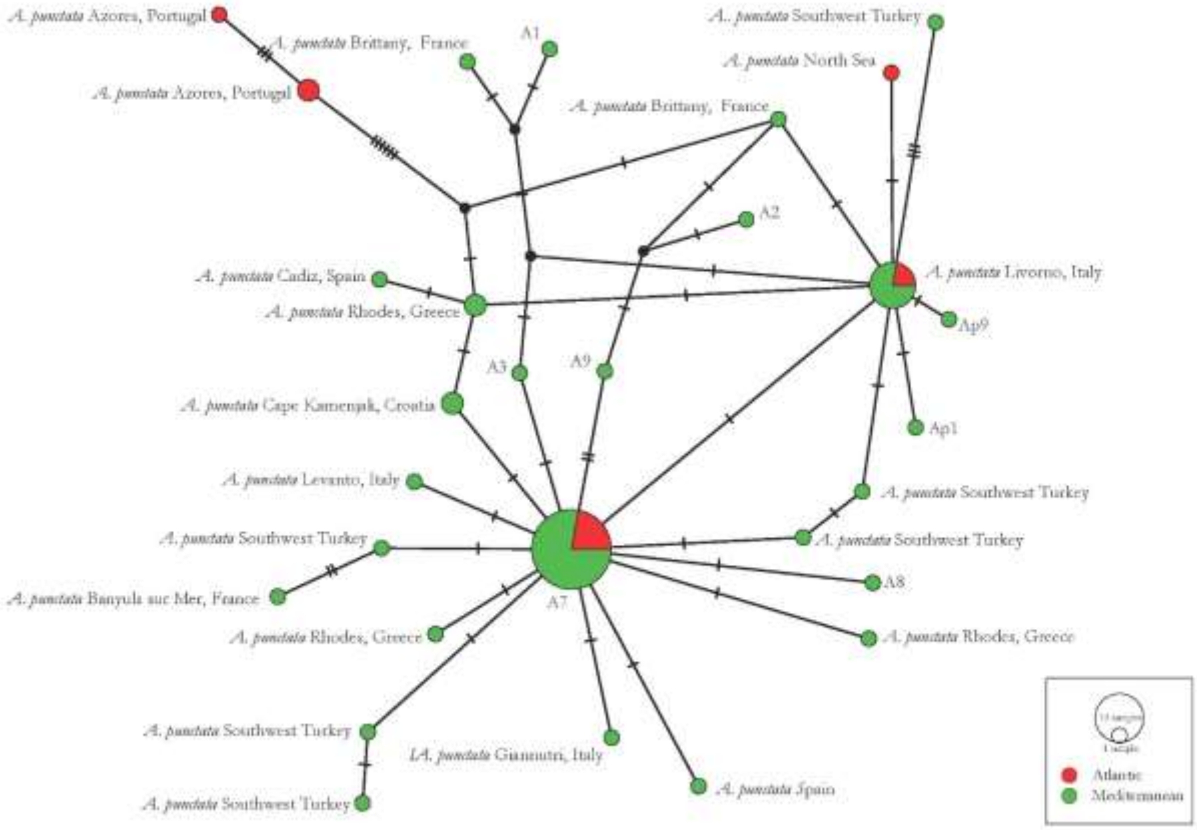

Figure 4. Haplotype networks based on COI sequence data, the geographic region of origin of the specimens is represented in color. The relative size of the circles is proportional to the number of sequences of the same haplotype.

From about 25 mm in length up (APA), specimens are more or less dark olive green with numerous white marks throughout the body, including the rhinophores and the dorsal area of the foot, sometimes gathered in specific areas. In these larger specimens the black pigmentation of cephalic tentacles, rhinophores, margin of the parapodium and anterior and posterior borders of the foot is no longer observed. In some darker specimens a white line is very apparent on the edge of the parapodium. The largest specimens (10–15 cm) are usually brownish in color and the white spots can cover a large part of the body or be very small and widely dispersed. In some of the larger specimens the spots are cream-colored with a whitish central area. The foot is wide behind and acts like a suction cup.

Figure 5. Specimens of APA 65 mm length (left) and APJ 20 mm length (right). Localities. A: Es Caials; B: La Fosca; C: Fòrum; D: Fòrum; E: Bau del Cap Falcó; F: La Fosca; G: Cap Falcó; H: Bau del Cap Falcó

The shells of the *A. punctata* (Figure 6) specimens measure 10 mm in a 25 mm living animal and 35 mm in a 65 mm specimen, they are oval shells, wider about half their length, with a curved posterior end, the right part adjacent to the protoconch is slightly concave.

Figure 6. Shells of specimens. A: APJ (A3). Collected in La Fosca, Barcelona. B: APA (Ap3) from El Fòrum, Barcelona

4.5.5. ***Radular and jaw structure***

The radular formula of a 20 mm APJ specimen collected alive in La Fosca, Palamos, Barcelona, NE Spain was 35×5.10.1.10.5. The central tooth has a geometric shape similar to a trapezium with a very elongated base, a central triangular cusp and several lateral protuberances without clearly defined denticles, the teeth measure on average 54.91 wide × 111.95 µm long; the lateral teeth are narrow and have a main cusp with an inner lateral denticle and 2–3 denticles on the outer side; the outermost teeth are undeveloped, have an outer margin and an inner margin with a well-defined stalk, 79.49 µm long × 12.34 µm wide (Fig. 7 A, B and C right).

In a 85 mm APA specimen collected alive at the Forum, Barcelona, NE Spain the radular formula was 51×8.10.1.10.8. The central tooth has a trapezoidal geometric shape, with a serrated main cusp flanked with 2 denticles on each side; this rachidian tooth measures 94.22 µm long × 54.91 µm wide; lateral teeth are narrow and have a serrate main cusp, inner flanking cusp and reduced outer flanking cusp; they are 94.09 µm long × 48.56 µm wide; outermost they are 126.20 µm long × 16.99 µm wide (Fig. 7 A, B and C left). The jaws of the APA and APJ specimens are formed by tiny curved and smooth hook-shaped rods called uncinas that serve to scrape food, having two to four cusps at the apex (Fig, 7D).

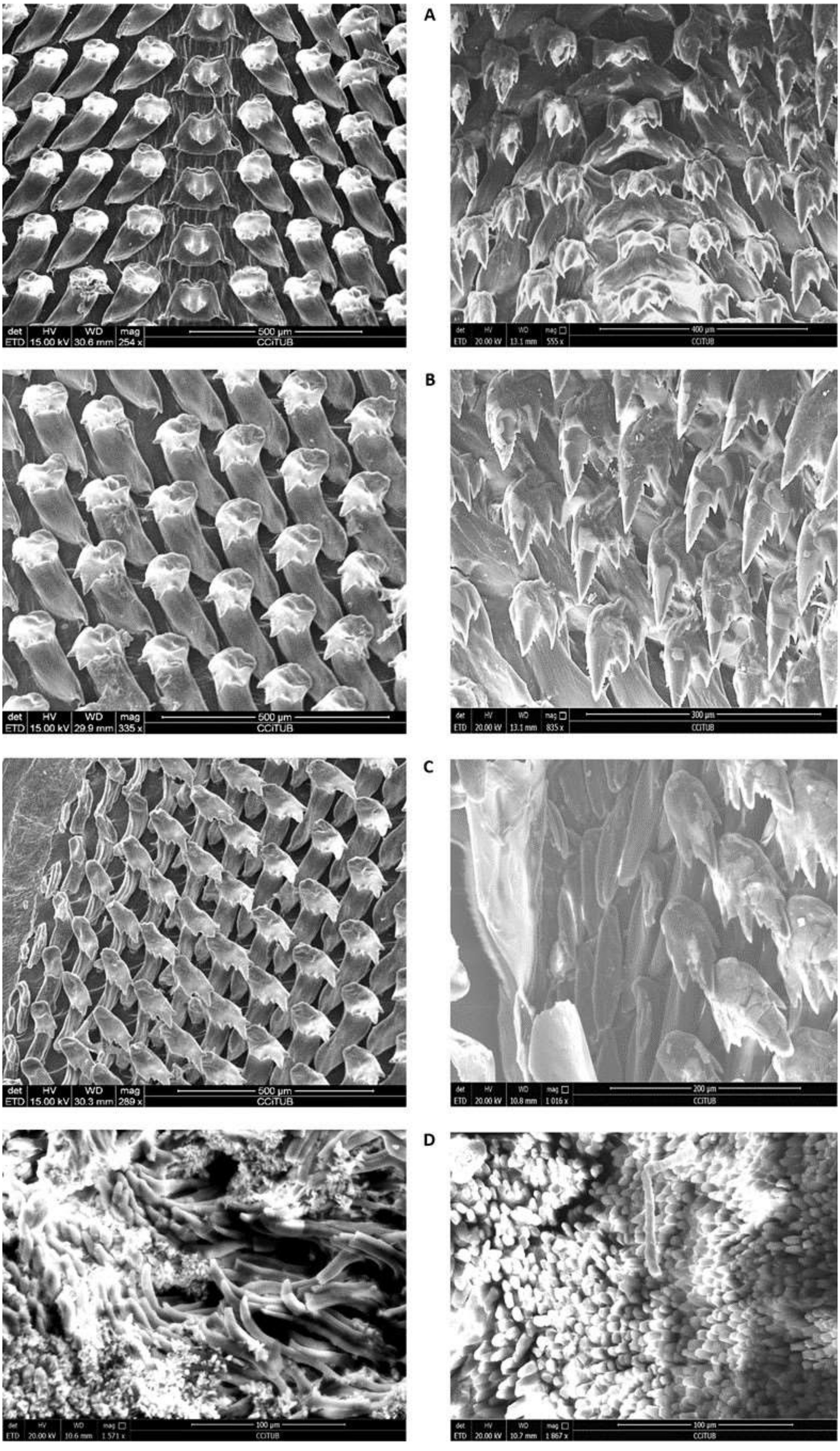

Figure 7. Scanning electron micrographs of the radular teeth and jaw elements of APA (left) from Fòrum (Barcelona, NE Spain) and APJ (right) from La Fosca (Palamós, NE Spain). A. Rachidian and first lateral teeth, B. lateral teeth, C. marginal and external lateral teeth D. uncinas of the jaw.

4.5.6. *Biology*

On the Catalonian coast, JPAs up to a size of about 20 mm (Figure 8B, C and D), preferentially live among the fronds of red algae soft red algae such as *S. coronopifolius* (Figure 8A) and *P. cartilagineum*. APJ specimens feed on different red algae and presumably obtain pigments that help them camouflage themselves to hide from predators. Specimens change from APJ (reddish) to APA (olive green) as they get larger. Due to their larger size, APA specimens no longer go unnoticed by predators in small red algae and have to implement alternative defensive strategies; therefore, they move to a different habitat, living under the rocks; at the same time, they begin to ingest green algae of the genera *Ulva* Linnaeus 1753 (such as *Enteromorpha* Link 1820), preferably *Ulva lactuca* Linnaeus 175 which is a very common green algae in the Mediterranean; their bodies change from reddish to an olive-green hue with white spots, as they probably acquire pigments from their food and incorporate them into their tissue. Therefore, APA specimens acquire other green or brown tones depending on the algae available to feed on, in addition to the typical white spots that characterize the species. When specimens are disturbed, they can secrete a defensive whitish fluid, sometimes mixed with purple ink (Fig. 8C).

Figure 8. A: the red algae *Sphaerococcus coronopifolius*; B, C and D: APJ of 20 mm length (known until recently as *A. parvula*) on the same alga, note the black margins of oral tentacles, rhinophores, parapodia, and anterior and posterior end of the foot; in C a specimen emitting the defensive violaceous substance after being disturbed.

