






Aggregations of a Sessile Ctenophore, *Coeloplana* sp., on Indo-West Pacific Gorgonians

Kaveh Samimi-Namin ^{1,2,3,*}, Michel R. Claereboudt ⁴, Bert W. Hoeksema ^{1,5}, Catherine S. McFadden ⁶,
Nicholas Bezio ^{7,8} and Gustav Paulay ⁹

- ¹ Marine Evolution and Ecology Group, Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands; bert.hoeksema@naturalis.nl
 - ² Department of Biology, University of Oxford, Oxfordshire, Oxford OX1 3SZ, UK
 - ³ Natural History Museum, Cromwell Road, London SW7 5BD, UK
 - ⁴ Department of Marine Science and Fisheries, College of Agricultural and Marine Sciences, Sultan Qaboos University, Muscat 123, Oman; mclaereboudt@mac.com
 - ⁵ Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands
 - ⁶ Department of Biology, Harvey Mudd College, Claremont, CA 91711, USA; mcfadden@g.hmc.edu
 - ⁷ Biology Department, University of Maryland, College Park, MD 20742, USA; nickbezio@gmail.com
 - ⁸ National Systematics Laboratory, Office of Science and Technology, NOAA National Marine Fisheries Service, MRC-153, Washington, DC 20013-7012, USA
 - ⁹ Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA; paulay@flmnh.ufl.edu
- * Correspondence: kaveh.samimi@naturalis.nl

Abstract: We document the benthic ctenophores *Coeloplana* sp. and *Vallicula multiformis* from Oman, extending their geographic range. A new *Coeloplana* species was found forming aggregations on gorgonians of two octocoral host genera, *Melithaea* and *Euplexaura*, representing associations previously unknown to occur in the Indo-West Pacific region. Our findings also illustrate the concurrent presence of the ectocommensal ophiuroid *Ophiothela mirabilis*, which adversely affects other *Coeloplana* species in the tropical West Atlantic, where it is considered invasive. This exploration contributes to our understanding of the biogeography, species distribution, and ectosymbiotic associations of these genera, setting the stage for a comprehensive species description and in-depth analysis of host relationships in future studies.



Citation: Samimi-Namin, K.; Claereboudt, M.R.; Hoeksema, B.W.; McFadden, C.S.; Bezio, N.; Paulay, G. Aggregations of a Sessile Ctenophore, *Coeloplana* sp., on Indo-West Pacific Gorgonians. *Diversity* **2023**, *15*, 1060. <https://doi.org/10.3390/d15101060>

Academic Editor: Michael Wink

Received: 11 August 2023

Revised: 25 September 2023

Accepted: 29 September 2023

Published: 3 October 2023



Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

Keywords: Ctenophora; Octocorallia; Arabian Sea; Platyctenida; Oman; Masirah Island; ectosymbiotic

The realization that ctenophores are the sister group to all other Metazoa [1,2] and that many aspects of their biology are likely convergent with other phyla, is attracting attention to this small phylum. Ctenophores, commonly known as comb jellies, are most diverse, and thought to have originated in the plankton, but three lineages have taken up a benthic existence [1–4].

The order Platyctenida is the main group of benthic ctenophores, characterized by an expanded oral region that forms a creeping sole, loss of ctenes in the adults of most species, and extensive tentacles extended by flow for prey capture [5–7]. They predominantly exhibit two distinct body types: the “lyre-shaped” form, which has two large aboral projections to extend tentacles into the water column, and the “flat” form with oral-aboral compression.

Most platyctenes are ectosymbiont commensals that live in close association with cnidarians, echinoderms, and algae [6–10]. The number of individuals per host depends on the species, host, and environmental conditions and can vary from one to hundreds [7,8,11]. Brooding, paedogenesis, and fragmentation are the main modes of propagation. Hermaphroditism, larval dispersal, and rapid development are likely traits that promote colonization, sustain high population densities, and provide resilience [12].

They are consumed by various predators, including sea anemones, molluscs, brachyuran crabs, and fishes [8,13,14].

The order Platyctenida is currently divided into five families, with Coeloplanidae being the most diverse [15]. Coeloplanidae includes two genera, *Coeloplana* Kowlevsky, 1880, with about 35 species [15], one species in the West Atlantic, and the rest in the Indo-West Pacific region; and the monotypic *Vallicula* Rankin, 1956, recorded across all warm oceans (Figure 1). Recent molecular studies suggest that the genus *Vallicula* belongs to a different family (Bezio and Collins, pers. comm.). *Coeloplana* is differentiated by its flask-shaped tentacle sheaths from *Vallicula*, which has anchor-shaped (or H-shaped) sheaths with a prominent cross-piece [5]. Six species of *Coeloplana* have been reported from the northwestern Indian Ocean, one from the Persian Gulf [16] and Somalia [17], and five from the Red Sea [6,18] (Figure 1A,B). No coeloplanids have been previously recorded from Oman.