APJ and APA specimens reproduce at the end of spring (April-June), both in the field and in the laboratory, forming aggregations of up to 9-10 individuals (APA) and 4-5 individuals (APJ) (Figure 9).

During this period numerous APA specimens migrate to shallow depths to copulate and lay eggs. The breeding period is simultaneous in various locations such as Cubelles, Cadaqués and Fòrum de Barcelona; In this last place we have counted up to more than 150 APA specimens in one hour of sampling copulating and depositing their egg masses under stones at a depth of about 2 m. After copulation, the animals lay a row of orange-yellow eggs (Figure 10) sometimes reddish to pink and sometimes mauve or orange, forming a compact mass. Inside the ribbon are capsules containing 3 or 4 eggs, each about 100 μm in diameter. Only APAs mate and lay eggs; APJs only copulate, but do not lay eggs (Figure 11). In the last 40 years, on the Catalonian coasts, 366 observations, 225 copulations and 92 APA clutches, 182 observations and two APJ matings were recorded (Figure 11 and Table 3).

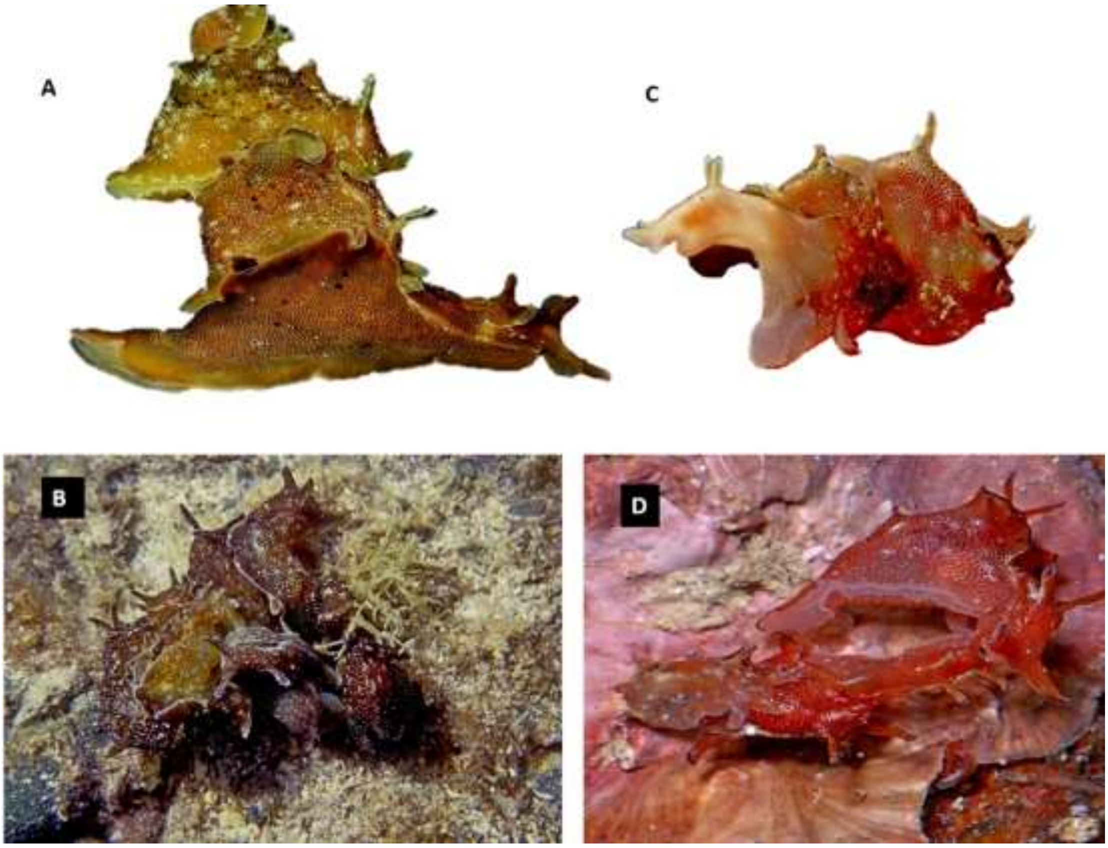

Figure 9. Reproduction in *Aplysia punctata*. A and B: multiple copulas in APA of 65 mm length; C and D: multiple copulas in APJ of 20 mm length (known until recently as *Aplysia parvula*).

Figure 10: Typical specimen of *Aplysia punctata* (APA) of 65 mm length with its eggs mass

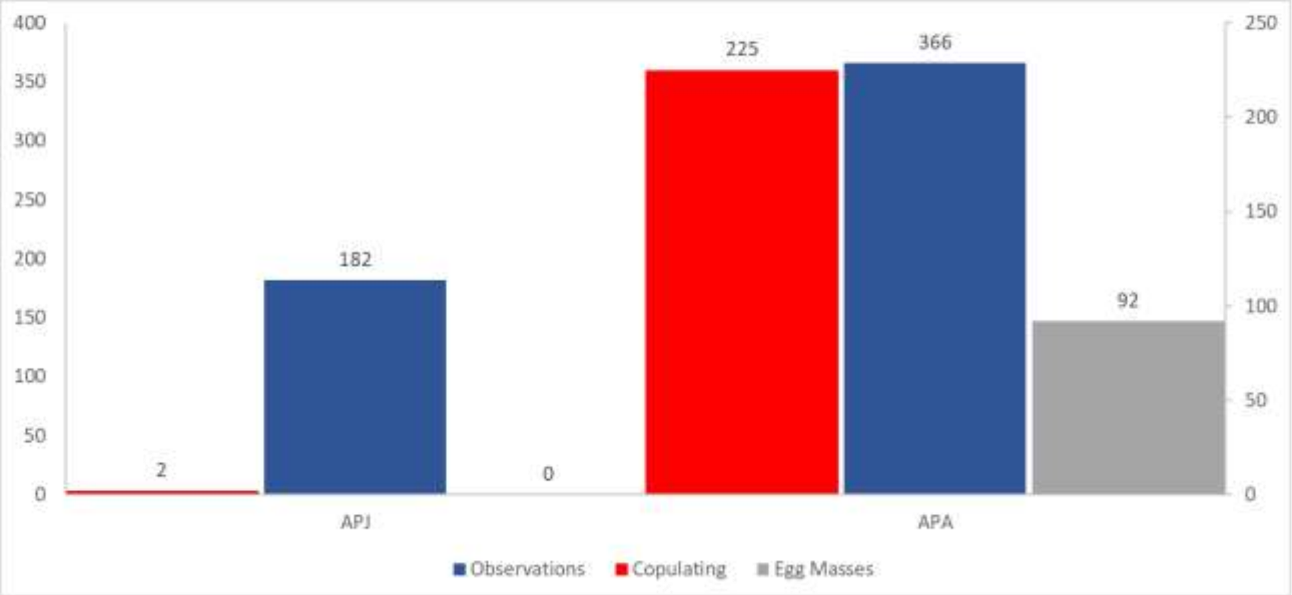

Figure 11: Comparison of sightings, mating and spawning of APJ and APA, on the left vertical axis is the number of observations and on the right vertical axis the copulas and egg masses.

4.6. Discussion

The morphological differences between APJ and APA in body color (Figure 5), shell (Figure 6), and radular and jaw morphology (Figure 7) examined here suggest that they could be different species, and even that APJ could be a possible new species of *Aplysia*. However, the results of the molecular analyses, including the phylogenetic tree, the species delimitation analysis with the ASAP algorithm (Figure 3) and the haplotype network (Figure 4), clearly show that all the specimens from the Catalonian coast of APJ and APA belong to a single species that corresponds to *A. punctate*. Although in Figure 3, there is divergence in the phylogenetic results between the intraspecific genetic biodiversity of some *A. punctata* collected by us with others from the eastern Atlantic (Azores, Portugal) and added to the small mutations observed among these specimens in Figure 4, but molecularly they are all still *A. punctata* (both APJ and APA and *A. punctata* from the Mediterranean and the eastern Atlantic).

We have concluded this because, both in the paper of Golestani *et al.* (2019) as in ours we have verified that molecularly there is no *A. parvula* in the Mediterranean and in the eastern Atlantic, that possibly the phenotypical resemblance of the APJ to the adults of *A. parvula*, is due to a protective action of the APJ from predators, to be able to hide better in the red algae, although there is also a very high probability that both species (both *A. puntata* and *A. parvula*) have hybrid populations, an aspect that makes it very difficult to distinguish the small ones with the naked eye. APJ from *A. parvula* adults, unless molecular testing is performed.

Regarding interspecific biodiversity, it is very evident in Figure 3 that the APJ, APA and the other *A. punctata* of the Mediterranean and the Eastern Atlantic are very different from the *A. fasciata* of the Eastern Atlantic, the *A. nigrocincta* of the Indo-Pacific and the *A. punctata* recorded in Azores, Portugal; We can even see this in Figure 4, where numerous mutations occur between the APJ, APA and the other *A. punctata* from the Mediterranean and the Eastern Atlantic with the *A. fasciata* from the Eastern Atlantic, the *A. nigrocincta* from the Indo-Pacific and including the *A. punctata* recorded in Azores, Portugal; the latter according to this paper and the one carried out by Golestani *et al.* (2019) are a different species, despite the fact that in our paper we found in Figure 3, an *A. punctata* from southwest Turkey within the clade of *A. punctata* from Azores, Portugal; this is part of this group of specimens that may be another species; although all specimens from southwest Turkey were mistakenly recorded by Yokes in 2018 as *A. parvula*, one year before the paper of Golestani *et al.* (2019), who records all those specimens from southwest Turkey as *A. punctata*.

Garstang (1890) and Eales (1921) found that *A. punctata* in the Mediterranean feeds on eight species of algae, red algae in the juvenile stage and green algae as adults. On the other hand, in Atlantic coasts Niell

(1977) pointed out that *A. punctata* can feed up to 32 species of red and green algae, but almost always prefers *Ulva gigantea* Bliding 1969 and Eales (1921) indicated that this species prefers *Delesseria* sp., *Fucus cartilagineus* Linneo 1753, *Laminaria* sp., and *Ulva* sp, 1753. Carefoot (1967a) in the British Islands found that juveniles of *A. punctata* feed preferentially on red algae of different genera, such as *Plocamium* Lamouroux, 1813, *Heterosiphonia* Montagne 1842, *Cryptopleura* Kützing 1843, and *Delesseria* Lamouroux 1813 (in that order) when available. Also, Carefoot (1967b) used a combination of these red algae in the laboratory to feed specimens of *A. punctata* and found that they used the energy obtained by ingesting these algae for growth, nitrogen production, carbohydrates, and amino acid synthesis, and that they grew faster feeding on the species *P. cartilagineum* (as *Plocamium coccineum* Lyngbye 1819).

In this chapter, we have seen how the APJ of the Catalonian coasts feed on a great variety of types of red algae, such as *S. coronopifolius* and *P. cartilagineum*; acquiring a reddish hue very similar or phenotypically similar to the adults of *A. parvula*, due to the fact that they incorporate the pigments of the algae into their body; but as they increase in size, they no longer go unnoticed by predators in the small red algae and have to implement alternative defensive strategies, and one of them is to feed on green algae of the *Ulva lactuca* species available in the environment and as they take pigments from the algae, their body changes to an olive green hue with many white spots, which is the hue of the APA specimens; they also move to a different habitat that may provide better protection, such as under rocks. These APA specimens acquire other green or brown tones, in addition to the typical white spots that characterize the species in its adult state, which help it to go unnoticed by predators, managing to conserve the species and make it very common in the Mediterranean.