Identification of Coeloplanidae is based on colour pattern, patterns of aboral papillae, development of oral groove and oral lappets, and host [5–7,19]. Additionally, recent studies have utilized *Cytochrome c Oxidase Subunit I* (COI) sequences for species differentiation [10,18]. *Vallicula multiformis* is a habitat generalist with low host specificity, whereas most *Coeloplana* species are habitat specialists with high host specificity and are restricted to a specific host or a group of morphologically similar hosts [6–8,19].

This ectosymbiont/host association in coeloplanids can provide insights into species distributions and biogeography. Cnidarians are the most common hosts, with at least 19 described (and numerous undescribed) species of *Coeloplana* recorded from them, 17 obligately so. One species (*C. loyai*) lives on mushroom corals (Fungiidae), while the rest occur on octocorals, all but three on soft corals (Table 1). The only exceptions are the Atlantic *C. waltoni* and the Indo-West Pacific *C. sophiae* both known only from gorgonians, and the generalist *C. duboscqui* recorded from sea pens [6,7,12,20–22]. This suggests that soft-coral morphology is better suited for *Coeloplana*, and the low diversity of *Coeloplana* in the Atlantic compared to Indo-West Pacific reefs may be due to the practical absence of soft corals from Atlantic reefs [23]. *Coeloplana* species on gorgonians are generally also smaller than those on soft corals.

During a large-scale survey of the marine biodiversity of Oman (2019–2023) that aimed to characterize macroinvertebrate fauna, we encountered aggregations of an undescribed *Coeloplana* species on two gorgonian hosts, *Melithaea* Milne Edwards, 1857 (Melithaeidae) and *Euplexaura* Verrill, 1869 (Euplexauridae), around Masirah Island (Figures 1–3, Videos S1 and S2). The animals were a few millimetres long and appeared to occupy the hosts without particular preference for location or orientation on the colony (Figures 2 and 3). Approximately 15–30 individuals were found on *Melithaea* sp. colonies (Figure 2C,D), and over 60 individuals on *Euplexaura* sp. colonies (Figure 2A,B). They were noted in situ on *Euplexaura* colonies, but were cryptic on the orange-yellow *Melithaea* colonies and only noticed in the lab, when they crawled off the colony as water quality in their tank declined. Two colour forms, pink and yellow, cooccurred on both hosts and likely represent morphotypes of the same species. The yellow form is effectively invisible on the similar-coloured *Melithaea* (Figure 3). We reviewed all known species of *Coeloplana* and these specimens do not match any described species. In addition, we encountered *Vallicula multiformis* on a green alga host (Figure 4, Video S3).

The ctenophores co-occurred with the ectocommensal ophiuroid *Ophiothela mirabilis* (Verrill, 1867) (Figure 2B,C). This ophiuroid is invasive in the tropical West Atlantic and appears to negatively impact *Coeloplana waltoni* in south Florida [24].

Our observations constitute the first report of such aggregations on gorgonians in the Indo-West Pacific, as well as the first record of *Coeloplana* sp. and *Vallicula multiformis* in Oman. This discovery contributes to our understanding of ectosymbiont-host associations, biogeography, and species distribution of *Coeloplana* and *Vallicula*. Future research will focus on formally describing the species and its gorgonian hosts.