Lo Bianco (1909) found that the Mediterranean *A. punctata* reproduces from February to July; while Eales (1921) indicated that the reproductive period is from spring to summer, Miller (1960) from March to August, Carefoot (1967a) from May to October and Thompson (1976) in spring; all of them for the specimens of the Atlantic. We found Mediterranean APA, copulating and ovilaying, and APJ only copulating in April and June, but not copulating with each other, forming reproductive aggregates of 9-10 individuals of APA (Figure 9A and 9B) and 4-5 individuals of red APJ (Figure 9C and 9D) confirming that APJ specimens are sexually mature and therefore smaller adults. Carefoot (1987) observed breeding APA groups of 22 to 30 individuals.

Ballesteros & Templado (1987) indicated that the eggs in APA are aligned forming a ribbon of 0.6 mm in diameter with abundant reddish or pinkish eggs, each with a diameter between 80 and 105 μm. We found that the egg masses change color depending on the size of the animal, probably a defensive mechanism against predators. Our APA specimens produced pink or reddish egg masses, very similar in color to the algae they feed on (Figure 10). They also produce egg masses that vary from yellow to pink, and also mauve (Carefoot, 1967b) or orange (Eales 1921), the latter coinciding with those observed in this study; APJs do not produce egg masses, they were only observed copulating (Figure 11), because despite maturing early, they may not be able to fertilize their eggs. Also, despite the fact that in the last 40 years there are records of the observations of APJ and APA, both of their copulations and their laying, the records for the amount of time seem very low, this is due to the large number of predators that it has. the species, climate change, the loss of its habitat and food also influence this. We believe that veliger larvae retain their reddish egg coloration because they are more likely to survive after metamorphosis when recruited on red algae than on other types of algae or substrates, since according to Carefoot (1987) mortality in the larval stage is very high. high due to the large number of predatory organisms that exist in its environment.

Based on the results of this study, it appears that changes in the diet of *A. punctata* determine body color, providing this species with a dynamic, adaptable defensive mechanism that would explain the dominance of this species in the western Mediterranean.

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4.8. References

Andrews K.R., Norton E.L., Fernandez-Silva I., Portner E. & Goetze E. 2014. Multilocus evidence for globally distributed cryptic species and distinct populations across ocean gyres in a mesopelagic copepod. *Molecular Ecology*, 23: 5462–5479. https://doi.org/10.1111/mec.12950

Ballesteros M. 2007. Lista actualizada de los opistobranquios (Mollusca: Gastropoda: Opisthobranchia) de las costas catalanas. *Spira*, 2(3): 163-188.

Ballesteros M. & Templado J. 1987. *Aplysia parvula* Guilding in Mörch, 1863 en las costas de la península ibérica. *Publicaciones del Departamento de Zoología*, 13: 55-62.

Ballesteros M., Madrenas E. & Pontes M. 2016. Actualización del catálogo de los moluscos opistobranquios (Gastropoda, Heterobranchia) de las costas catalanas. *Spira* 6:1-28.

Ballesteros M., Madrenas E. & Pontes M. 2021. "*Aplysia parvula*" in OPK-Opistobranquis. Published: 15/05/2012. Accessed: 26/11/2021. (https://opistobranquis.info/en/fImKM)

Barash A. & Danin Z. 1971. Opisthobranchia (Mollusca) from Mediterranean waters of Israel. *Israel Journal of Zoology*, 20: 151-200.

Barco A., Raupach M.J., Laakmann S., Neumann H. & Knebelsberger T. 2016. Identification of North Sea molluscs with DNA barcoding. *Molecular and Ecology Resources*, 16(1): 288-97.

Bebbington A. 1975. On a collection of *Aplysia* species from Naples with a note on the distribution of *Aplysia parvula* (Gastropoda, Opisthobranchia) in the Mediterranean. *Pubblicazioni della Stazione Zoologica di Napoli*, 39: 121–128.

Bebbington A. & Brown G.H. 1975. *Aplysia parvula* Guilding in Morch, an opisthobranch new to the British fauna. *Journal of Conchology*, 28: 329–333.

Bernhard D. 1999. Several highly divergent histone H3 genes are present in the hypotrichous ciliate *Stylonychia lemnae*. *FEMS Microbiology Letters* 175: 45-50.

Bouchet P. & Gofas S. (2015). *Aplysia*. In: MolluscaBase (2022). Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=137654

Carefoot T.H. 1967a. Growth and nutrition of *Aplysia punctata* feeding on a variety of marine algae. *Journal of the Marine Biological Association of the U.K.*, 47: 565-589.

Carefoot T.H. 1967b. Studies on a sublittoral population of *Aplysia punctata*. *Journal of the Marine Biological Association of the U.K.*, 47: 335-350.

Carefoot T.H. 1987. *Aplysia*: its biology and ecology. *Oceanography and Marine Biology: Annual Review*, 25: 167–284.

Cervera J.L., Calado G., Gavaia C., Malaquias M.A.E., Templado J., Ballesteros M., García-Gómez J.C., & Megina, C. 2004. An annotated and updated checklist of the opisthobranchs (Mollusca: Gastropoda) from Spain and Portugal (including islands and archipelagos). *Boletin del Instituto Español de Ocean*ografía, 20: 1–111.

Clement M., Posada D. & Crandall K.A. 2000. Graphicraft Limited, Hong Kong TCS: a computer program to estimate gene genealogies. *Molecular Ecology*, 9: 1657–1659.

Cooke S., Hanson D., Hirano Y., Ornelas-Gatdula E., Gosliner T.M., Chernyshev A.V. & Valdés, A. 2014. Cryptic diversity of *Melanochlamys* sea slugs (Gastropoda, Aglajidae) in the North Pacific. *Zoologica Scripta*, 43: 351–369. https://doi.org/10.1111/zsc.12063

de Oliveira L., Cunha C.M., Colpo K.D. & Valdes A. 2014. It's not what it looks like: molecular data fails to substantiate morphological differences in two sea hares (Mollusca, Heterobranchia, Aplysiidae) from southern Brazil. *Helgoland Marine Research*, 68:(4): 523-530

Domènech A., Avila C. & Ballesteros M. 2002. Spatial and Temporal variability of the Opisthobranch molluscs of Port Lligat Bay (Catalonia, NE Spain). *Journal of Molluscan Stud*ies, 68:29-37.

Doyle. J.J. 1992. Gene trees and species trees: molecular systematics as one-character taxonomy. *Systematic Botany*, 17: 144–163. https://doi.org/10.1146 /annurev.ecolsys.27.1.423

Drummond A.J., Ashton B., Buxton S., Cheung M., Cooper A., Heled J., Kearse M., Moir R., Stones-Havas S., Sturrock S., Thierer T. & Wilson A. 2010. Geneious v5.1. URL http:// www.geneious.com.

Eales N.B. 1921. *Aplysia.* L.M.B.C. *Mem. typ. Br. mar. PI. Anim.*, 24: 84.

Eales N.B. 1970. On the migration of tectibranch molluscs from the Red Sea to the eastern Mediterranean. *Journal of Molluscan Studies*, 39: 217–220.

Field K.G., Olsen J.J., Lane D.J., Giovannoni S.J., Ghiselin M.T., Raff E.C., Pace N.R. & Raff R.A. 1988. Molecular phylogeny of the animal kingdom. *Science*, 239 (4841 Pt 1):748-53. doi: 10.1126/science.3277277.

Folmer O., Black M., Hoeh W., Lutz R. & Vrijenhoek, R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol*ecular *Mar*ine *Biol*ogy *and Biotechnol*ogy, 3: 294–9.

Fukami H., Budd A.F., Paulay G., Solé-Cava A., Chen C.A., Iwao K. & Knowlton N. 2004. Conventional taxonomy obscures deep divergence between Pacific and Atlantic corals. *Nature*, 427: 832.

Gaither M.R., Bowen B.W., Rocha L.A. & Briggs J.C. 2016. Fishes that rule the world: circumtropical distributions revisited. *Fish and Fisheries*, 17: 664–679. https://doi.org/10.1111/faf.12136

Garstang W. 1890. A complete list of the opisthobranchiate Mollusca found at Plymouth; with further observations on their morphology, colours, and natural history. *Jounal of the marine biological Associtiion of the U.K.*, 1: 399-457.

Glanzman D.L. 2006. The cellular mechanisms of learning in *Aplysia*: of blind men and elephants. *Biological Bulletin,* 210(3):271-9. doi: 10.2307/4134563.

Grande C., Templado J., Cervera J.L. & Zardoya R. 2004. Molecular phylogeny of euthyneura (mollusca: gastropoda). *Molecular Biology and Evoution.*, 21(2): 303-313.

Gofas S., Luque A.A., Templado J. & Salas C. 2017. A national checklist of marine Mollusca in Spanish waters. *Sci. Mar.*, 81(2): 241-254. http://dx.doi.org/10.3989/scimar.04543.21A

Golestani H., Crocetta F., Padula V., Camacho-García Y., Langeneck J., Poursanidis D., Pola M., Yokeş B., Cervera J.L., Jung D.-W., Gosliner T., Araya J.F., Hooker Y., Schrödl M. & Valdés A. 2019. The little *Aplysia* coming of age: from one species to a complex of species complexes in *Aplysia parvula* (Mollusca: Gastropoda: Heterobranchia). *Zoological Journal of the Linnean Society*,187(2):279-330. https://doi.org/10.1093/zoolinnean/zlz028/5509942

Hillis D.M. & Bull J.J. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analyses. *Systematic Biology*, 42: 182–192.

Howells H.H. 1942. The structure and function of the alimentary canal of *Aplysia punctata*. Q*uarterly Journal of microscopical Sci*ence, 83: 357-97.

Huelsenbeck J.P. & Rannala B. 2004. Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. *Systematic Biology*, 53: 904–913.

Kelaart E.F. 1858. Description of new and little-known species of Ceylon nudibranchiate molluscs and zoophytes. *Journal of the Ceylon Branch of the Royal Asiatic Society, Columbo*, 3(1): 84-139.

Kienberger K., Carmona L., Pola M., Padula V., Gosliner T.M. & Cervera J.L. 2016. *Aeolidia papillosa* (Linnaeus, 1761) (Mollusca: Heterobranchia: Nudibranchia), ¿single species or a cryptic species complex? A morphological and molecular study. *Zoological Journal of the Linnean Society*, 177: 481–506.

Kimura M. 1980. A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16:111–20.

Knowlton N. 2000. *Molecular genetic analyses of species boundaries in the sea*. In: Solé-Cava AM, Russo CAM, Thorpe JP, eds. Marine genetics. Dordrecht: Springer, 73–90.

Kumar S., Stecher G. & Tamura K. 2016. MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, 33: 1870–1874.

Lanfear R., Frandsen P.B., Wright A.M., Senfeld T. & Calcott B. 2017. Partition Finder 2: New Methods for Selecting Partitioned Models of Evolution for Molecular and Morphological Phylogenetic Analyses. *Molecular Biology and Evolution,* 34(3): 772–773.

Leigh J.W. & Bryant D. 2015. PopART: full-feature software for haplotype network construction. *Methods in Ecology and Evolution*, 6: 1110–1116.

Lindsay T. & Valdés, Á. 2016. The model *Hermissenda crassicornis* (Gastropoda: Heterobranchia) is a species complex. *PloS One*, 11: pe0154265. https://doi.org/10.1371/journal.pone.0154265

Lo Bianco S. 1909. Notizie biologiche riguardianti specialimente il periodo di maturita sessuale degli animale del golfo di Napoli. *Mittheilungen aus der Zoologischen Station zu Neapal*, 19: 513-761.

MacGinitie G.E. & MacGinitie N. 1968. *Natural History of Marine Animals*. McGraw-Hill Book Company, New York.

Martín D., Dantart L. & Ballesteros M. 1990. Moluscos de las concreciones de algas calcáreas del litoral catalán (NE España). *Lavori S.I.M.*, 23:445-456.

Martínez E. 1995. *El orden Anaspidea (Mollusca: Opisthobranchia) en el Atlantico y Mediterraneo próximo; revisión taxonómica y estudio de los metabolitos secundarios*. Tesis doctoral. Universidad de Oviedo, España.

Medina M. & Walsh P.J. 2000. Molecular systematics of the order Anaspidea based on mitochondrial DNA sequence (12S, 16S, and COI). *Molecular Phylogenetic and Evolution*, 15:41–58. https://doi.org/10.1006/mpev.1999.0736

Medina M., Collins T. & Walsh P. 2001. mtDNA Ribosomal Gene Phylogeny of Sea Hares in the Genus *Aplysia* (Gastropoda, Opisthobranchia, Anaspidea): Implications for Comparative Neurobiology. *Syst. Biol.*, 50(5): 676–688. https://doi.org/10.1080/106351501753328802

Medina M., Collins T. & Walsh P. 2005. Phylogeny of Sea Hares in the *Aplysia* Clade Based on Mitochondrial DNA Sequence Data. *Bulletin of Marine Science*, 76: 691-698.

Miller M.C. 1960. A note on the life history of *Aplysia punctata* Cuvier in Manx waters. *Procedings of the malacological Society of London*, 34: 165-167.

Niell F.X. 1977. L'alimentation d'*Aplysia punctata* (GASTROPODA, Opisthobranchia) Cuvier dans la Ría de Vigo (Galice). I. Analyse du contenu digestif d'individus de la zone intertidale. *Malacologia*, 16 (1): 207-209.

Nolen T.G., Johnson P.M., Kicklighter C.E. & Capo T. 1995. Ink secretion by the marine snail *Aplysia californica* enhances its ability to escape from a natural predator. *Jounal of Comparative Physiology A.*, 176: 239-254.

Ornelas-Gatdula E., Camacho-García Y., Schrödl M., Padula V., Hooker Y., Gosliner T.M. & Valdés, Á. 2012. Molecular systematics of the '*Navanax aenigmaticus*' species complex (Mollusca, Cephalaspidea): coming full circle. *Zool. Scr.*, 41:374–385. https://doi.org/10.1111/j.1463-6409.2012.00538.x

Paine R.T. 1963. Food recognition and predation on opisthobranchs by *Navanax inermis* (Gastropoda: Opisthobranchia). *TheVeliger*, 6: 1-9.

Palumbi S., Martin A., Romano S., McMillan W.O., Stice L. & Grabowski, G. 1991. *The simple fool's guide to PCR, Ver. 2.0* Honolulu, University of Hawaii.

Pennings S.C. 1990a. Predator-prey interactions in opisthobranch gastropods: effects of prey body size and habitat complexity. *Marine Ecology Progress Series,* 62: 95-101.

Pennings S.C. 1990b. Multiple factors promoting narrow host rage in the sea hare, *Aplysia californica*. *Oecologia*, 82: 192-200.

Puillandre N., Brouillet S. & Achaz G. 2021. ASAP: assemble species by automatic partitioning. *Molecular Ecology Resources*, 21: 609–620.

Ribero N., Martínez R. & Pauls S. 1998. Primer registro de *Aplysia* (*Pruvotaplysia*) *parvula* Mörch, 1863 (Mollusca, Opisthobranchia, Aplysiidae) para Venezuela. *Acta Biologica Venezolana*, 18(1): 43-47.

Rudman W.B. & Avern G. 1989. The genus *Rostanga* (Nudibranchia: Dorididae) in the Indo-West Pacific. *Zoological Journal of the Linnean Society*, 96(3): 281-338.

Rudman W.B. 1998. Opisthobranch defence. [In] Sea Slug Forum. Australian Museum, Sydney. Available from http://www.seaslugforum.net/factsheet/defcol

Rudman W.B. 2004. Colour in sea slugs. [In] Sea Slug Forum. Australian Museum, Sydney. Available from http://www.seaslugforum.net/factsheet/colour

Russell E. 1966. An investigation of the palatability of some marine invertebrates to four species of fish. *Pacific Sci*ence, 20: 452-460.

Salvador X. 2019. *Guía práctica para fotografiar nudibranquios del litoral español*. Editorial Marcombo, Barcelona, 360 pags.

Sánchez Tocino L. 2001. *Aplysia parvula* accessed through: Opistobranquios de la Costa de Granada on 2014-12-14. (http://www.ugr.es/~lstocino/aplysia_parvula.htm).

Sarver D.J. 1978. *The ecology and energetics of Aplysia juliana (Quoy and Qaimard, 1832)*. Ph.D. dissertation, University of Hawaii.

Simon C., Frati F., Beckenbach A., Crespi B., Liu H. & Flook, P. 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene-sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, 87: 651–701.

Stamatakis A. 2014. RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. Oxford University Press.

Swennen C. 1961. On a collection of Opisthobranchia from Turkey. *Zoologische Mededeelingen Leiden*, 38:41-75.

Templado J. & Villanueva R., 2010. Checklist of Phylum Mollusca. pp. 148-198 In supporting information Coll, M., et al., 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS ONE*, 5(8): e11842.

Thompson T.E. 1976. *Biology of Opisthobranch Molluscs*. Ray Society: London. 207 pp.

Uribe R., Sepúlveda F., Goddard J.H.R. & Valdés Á. 2018. Integrative systematics of the genus *Limacia* O. F. Müller, 1781 (Mollusca, Gastropoda, Nudibranchia, Polyceridae) in the Eastern Pacific. *Marine Biodiversity*, 48(4):1815–1832. https://doi.org/10.1007/s12526-017-0676-5

Ware C., Berge J., Jelmert A., Olsen S.M., Pellisier L., Wisz M., Kriticos D., Semenov G., Kwasniewski S. & Alsos I.G. 2015. Biological introduction risks from shipping in a warming Arctic. *Journal of Applied Ecology*, 53(2), 340-349. https://doi.org/10.1111/1365-2664.12566

Willan R.C. 1979. *The ecology of two New Zealand opisthobranch molluscs*. Ph.D. dissertation, University of Auckland.

Winkler L.R. & Tilton B.E. 1962. Predation on the California sea hare, *Aplysia californica* Cooper, by the solitary great green sea anemone, *Anthopleura xanthogrammica* (Brandt), and the effect of sea hare toxin and acetylcholine on anemone muscle. *Pacific Science,* 16: 286-290.

Wollscheid-Lengeling, E., Boore, J., Brown, W., Waegele, H., 2001. The phylogeny of Nudibranchia (Opisthobranchia, Gastropoda, Mollusca) reconstructed by three molecular markers. *Organims Diversity and Evolution*, 1(4): 241-324.

Yokes M.B. 2018. *Genetics of Aplysiidae from Turkish coastline*. Unpublished.

Yonge C.M. 1949. *The Sea Shore*. London: Collins, 311 pp.

General discussion

This thesis report has two well-differentiated parts, the first refers to the study of the biodiversity of sea slugs in a broad sense of the coasts of Panama in its two slopes, the Caribbean and the Pacific, and the second part deals with the study of three species from the Catalonian coasts (NE Spain) of which there were some doubts about their identification or origin. The most important part of the second part of this thesis is the incorporation of molecular analysis as an answer to the questions in the identification of species, such as a complex of species or a diversity of cryptic or pseudo-cryptic species. Therefore, the commonly used genetic markers, such as COI, 16S and H3, were amplified starting from specimens collected in the field; with the help of data sequences retrieved from the GenBank public database; a data set that amounts to a total of 564 concatenated sequences that were used to reconstruct a molecular phylogeny of the *Bursatella*, *Aplysia* and *Berthella* genera that have helped to clarify some aspects of their identification and origin.

Two oceans: biogeographic and taxonomic review of heterobranch sea slugs (Mollusca: Gastropoda) from waters of Panama.

The majority of marine research on Panama has been carried out in the Caribbean around Isla Colón, Bocas del Toro, primarily because the marine station of the Smithsonian Tropical Research Institute (STRI) is located there. Another area that has attracted the attention of marine scientists is the island of Coiba in the Coiba National Park, located in Pacific waters and where STRI also has a small research laboratory.

Whereas many publications cite species of Panamian heterobranch sea slugs, only 9 articles deal more or less exclusively with Panamanian species (Strong & Hertlein 1939; Olsson & McGinty 1958; Meyer 1977; Vega & González 2002; Hermosillo 2004; Hermosillo & Camacho-García 2006; Collin *et al.* 2005; Aviles 2010; Goodheart *et al.* 2016). Although no exhaustive work has been done in the coasts of Panama to document the total diversity of heterobranch sea slugs, in this work a total of 233 species are compiled from the literature, numerous online records and personal collections. Of the total number of species, 118 are from the Caribbean, representing 35.87% of the 329 species reported in the entire Caribbean (Valdés *et al.* 2006; García & Bertsch 2009). This is a somewhat low number compared to those reported from the Caribbean coast of Costa Rica according to Camacho-García *et al.* (2014), which currently stands at 152. Another 127 species are recorded from the Pacific coast, same as the neighboring country Costa Rica, which has 127 species recorded (Camacho-García, 2009); these 127 species constitute 32.07% of the 396 heterobranch sea slugs present in the Eastern Pacific between Point Concepción (California) and the Galapagos Islands (García & Bertsch 2009) and 57.73% of the 220 species recorded by these authors for the Pacific in the Panamic Province.

Recent studies have focused on the biodiversity of sea slugs in Panama's neighboring countries. For example, Ardila *et al.* (2007) compiled a list of 109 species in Colombia, 83 of them for the Caribbean coast and 29 for the Pacific. In Venezuela, Caballer *et al.* (2015), sampled 52 localities between 1993 and 2015, recording 134 species. Considering these data and the previous studies, it can be concluded that the biodiversity of Panamanian heterobranch sea slugs is relatively well known, despite the fact that exhaustive or long-term studies have not been carried out.

In the Panamanian Pacific, the best-known area in terms of heterobranch sea slug biodiversity is the island of Coiba in the Coiba National Park, Veraguas province. Hermosillo (2004) recorded 75 species for Coiba Island, expanding the distribution of some species such as *Haminoea ovalis, Philinopsis speciosa* (as *Philinopsis cyanea*), *Berthella agassizii* and *Phyllaplysia padinae*. Subsequently, Hermosillo & Camacho-García (2006) recorded another 14 species on Coiba Island that had not been previously mentioned, bringing the total number of heterobranch sea slug species in the Coiba National Park to 89.

There is no doubt that molecular analyses have contributed substantially to improvements in the taxonomy and classification of the species of marine slugs of Panama. For example, here we cite papers such as Valdés *et al.* (2017) that separate the species *Dolabrifera dolabrifera* into a complex of five cryptic species of which three are present in Panama (*Dolabrifera nicaraguana* in the Pacific, *D. ascifera* and *D. virens* in the Caribbean); or Golestani *et al.* (2019) that separate *Aplysia parvula* into four genetically distinct lineages of which *A. hooveri* is found in the Pacific of Panama; or Bazzicalupo *et al.* (2020) that separates *Stylocheilus striatus* into three cryptic species of which two are in Panama (*Stylocheilus striatus* in the Caribbean and *S. rickettsi* in the Pacific).

As general conclusions, it can be said that although a relatively large number of species of sea slugs are known in Panamanian waters, it is necessary to extend the study to more localities, mainly on the Pacific coast but also to others on the Caribbean coast and especially on substrates where sea slugs can potentially appear, such as the underside of stones and coral debris, herbivorous species among algae, the surface of sponges and corals, on hydrariam colonies or soft substrates for species that have ability to bury itself in sediment.

However, these investigations have often been hampered by the lack of up-to-date field guides. This is particularly problematic for the study of sea slugs, because their taxonomy and systematics have changed drastically in recent years due to new data resulting from molecular studies. For this reason, a new illustrated species list, including all past and recent bibliographic information is necessary to support research projects dealing with sea slug species from the Panamanian coasts.

Where do the populations of *Bursatella leachii* of the Mediterranean come from, especially those of the Catalonian coasts?

The sea hare *Bursatella leachii* is a species that has been widely known since the beginning of the 19th century. Since then and due to its chromatic variability and its wide geographical dispersion, numerous species and subspecies have been described in practically all the tropical and subtropical zones of the Pacific, Indian and Atlantic, all of them except *B. ocelligera* and *B. hirsuta*, are currently considered synonyms of *B. leachii.*

From this we can deduce that after analyzing the results of both the species delimitation (ASAP) and the haplotype networks, we realize that everything is summarized in species of a group of *B. leachii* from a combination of the American Atlantic and Africa with that of the Mediterranean; that share morphological characteristics and genotypic sequences; coinciding in part with the paper of Bazzicalupo *et al.* (2018) who considered the association of *B. leachii* species between the Atlantic and the Mediterranean as the most common among the haplotype networks; which shows that the Atlantic Ocean is not a natural geographical barrier as such, there are species such as *B. leachii* that can travel long distances and establish themselves in favorable regions where they can settle and compete with their local species, thanks to warming. Mediterranean waters (Bianchi & Morri 2003, Raitsos *et al.* 2010). Many of these adaptations of these species are possible due to human intervention, climate change and the characteristics of the species itself. Specimens of *B. leachii* from Catalonia share haplotypes with specimens from both shores of the Atlantic and with others from the Mediterranean Sea but not with those from the Indo-Pacific, which confirms the hypothesis that they entered the Mediterranean Sea through the Strait of Gibraltar.

On the other hand, the characteristics of *B. leachii* allow it to colonize territories other than those most common for it (Blackburn *et al.* 2009), because it adapts to unfavorable conditions in terms of the amount of food available (Clarke 2006), other A very important aspect is that their larvae can be kept for more than three months immediately to hatch and their life cycle is short, the adults reach maturity very quickly in a few months (Paige 1988).

Although there are biotic and abiotic factors, demographic and environmental stochasticity that affect the adaptation of invasive species (Lockwood *et al.* 2007); In the case of Lessepsian invaders, such as *B. leachii,* they are said to have sufficient phenotypic plasticity (the ability to cope with a variety of environmental conditions) to survive, mate, have offspring, and be successful in their new habitat, without doing so. no use of evolutionary adjustments (Bernardi *et al.* 2010); which allowed him to invade through the Strait of Gibraltar for those of the Atlantic. In addition to that, there are currently two more species of the *Bursatella* genus, which could be considered cryptic, these are *B. occelligera* from the Indo-Pacific and *B. hirsuta* from South Australia.

Molecular analysis and population monitoring of *Berthella stellata.*

Although with fluctuations in the abundance of individuals, the population of *Berthella stellata* in Es Caials (Costa Brava, NE Spain) remains stable over years, and it can be verified that it is a place where individuals copulate and lay their eggs. In this locality there is a great chromatic variability between the specimens, with clear specimens, others brown with scattered white spots and others with the typical Y-shaped white spot.

According to Gosliner and Bertsch (1988), simple morphological characteristics such as body coloration, shell shape, radular teeth, jaw parts, and reproductive appearance were considered intraspecific elements to be considered to designate a species. For these authors, all the specimens from different populations with similar external morphologies were of the same species, premise that molecular analyzes deny because we have seen that specimens of the same coloration can be from different species and others that have various colorations belong to the same population and therefore are of the same species.

Three different colorations were found in the morphological aspects of the populations of *B. stellata* from Es Caials and according to the results of our molecular species delimitation analyzes and the phylogenetic trees they are the same species; this indicates that the joint use of a molecular and morphological approach can help to improve the determination of the populations of Heterobranchia sea slug species as also Ghanimi *et al* (2020) think for the identification of species.

Finally, we see that the Mediterranean populations of *B. stellata* from Es Caials and those from Italy share both morphological and molecular aspects with populations from the European Northeast Atlantic region such as Portugal.

Changing feeding habits and ontogenetic dimorphism in juvenile and adult ***Aplysia punctata*****.**

The juveniles of *Aplysia punctata* (APJs) have almost always been found on the Catalonian coast (NE Spain) associated with soft red thalli of algae such as *S. coronopifolius* and *P. cartilagineum*, where they are very cryptic, acquiring a color very similar to that of adults of *A. parvula.* Carefoot (1967) found that in the Atlantic Ocean juveniles of *A. punctata* preferentially feed on red algae such as *Plocamium* Lamouroux, 1813, *Heterosiphonia* Montagne 1842, *Cryptopleura* Kützing 1843 and *Delesseria* Lamouroux 1813 in that order when they are available. Also, Carefoot (1967) used a combination of these red algae in the laboratory to feed specimens of *A. punctata* and found that they used the energy obtained from eating these algae for growth, nitrogen production, carbohydrates, and amino acid synthesis, and that grew faster feeding on the species *P. cartilagineum* (such as *Plocamium coccineum* Lyngbye 1819). Juvenile specimens of *Aplysia punctata* (APJ) change from reddish to olive green when they reach larger sizes and begin to ingest the green algae *U. lactuca*; their bodies change color as they acquire pigments from their food and incorporate them into their tissue. It is known from Garstang (1890) and Eales (1921) that *A. punctata* in the Mediterranean feeds on eight varieties of algae, of which in its juvenile state it consumes red algae, then in its adult state it feeds on green algae. On the Catalonian coast, APJ up to a size of about 20 mm live preferably among the fronds of these red algae where they feed on them and obtain the pigmentation they have on their body to protect themselves from predators by imitating the color of the algae. As they age, the specimens of *A. punctata* become independent from red algae and live under stones feeding on a wide variety of algae (APA); in this way they lose their cryptic characteristics similar to "*parvula*" adults and acquire other green or brown tones on the body in their adult phase, in addition to the typical white spots that characterize the species.

We found that APA copulate and lay their eggs between April and June, which according to Thompson (1976) occurs in spring but only in adults, something that varied in what we could observe both in nature and in the laboratory, that up to 9- 10 individuals of APAs and 4-5 individuals of red specimens of APJs copulated, which is novel because it was thought that only in their adult state was the stage in which they are capable of copulating because they are more mature. With this paper we demonstrate that the change of food that causes the coloration of the body according to the type of algae that it ingests, the early maturation to be able to copulate, the coloration of the masses of eggs and larvae and the secretion of purple substances are very efficient strategies that uses this species to remain the dominant species and to be very successful in the Mediterranean.

All this has given us a perspective of the things that must be done in the future; that still in some regions of the world, there are species that are considered unique or circumtropical that could be a complex of species or cryptic or pseudo-cryptic species, that if we use molecular analysis well we could elucidate their status worldwide; also, that despite the fact that Panama is a small country in territorial extension, it is very diverse in terms of the number of species of sea slugs and that finally, the width of the Atlantic does not constitute an insurmountable barrier for the dispersal of larvae of highly adaptive species to different conditions.

Conclusions

- Although an exhaustive work has not been carried out on the Panamanian coast to document the total diversity of heterobranchial sea slugs, in this work a total of 233 species from numerous records, studies and collections are compiled. Likewise, despite the fact that Panama is a small country in territorial extension, it is very diverse in terms of the number of species of sea slugs and also confirms the high biodiversity of heterobranch sea slugs that inhabit the Panamanian coasts, but it is considered necessary a extensive sampling on Pacific coasts, which have been less studied.

- *Bursatella leachii* has the ability to cope with a variety of environmental conditions to survive, mate, have offspring and succeed in new habitats, without making use of evolutionary adjustments; which allows it to invade the Strait of Gibraltar for those coming from the Atlantic; that the Atlantic Ocean is not an insurmountable barrier for species like this one. It is confirmed that this species is expanding on the Catalan coast and that locally it can be abundant at certain times of the year.

- In the town of Es Caials there is a stable population of *B. stellata* with individuals present throughout the year, which reproduce between the months of May and June; individuals also have a great chromatic variability. The population of *Berthella stellata* from Es Caials shares both morphological and molecular aspects with specimens from the Northeast Atlantic and Mediterranean in Europe.

- With this chapter we have shown that in the Mediterranean there never existed or at present there are no confirmed specimens of *Aplysia parvula*; and that the true identity of these red small Mediterranean *Aplysia*, especially those from the coast of Catalonian, is that they are the juveniles of *Aplysia punctata*; that they have different feeding strategies that due to this they obtain the coloration in the different stages of their life.

- All this has given us a perspective of the things that must be done in the future; that still in some regions of the world, there are species that are considered unique or circumtropical that could be a complex of species or cryptic or pseudo-cryptic species, that if we use molecular analyzes well we could elucidate their status worldwide; as an answer to the questions in the identification of species considered unique, such as a complex of species or a diversity of cryptic or pseudo-cryptic species.

General References

Álvarez, L.A.; García, F.J. & Villani, G. 1993. A new Mediterranean species of Haminaea Leach, 1820 (Gastropoda: Opisthobranchia: Cephalaspidea). *Journal of Molluscan Studies*, 59: 339–345.

Alvim, J. & Pimenta, A. 2015. Taxonomic review of *Berthella* and *Berthellina* (Gastropoda: Pleurobranchoidea) from Brazil, with description of two new species. *ZOOLOGIA*, 32 (6): 497-531.

ANAM. 2009. *Plan de Manejo del Parque Nacional Coiba*. Compiladores Maté J.L, Tovar D, Arcia E, Hidalgo Y. Ciudad de Panamá, República de Panamá. 168 pp.

Appeltans, W.; Ahyong, S.T.; Anderson, G.; Angel, M.V.; Artois, T.; Bailly, N.; Bamber, R.; Barber, A.; I Bartsch, I. & Berta, A. 2012. *Current Biology*, 22(23): 2189-2202.

Ávila, C. 1995. Natural products of Opisthobranch molluscs: a biological review. *Oceanography and Marine Biology: An Annual Review*, 33: 487-559.

Ávila, C.; Cimino, G.; Crispino, A. & Spinella, A. 1991a. Drimane sesquiterpenoids in Mediterranean *Dendrodoris* nudibranchs: anatomical distribution and biological role. *Experientia*, 47: 306-310.

Ávila, C.; Cimino, G.; Crispino, A.; Fontana, A. Gavagnin, M.; Ortea, J. & Trivellone, E. 1991b. Defensive strategy of two *Hypselodoris* nudibranchs from Italian and Spanish coasts. *Journal of Chemical Ecology*, 17: 625-636.

Avilés, M.C. 2010. Listado preliminar de moluscos opistobranquios de la República de Panamá. *MUMAUP*, 3: 1-23.

Barker, G.M. 2001. Gastropods on land: phylogeny, diversity, and adaptive morphology. In Baker, G.M. (ed.) *The biology of terrestrial molluscs*. Wallingford, United Kingdom: CABI Publishing.

Ballesteros, M. 1980. *Contribución al conocimiento de los Sacoglosos y Nudibranquios (Mollusca: Opisthobranchia)* (Tesis Doctoral). Universitat de Barcelona, España.

Ballesteros, M. & Weitzmann, B. 2016. La liebre de mar *Bursatella leachii* continua su expansión en las costas catalanas. *Noticiario* SEM, 65:23-24.

Ballesteros, M.; Madrenas, E. & Pontes, M. 2012-2017a. "*¿Qué es un Opistobranquio?*" in OPK-Opistobranquis, published: 05/12/2016, Accessed: 19/05/2017 at (http://opistobranquis.info/es/qLtEX)

Ballesteros, M.; Madrenas, E. & Pontes, M. 2012-2017b. "*Anatomía de los opistobranquios*" in OPK-Opistobranquis, Published: 25/12/2012, Accessed: 19/05/2017 at (http://opistobranquis.info/es/BgXgw)

Ballesteros, M.; Madrenas, E. & Pontes, M. 2012-2017c. "*Coloración: Estrategia de defensa*" in OPK-Opistobranquis, Published: 25/12/2012, Accessed: 19/05/2017 at (http://opistobranquis.info/es/WQsK2)

Ballesteros, M.; Madrenas, E. & Pontes, M. 2012-2017d. "*Alimentación y rádula*" in OPK-Opistobranquis, Published: 25/12/2012, Accessed: 19/05/2017 at (http://opistobranquis.info/es/BlQHq)

Ballesteros, M.; Madrenas, E. & Pontes, M. 2012-2017e. "*Órganos sensoriales y rinóforos*" in OPK-Opistobranquis, Published: 25/12/2012, Accessed: 19/05/2017 at (http://opistobranquis.info/es/Tq7u9)

Ballesteros, M.; Madrenas, E. & Pontes, M. 2012-2017f. "*Respiración, cerata y branquias*" in OPK-Opistobranquis, Published: 25/12/2012, Accessed: 19/05/2017 at (http://opistobranquis.info/es/eyql5)

Ballesteros, M.; Madrenas, E. & Pontes, M. 2012-2017g. "Reproducción" in OPK-Opistobranquis, published: 25/12/2012, Accessed: 19/05/2017 at (http://opistobranquis.info/es/ILVvN)

Ballesteros, M.; Madrenas, E. & Pontes, M. 2012-2019. "*Bursatella leachii*" in OPK-Opistobranquis, published: 15/05/2012, Accessed: 29/01/2019 at https://opistobranquis.info/es/NNgfg

Bazzicalupo, E.; Crocetta, F.; Estores-Pacheco, K.; Golestani, H.; Bazairi, H.; Giacobbe, S.; Jaklin, A.; Poursanidis, D.; Chandran, B.K; Cervera, J.L. & Valdés, Á. 2018. Population genetics of *Bursatella leachii* (De Blainville, 1817) and implications for the origin of the Mediterranean population. *Helgoland Marine Research*, 72: 19.

Bazzicalupo, E.; Crocetta, F.; Gosliner, T.; Berteaux-Lecellier, V.; Camacho-García, Y., Sneha B. & Valdés, Á. 2020. Molecular and morphological systematics of *Bursatella leachii* de Blainville, 1817 and *Stylocheilus striatus* Quoy & Gaimard 1832 reveal cryptic diversity in pantropically distributed taxa (Mollusca: Gastropoda: Heterobranchia). *Invertebrate Systematics,* 34: 535–568.

Bebbington, A. 1970. Aplysiid species from Malta with notes on the Mediterranean Aplysiomorpha (Gastropoda, Opisthobranchia). *Pubblicazioni della Stazione Zoologica di Napoli*, 38: 25-46.

Bebbington, A. & Brown, G.H. 1975. *Aplysia parvula* Guilding in Morch, an opisthobranch new to the British fauna. *Journal of Conchology*, 28: 329–333.

Behrens, D.W. & Hermosillo, A. 2005. *Eastern Pacific Nudibranchs. Sea Challengers.* Mexico: Monterrey.

Bernardi, G.; Golani, D. & Azzuro, E. 2010. *The genetics of Lessepsian bioinvasions.* In: Golani, D., Appelbaum-Golani, B. (Eds.), Fish Invasions of the Mediterranean Sea: Change and Renewal, p. 71 (Sofia, Moscow).

Best, M. & Kidwell, S. 2000. Bivalve taphonomy in tropical mixed siliciclastic–carbonate settings. I. Environmental variation in shell condition. *Paleobiology*, 26:80–102.

Bianchi, C.N. & Morri, C. 2003. Global sea warming and "tropicalization" of the Mediterranean Sea: biogeographic and ecological aspects. *Biogeographical Journal of Integrated Biogeography* 24:319–27.

Bieler, R. 1992. Gastropod phylogeny and systematics. *Annual Review of Ecology and Systematics*, 23: 311–338.

Blackburn, T.M.; Cassey, P. & Lockwood, J.L. (2009). The role of species traits in the establishment success of exotic birds. *Global Change Biololgy*, 15(12):2852–60.

Bonar, D.B. 1978. Morphogenesis at metamorphosis in opisthobranch molluscs. Chia, F.S. & Rice, M.E. (eds). In: *Settlement and metamorphosis of marine invertebrate larvae.* New York, United State: Elsevier.

Briggs, J.C. 2003. Marine centres of origin as evolutionary engines. *Journal of Biogeography*, 30: 1–18.

Camacho-García, Y. 2009. *Benthic opisthobranchs*. In Wehrtmann, I. & Cortes, J. *Marine biodiversity of Costa Rica*. Springe Science.

Camacho-García, Y.; Pola, M.; Carmona, L.; Padula, V.; Villani, G. & Cervera, L. 2014. Diversity and distribution of the heterobranch sea slug fauna on the Caribbean of Costa Rica. *Cahiers de Biologie Marine*, 55:109-127.

Capper, A.; Tibbetts, I.R.; O'Neil, J.M. & Shaw, G.R. 2005. The fate of *Lyngbya majuscula* toxins in three potential consumers. *Journal of Chemical Ecology*, 31:1595-1606.

Castillo-Rodríguez, Z. (2014). Biodiversidad de moluscos marinos en México. *Revista Mexicana de Biodiversidad*, Suplemento 85: S419-S430

Cervera, J.L.; Calado, G.; Gavaia, C.; Malaquías, A.E.; Templado, J.; Ballesteros, M.; García-Gómez, J.C. & Megina, C. 2004. An annotated and updated checklist of the opisthobranchs (Mollusca: Gastropoda) from Spain and Portugal (including islands and archipelagos). *Boletín Instituto Español de Oceanografía*, 20(1-4): 1-111.

Cervera, J.L.; Tamsouri, N.; Moukrim, A. & VILLANI, G. 2010. New records of two alien opisthobranch molluscs from the north-eastern Atlantic: *Polycera hedgpethi* and *Godiva quadricolor*. *Marine Biodiversity Records*, 3: 1–4.

Cimino, G. & Ghiselin, M.T. 1999. Chemical defense and evolionary trends in biosynthetic capacity among dorid nudibranchs (Mollusca: Gastropoda: Opisthobranchia). *Chemoecology*, 9: 187-207.

Cimino, G. & Ghiselin, M.T. 2009. Chemical defense and the evolution of opithobranch gastropods. *Proceedings of the California Academy of Sciences*, 60: 175-422.

Cimino, G.; Fontana, A.; Giménez, F.; Marin, A.; Mollo, E.; Trivellone, E. & Zubia, E. 1993. Biotransformation of a dietary sesterpenoid in the Mediterranean nudibranch *Hypselodoris orsini*. *Experientia*, 49: 582-586.

Cimino, G.; Ciavatta, M.L.; Fontana, A. & Gavagnin, M. 2001. Metabolites of marine opistobranchs: chemistry and biological activity. In Tringali, C. (ed.) Bioactive compounds from natural sources. Isolation, characterization and biological properties. *Catania*, 577-637.

Claremont, M.; Williams, S.T.; Barraclough, T.G. & Reid, D. 2011. The geographic scale of speciation in a marine snail with high dispersal potential. *Journal of Biogeography*, 38: 1016–1032.

Clark, K. & Jensen, K.R. 1981. A comparison of egg size, capsule size, and development patterns in the order Ascoglossa (Sacoglossa) (Mollusca: Opishtobranchia). *International Journal of Invertebrate Reproduction*, 3: 57–64.

Clarke, C.L. 2006. The population dynamics and feeding preferences of *Bursatella leachii* (Opisthobranchia: Anaspidea) in northeast Queensland, Australia. Records of the Western Australian Museum Suppl., 69:11–21.

Coates, A. & Obando, J. 1996. The geologic evolution of the Central American Isthmus. In Jackson, J.; Budd A. & Coates A. (eds). *Evolution and environment in tropical America*, Chicago, United State: University of Chicago Press.

Coates, A.; Aubry, M.; Berggren, W. & Collins, L. 2003. Early neogene history of the Central American arc from Bocas del Toro, western Panamá. *Geological Society of America Bulletin*, 115:271-287.

Coates, A.; Collins, L.; Marie-Pierre Aubry, M. & Berggren, W. 2004. The Geology of the Darien, Panamá, and the late Miocene-Pliocene collision of the Panamá arc witch northwestern South America. *Geological Society of America Bulletin*, 116:1327-1344.

Collen B.; Böhm, M.; Kemp, R. & Baillie J. 2012. *Spineless: status and trends of the world's invertebrates*. London, United Kingdom: Zoological Society of London.

Collier, C. &. Farmer, W. 1964. Additions to the nudibranch fauna of the east Pacific and the Gulf of California. *Transactions of the San Diego Society for Natural History*, 13: 377-396.

Collin R. 2005. Ecological Monitoring and Biodiversity Surveys at the Smithsonian Tropical Research Institute's Bocas del Toro Research Station. *Caribbean Journal of Science*, 41(3):367–73.

Collin, R.; Díaz, M.C.; Norenburg, J.; Rocha, R.M.; Sánchez, J.A. & Schulze, A. 2005. Photographic identification guide to some common marine invertebrates of Bocas Del Toro, Panama. *Caribbean Journal of Science*, 41:638-707.

Collins, L.; Coates, A.; Jackson, J. & Obando, J. 1995. Timing and rates of emergence of the Limón and Bocas del Toro basins: Caribbean effects of Cocos Ridge subduction? *Geological society of America*, special paper 295:263-289.

Cronin, T. & Dowsett, H. 1996. Biotic and oceanographic response to the Pliocene closing of the Central American Isthmus. In Jeremy Jackson, J.; Budd, A. & Coates, A. *Evolution and environment in tropical America*. Chicago, United State: University of Chicago Press.

D'Croz, L. & Robertson, D. 1997. Coastal oceanographic conditions affecting coral reefs on both sides of the Isthmus of Panamá. *Proceedings of the 8th International Coral Reef Symposium*. 2:2053-2058.

Eales, N.B. 1970. On the migration of tectibranch molluscs from the Red Sea to the eastern Mediterranean. *Journal of Molluscan Studies*, 39: 217–220

Edmunds, M. 1977. Larval development, oceanic currents, and origins of the Opisthobranch fauna of Ghana. *Journal of Molluscan Studies*, 43: 301–308.

Edmunds, M. 1981. Opisthobranchiate Mollusca from Ghana: Chromodorididae. *Zoological Joumal ofthe Linnean Society*, 72: 175-201.

Fontana, A.; Giménez, F.; Marin, A.; Mollo, E. & Cimino, G. 1994. Transfer of secondary metabolites from the sponges *Dysidea fragilis* and *Pleraplysilla spinifera* to the mantle dermal formations (MDFs) of the nudibranch *Hypselodoris webbi*. *Experientia*, 50: 510-516.

Fraser, C.I., Nikula, R. & Waters, J.M. 2011. Oceanic rafting by a coastal community. *Proceedings of the Royal Society of London*, 278: 649–655.

García, F.J. & Bertsch, H. 2009. Diversity and distribution of the Gastropoda Opisthobranchia from the Atlantic Ocean: a global biogeographic approach. *Scientia Marina*, 73: 153–160.

García-Talavera, F. 1983. *Los moluscos gasterópodos anfiatlánticos. Estudio paleo y biogeográfico de las especies bentónicas litorales*. Publicaciones de la Universidad de La Laguna. Monografías, no.10.

Ghanimi, H.; Schrödl, M.; Goddard, J.; Ballesteros, M.; Gosliner, T.; Buske, Y. & Valdés, Á. 2020. Stargazing under the sea: molecular and morphological data reveal a constellation of species in the *Berthella stellata* (Risso, 1826). *Marine Biodiversity*, 50:11. https://doi.org/10.1007/s12526-019-01027-w

Golestani, H.; Crocetta, F.; Padula, V.; Camacho-García, Y.; Langeneck, J.; Poursanidis, D.; Pola, M.; Yokeş, B.; Cervera, J.L.; Jung, D.-W.; Gosliner, T.; Araya, J.F.; Hooker, Y.; Schrödl, M. & Valdés, Á. 2019. The little *Aplysia* coming of age: from one species to a complex of species complexes in *Aplysia parvula* (Mollusca: Gastropoda: Heterobranchia). *Zoological Journal of the Linnean Society*, XX, 1–52. https://doi.org/10.1093/zoolinnean/zlz028/5509942

Goodheart, J.; Ellingson, R.; Vital, X.; Galvão, H.; McCarthy, J.; Medrano, S.; Bhave, V.; García-Méndez, K; Jiménez, L.; López, G.; Hoover, C.; Awbrey, J.; De Jesus, J.; Gowacki, W.; Krug, P. & Valdés, A. 2016 Identification guide to the heterobranch sea slugs (Mollusca: Gastropoda) from Bocas del Toro, Panamá. *Marine Biodiversity Records*, 9:1-31.

Gordon B. 1982. *A Panamá forest and shore: natural history and Amerindian culture in Bocas del Toro*. United State: Pacific Grove, Boxwood Press.

Gosliner, T.M. 1995. Introduction and spread of *Philine auriformis* (Gastropoda: Opisthobranchia) from New Zealand to San Francisco Bay and Bodega Harbor. *Marine Biology*, 122: 249–255.

Gosliner, T.M. & Behrens, D.W. 2006. Anatomy of an invasion: systematics and distribution of the introduced Opisthobranch snail, *Haminoea japonica* Pilsbry, 1895 (Gastropoda: Opisthobranchia: Haminoeidae). *Proceeding of the California Academy of Sciences*, 57: 1003–1010.

Gosliner, T.M. & Bertsch, H. 1988. A Review of the Genus *Berthella* (Opisthobranchia: Notaspidea) from the Pacific Coast of North America. *The Veliger*, 31(1/2): 46-67.

Gosliner, T.M., Behrens, D.W. & Valdés, A. 2008. *Indo-Pacific nudibranchs and sea slugs: a field guide to the world's most diverse fauna*. San Francisco, United States: California Academy of Sciences/Sea Challengers Natural History Books.

Hadfield, M.G. & Karlson, H. 1969. Externally induced metamorphosis in a marine gastropod. *American Zoologist*, 9: 1122.

Händeler, K.; Grzymbowski, Y.P.; Grug, P.J. & Wägele. H. 2009. Funtional chloroplasts in metazoan cells – a unique evolutionary strategy in animal life. *Frontiers in zoology*, 6: 28.

Haszprunar, G. 1985. The Heterobranchia: a new concept of the phylogeny and evolution of the higher Gastropoda. *Journal of Zoological Systematics and Evolutionary Research*, 23: 15-37.

Hermosillo, A. 2004. Opisthobranch mollusks of Parque Nacional de Coiba, Panamá (tropical eastern Pacific). *The Festivus*, 36: 105-117.

Hermosillo, A. & Camacho-García, Y. 2006. A note on the opisthobranchs of Parque Nacional de Coiba, Panama (Tropical Eastern Pacific). *The Festivus*, 38(9): 95-98.

Ibáñez-Yuste, A.J., Garrido-Díaz, A., Espinosa-Torre, F. & Terrón-Sigler, A. 2012. Primera cita del molusco exótico *Bursatella leachii* de Blainville, 1817 (Mollusca: opistobranchia) en el litoral mediterráneo andaluz. *Chronica naturae*, 2, 25-31.

Jackson, J. & Budd, A. 1996. Evolution and environment: Introduction and overview. In Jeremy, J.; Budd, A. & Coates, A.(eds.) *Evolution and Environment in Tropical America.* Chicago, United States: University of Chicago Press.

Jackson, J. & D'Croz, L. 1997. The ocean divided. In Coates, A. (ed.) *Central America: A Natural and Cultural History.* New Haven, United States: Yale University Press.

Jensen, K. 2001. Review of reproduction in the Sacoglossa (Mollusca, Opisthobranchia). *Bollettino Malacologico*, 37: 81–98.

Johnson, R. & Gosliner, T. 2012. Traditional taxonomic groupings mask evolutionary history: A molecular phylogeny and new classification of the chromodorid nudibranchs. *PLoS ONE*, 7(4): e33479.

Jörger, K. M.; Stöger, I.; Kano, Y.; Fukuda, H.; Knebelsberger, T. & Schrödl, M. 2010. On the origin of Acochlidia and other enigmatic euthyneuran gastropods, with implications for the systematics of Heterobranchia. BMC *Evolutionary Biology*, 10.

Katsanevakis, S.; Zenetos, A.; Belchior, C. & Cardoso, A.C. 2013. Invading European seas: assessing pathways of introduction of marine aliens. *Ocean and Coastal Management*, 76: 64–74.

Kirby, M. & Jackson, J. 2004. Extinction of a fast-growing oyster and changing ocean circulation in Pliocene Tropical America. *Geology*, 32:1025–1028.

Knowlton, N. 1993. Sibling species on the sea. *Annual Review in Ecology and Systematics*, 24: 189–216.

Krug, P.J.; Morlet, M.S.; Asif, J.; Hellyar, L.L. & Blom, W.M. 2008. Molecular confirmation of species status for the rare cephalaspidean *Melanochlamys lorrainae* (Rudman, 1968), and comparison with its sister species *M. cylindrical* Cheesman, 1881. *Journal of Molluscan Studies*, 74: 267–276.

Krug, P.J.; Caplins, S.A.; Algoso, K.; Thomas, K.; Valdés, Á.A., Wade, R.; Wong, N.L.W.S.; Eernisse, D.J. & Kocot, K.M. 2022. Phylogenomic resolution of the root of Panpulmonata, a hyperdiverse radiation of gastropods: new insight into the evolution of air breathing. *Procedings of the Royal Society B.*, 289: 20211855. https://doi.org/10.1098/rspb.2021.1855

Lockwood, J.L.; Hoopes, M.F. & Marchetti, M.F. 2007. *Invasion Ecology*. Blackwell Publishing, Malden, p. 304.

Lovelock, C.E.; Feller, I.C.; McKee, K.L.; Engelbrecht, B.M. & Ball, M.C. 2004. The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panamá. *Functional Ecology*, 18:25–33.

Maestrati, P. & Lozouet, P. 1996. Les Glycymerididae (Mollusca: Bivalvia) de l'Oligoce`ne superior (Chattien) du Basin de l'Adour, France. *Annalles de Paleontologie (Vert-Invert.)*, 82: 3–25.

Malaquías, M.A.E. & Reid, D.G. 2008. Systematic revision of the recent species of Bullidae (Mollusca: Gastropoda: Cephalaspidea), with a molecular phylogenetic analysis. *Zoological Journal of the Linnean Society*, 153: 453–543.

Malaquías, M.A.E. & Reid, D.G. 2009. *Tethyan vicariance*, relictualism and speciation: evidence from a global molecular phylogeny of the opisthobranch genus *Bulla*. *Journal of Biogeography*, 36: 1760–1777.

Malaquías, M.A.E.; Calado, G.P.; Padula, V.; Villani, G. & Cervera, J.L. 2009. Molluscan diversity in the North Atlantic Ocean: new records of opisthobranch gastropods from the Archipelago of Azores. *Marine Biodiversity Records*, 2: 1–9.

Marcus, Ev. 1958 On Western Atlantic opisthobranchiate gastropods. *American Museum of Natural History, Novitates*, 1906: 1-81.

Marcus, Ev. 1977. An annotated checklist of the Western Atlantic warm water Opisthobranchs. *Journal of Molluscan Studies*, 4 (Supplement): 1-22.

Marcus, Ev. & Marcus, Er. 1967. Opisthobranchs from the gulf of California. *Studies in Tropical Oceanography*, 6:1-137.

Marín, A. & Ros, J. 1989. The chloroplast-animal association in four Iberian sacoglossan opisthobranchs: *Elysia timida*, *Elysia translucens*, *Thuridilla hopei* and *Bosellia mimetica*. *Scientia Marina*, 53: 429–440.

Marín, A. & Ros, J. 1992. Dynamics of a peculiar plant-herbivore relationship: the photosyntetic ascoglossan *Elysia timida* and the chlorophycean *Acetabularia acetabulum*. *Marine Biology*, 112: 677–682.

Marín, A. & Ros, J. 1993. Ultrastructural and ecological aspects of the development of chloroplast retention in the sacoglossan gastropod *Elysia timida*. *Journal of Molluscan Studies*, 59: 95–104.

Medina, M.; Lal, S.; Vallès, Y.; Takaoka, T.L.; Dayrat, B.A.; Boore, J.L. & Gosliner, T. 2011. Crawling through time; transition of snails to slugs dating back to the Paleozoic, based on mitochondrial phylogenomics. *Marine Genomics*, 4: 51-59.

Meyer, C.P. 2003. Molecular systematics of cowries (Gastropoda: Cypraeidae) and diversification patterns in the tropics. *Biological Journal of the Linnean Society*, 79: 401–459.

Meyer, K.B. 1977. Dorid nudibranchs of the Caribbean coast of the Panama Canal Zone. *Bulletin of Marine Science*, 27: 299-307.

Moles, J. 2016. *Antarctic heterobranch molluscs diving into their challenging ecology, taxonomy, and systematics* (Doctoral Thesis). Universitat de Barcelona, España.

Molnar, J.L.; Gamboa, R.L.; Revenga, C. & Spalding, M.D. 2008. Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecolology and Environ*ment, 6(9): 485-492.

Nunes, A.L.; Katsanevkis, S.; Zenetos, A. & Cardoso, A.C. 2014. Gateways to alien invasions in the European seas. *Aquatic Invasions*, 9(2):133-144.

O'Dea, A.; Jackson, J.; Fortunato, H.; Smith, J.; D'Croz, L.; Johnson, K. & Todd, J. 2007. Environmental change preceded Caribbean extinction by 2 million years. *Proceedings of the National Academy of Sciences* 104(13): 5501-5006.

O'Donoghue, C.H. & White, K.M. 1940. A collection of marine molluscs, mainly opisthobranchs, from Palestine. *Proceedings of the Malacological Society of London*, 24 (3): 92-96.

Olsson, A & McGinty, T.L. 1958. Recent marine mollusks from the caribbean coast of Panama with the description of some new genera and species. *Bulletin of American Paleontology*, 39(177): 5-59.

Ortea, J.; Moro, L.; Caballer, M. & Bacallado, J.J. 2003. *Revista de la Academia Canaria de Ciencias*. XIV(3-4): 165-180.

Paige, J.A. 1988. Biología, metamorfosis y desarrollo postlarval de *Bursatella leachii plei* Rang (Gastropoda: Opisthobranchia). *Boletín de Ciencias del Mar*, 42: 65-75.

Petuch, E.J. 1997. *Coastal paleoceanography of eastern North America*. United State: Kendall Hunt Publishing, Dubuque, IA.

Ponder, W.F. & Lindberg, D.R. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society*, 119: 83-265.

Putz, A.; König, G.M. & Wägele H. 2010. Defense strategies of Cladobranchia (Gastropoda, Opisthobranchia). *Natural product reports*, 27: 1386-1402.

Rahat, M. 1976. Direct development and symbiotic chloroplasts in *Elysia timida* (Mollusca: Opisthobranchia). *Israel Journal of Zoology*, 25: 186–193.

Raitsos D.E., Beaugrand G., Georgopoulos D., Zenetos A., Pancucci-Papadopoulou A.M., Theocharis A. & Papathanassiou E. 2010. Global climate change amplifies the entry of tropical species into the Eastern Mediterranean Sea. *Limnology and Oceanography*, 55(4):1478–84.

Ramos, L.J.; López, R. J.L. & MILLER, M.W. 1995. Behavior patterns of the aplysiid gastropod *Bursatella leachii* in its natural habitat and in the laboratory. *Neurobiology of Learning and Memory*, 63: 246-259.

Reid, D.G.; LAL, K.; Mackenzie-Dodds, J.; Kaligis, F.; Littlewood, D.T.J. & Williams, S.T. 2006. Comparative phylogeography and species boundaries in *Echinolittorina* snails in the central Indo-West Pacific. *Journal of Biogeography*, 33: 990–1006.

Rilov, G. & Galil, B. 2009. Marine Bioinvasions in the Mediterranean Sea- History, distribution and Ecology. En: Rilov, G. & Crooks, J.A. (eds.). *Biological Invasions in Marine Ecosystem*, capítulo 31: 549-575.

Rodríguez E, Almanza R. & Alvarado, R. 1993. Situación bíofísica y ambiental de la Provincia de Bocas del Toro. In Heckadon S. (ed.) *Agenda Ecológica y Social para Bocas del Toro*. Panamá: Impresora Continental.

Sánchez, L. 2017. *Sistemas de defensa*. Accessed: 19/05/2017 at (http://wpd.ugr.es/~lstocino/wordpress/?page_id=558)

Schaefer, K. 1996. Review of data on cephalaspid reproduction, with special reference to the genus *Haminaea* (Gastropoda: Opisthobranchia). *Ophelia*, 45: 17–37.

Scheltema, R.S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biological Bulletin*, 140: 284–322.

Scheltema, R.S. 1979. Dispersal of pelagic larvae and the zoogeography of Tertiary marine benthic gastropods. In: Gray, J. & Boucot, A.J. (eds) *Historical biogeography, plate tectonics, and the changing environment.* Corvallis, Oregon, United States: Oregon State University Press

Scheltema, R.S. 1995. The relevance of passive dispersal for the biogeography of Caribbean mollusks. *American Malacological Bulletin*, 11: 99–115.

Schneider, B. & Schmittner, A. 2006. Simulating the impact of the Panamánian seaway closure on ocean circulation, marine productivity and nutrient cycling. *Earth and planetary science letters*, 246:367–380.

Schrödl, M. & Neusser, T.P. 2010. Towards a phylogeny and evolution of Acochlidia (Mollusca: Gastropoda: Opisthobranchia). *Zoological Journal of the Linnean Society*, 158: 124–154.

Schrödl, M.; Jörger K.M.; Klussmann-Kolb, A. & Wilson, N.G. 2011. Bye bye “opisthobranchia”! a review on the contribution of mesopsammic sea sligs to euthyneuran systematics. *Thalassas*, 27:101-112.

Selfati, M.; El Ouamari, N.; Croetta, F.; Mesfioui, A.; Boissery, P. & Bazairi, H. 2017. Closing the circle in the Mediterranean Sea: *Bursatella leachii* Blainville, 1817 (Mollusca: Gastrooda: Anaspidea) has reached Morocco. *BioInvasions Records*, 6 (2): 129-134.

Stehli, F. & Webb, D. 1985. *The great American biotic interchange*. New York, United States: Plenum Press.

Streftaris, N. & Zenetos, A. 2006. Alien marine species in the Mediterranean—the 100 ‘worst invasives’ and their impact. *Mediterranean Marine Science*, 7: 87–118.

Streftaris, N.; Zenetos, A. & Papathanassiou, E. 2005. Globalisation in marine ecosystems: the story of non-indigenous marine species acroos European seas. *Oceanography and Marine Biology Annual Review*, 43:419-453.

Strong, A.M. & Hertlein, L.G. 1939. Marine mollusks from Panama collected by the Allan Hancock Expedition to the Galapagos Islands, 1931-1932. *Allan Hancock Pacific Expeditions*, 2: 177-246.

Teranes, Jane, Danna Geary y Brayan Bemis, B. 1996. The oxygen isotope record of seasonality in Neogene bivalves from the Central American Isthmus. In Jackson, J.; Budd, A. & Coates, A. (eds.) *Evolution and environment in tropical America*. Chicago, United States: University of Chicago press.

Teske, P.R.; Cherry, M.I. & Matthee, C.A. 2004. The evolutionary history of seahorses (Syngnathidae: Hippocampus): molecular data suggest a west Pacific origin and two invasions of the Atlantic Ocean. *Molecular Phylogenetics and Evolution*, 30: 273–286.

Thompson, T.E. 1958. The natural history, embryology, larval biology, and post-larval development of *Adalaria proxima* (Alder and Hancock) (Gastropoda: Opisthobranchia). *Philosophical Transactions of the Royal Society*, 242B: 1–58.

Thompson, T.E. 1962. Studies on the ontogeny of *Tritonia hombergi* Cuvier (Opisthobranchia). *Philosophical Transactions of the Royal Society of London*, 24: 171–218.

Thompson, T.E. 1980. Jamaican Opisthobranch molluscs II. *Journal of Molluscan Studies*, 46: 74-99.

Thompson, T.E. & Crampton, D.M. 1984. Biology of *Melibe fimbriata*, a conspicuous opisthobranch mollusc of the Indian Ocean, which has now invaded the Mediterranean Sea. *Journal of Molluscan Studies*, 50: 113–121.

Sylvester, F., Kalaci, O.; Leung, B.; Rousse, L.; Murray, C.; Choi, F.; Bravo, M.; Therriault, T. & MacIsaac, H. 2011. on? *Journal of Applied Ecology*, 48: 415-423.

Valdés A., Hamann, J., Behrens, D.W. & Dupont, A. 2006. *Caribbean Sea slugs: a field guide to the opisthobranch mollusks from the tropical northwestern Atlantic*. United States: Sea Challengers Natural History Books, Gig Harbor, WA.

Valdés, A.; Alexander, J.; Crocetta, F.; Yokeş, M.B.; Giacobbe, S.; Poursanidis, D.; Zenetos, A.; Cervera, J.L.; Caballer, M.; Galil, B.S. & Schembri, P.J. 2013. The origin and dispersal pathway of the spotted sea hare *Aplysia dactylomela* (Mollusca: Opisthobranchia) in the Mediterranean Sea. *Aquatic Invasions*, 8 (4) :427–36.

Vega, A. & González, A. 2002. Moluscos del pacífico veragüense, parte II (Gasteropoda). *Tecnociencia*, 4(1): 23-45.

Vermeij, G.J. (1995). Morphology and possible relationships of *Ecphora* (Cenozoic Gastropoda: Muricidae). *Nautilus*, 109: 120–126.

Vermeij, G.J. & Rosenberg, G. 1993. Giving and receiving: the tropical Atlantic as a donor and recipient region for invading species. *American Malacological Bulletin*, 10: 181–194.

Wägele, H., & Klussmann-Kolb, A. 2005. Opisthobranchia (Mollusca, Gastropoda) – more than just slimy slugs. Shell reduction and its implications on defense and foraging. *Frontiers in Zoology*, 2: 1-18.

Wägele, H. & Willian, R. 1994. The morphology and anatomy of the Antarctic gastropod *Bathyberthella* Antarctica (Opisthobranchia, Notaspidea, Pleurobranchidae). *Zoologica Scripta*, 23: 313-324.

Wägele, H.; Ballesteros, M. & Ávila, C. 2006. Defensive glandular structures in opistobranch molluscs – from histology to ecology. *Oceanography and Marine Biology: An Annual Review*, 44: 197-276.

Wägele, H.; Klussmann-Kolb, A.; Verbeek, E. & Schrödl, M. 2014. Flashback and foreshadowing – a review of the taxon Opisthobranchia. *Organisms Diversity & Evolution*, 14: 133-149.

Webb, D. 1985. Late Cenozoic mammal dispersals between the Americas. In Stehli, F. & Webb, D. (eds.) *The Great American Interchange*. New York, United States: Plenum press

Weitzmann, B.; Garcia, M. & Ballesteros, E. 2007. Primera cita de la liebre de mar *Bursatella leachii* Blainville, 1817 en la costa mediterránea peninsular. *Butlletí de la Institució Catalana d´Història Natural*, 75: 153-158.

Willan, R.C. 1987. Phylogenetic systematics of the Notaspidea (Opisthobranchia) with reappraisal of families and genera. *American Malacological Bulletin*, 5: 215–241.

Williams, S.T. & Reid, D.G. 2004. Speciation and diversity on tropical rocky shores: a global phylogeny of snails of the genus *Echinolittorina*. *Evolution*, 58: 2227–2251.

Wilson, N.G.; Maschek, J.A. & Baker, B.J. 2013. A species flock driven by predation? Secondary metabolites support diversification of slugs in Antarctica. *PloS one*, (: e80277.

Wysor, B. & Kooistra, W.H. 2003. An annotated list of marine Chlorophyta from the Caribbean coast of the Republic of Panamá. *Nova Hedwigia*, 77(3–4): 487–523.

WoRMS Editorial Board. 2022. World Register of Marine Species. http://www.marinespecies.org at VLIZ. Accessed 2017/V/17.

Zapata, F; Wilson, N.G.; Howison, M. Andrade, S.C.S.; Jörger, K.M.: Schrödl, M.; Goetz, F.E.; Giribet, G. & Dunn, C.W. 2014. Phylogenomic analyses of deep gastropod relationship reject Orthogastropoda. *Proceedings of the Royal Society B: Biological Science*, 281.

Zenetos, A.; Gofas, S.; Russo, G. & Templado, J. 2004. CIESM *Atlas of Exotic Species in the Mediterranean*. Vol. 3 Molluscs. (F. Briand, Ed). CIESM, Mónaco: 376 pp.

Zenetos, A.; Vassilopoulou, V.; Salomidi, M. & Pursanidis, D. 2008. Additions to the marine alien fauna of Greek waters (2007 update). *Marine Biodiversity Records*, 1: 1–8.

Zenetos, A.; Katsanevakis, S., Poursanidis, D.; Crocetta, F.; Damalas, D.; Apostolopoulos, G., Gravili, C.; Vardala-Theodorou, E. & Malaquías, M. 2011. Marine alien species in Greek Seas: additions and amendments by 2010. *Mediterranean Marine Science*, 12: 95–120.

Zhi-Qiang, Z. 2011. Animal biodiversity: an introduction to higher-level classification and taxonomic richness. *Zootaxa*, 3148:7-12.