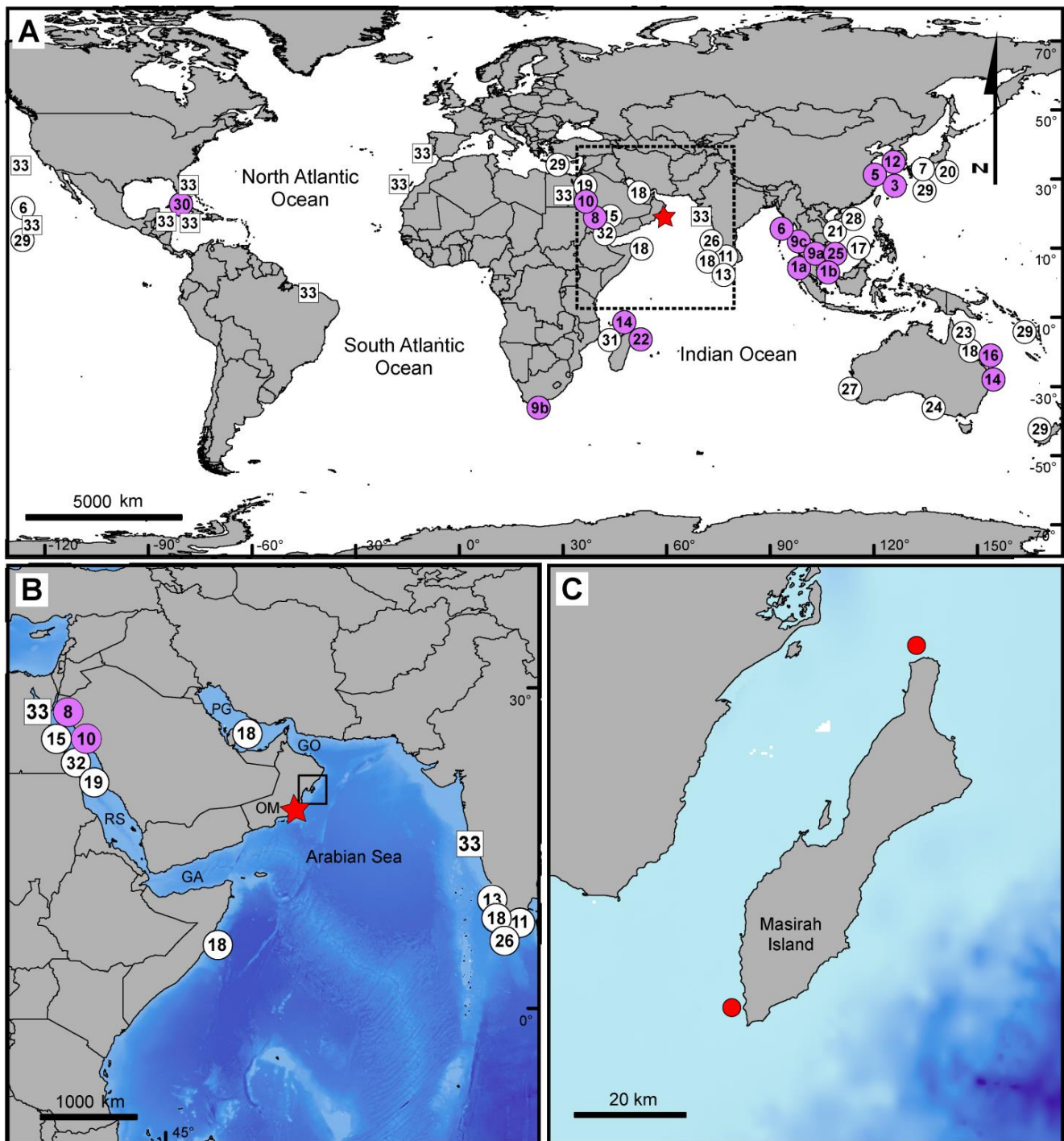


Figure 1. (A,B) Global distribution of *Coeloplana* (circles) and *Vallicula* (squares). *Coeloplana* records from octocoral hosts are purple in colour. The star represents the first record of the *Coeloplana* and *Vallicula* from Oman. (C) Locations of the observations and collections of *Coeloplana* sp. on gorgonian hosts in Masirah Island. Numbers indicate different species (Table 1, localities extracted from [6], and other publications). OM = Oman, PG = Persian Gulf, GO = Gulf of Oman, GA = Gulf of Aden, and RS = Red Sea. Blue shading in (B,C) represents depth.

Table 1. List of valid species of Coeloplanidae and their host based on [6,15]. Please note that the octocoral taxonomy has been updated in the table as accurately as possible. The *Coeloplana* records from octocoral host have been shaded purple (corresponding to Figure 1).

Record No.	Species	Host
1a	<i>C. agniae</i> Dawydoff, 1930	<i>Sclerophytum polydactylum</i> (Octocorallia)
1b	<i>C. agniae</i> var. <i>striata</i> Dawydoff, 1938	<i>Sclerophytum polydactylum</i> (Octocorallia)
2	<i>C. anthostella</i> Song & Hwang, 2010	<i>Dendronephthya spinulosa</i> and other <i>Dendronephthya</i> spp. (Octocorallia)
3	<i>C. astericola</i> Mortensen, 1927	<i>Echinaster luzonicus</i> (Asteroidea)
4	<i>C. bannwarthi</i> Krambach, 1933	<i>Diadema</i> spp. (Echinoidea)
5	<i>C. bocki</i> Komai, 1920	<i>Stereonephthya japonica</i> , <i>Dendronephthya spinulosa</i> , <i>D. dendricata</i> (Octocorallia), Hydrozoa, algae, Echinodermata
6	<i>C. duboscqui</i> Dawydoff, 1930	<i>Pteroides</i> (Octocorallia), <i>Hypnea</i> (red algae)
7	<i>C. echinicola</i> Tanaka, 1932	<i>Toxopneustes pileolus</i> (Echinoidea)
8	<i>C. fishelsoni</i> Alamaru, Brokovich & Loya, 2015	<i>Xenia umbellata</i> , <i>Paralemnalia</i> (Octocorallia)
9a	<i>C. gonoctena</i> Krempf, 1920	<i>Cladiella krempfi</i> , <i>Cladiella pachyclados</i> (Octocorallia)
9b	<i>C. gonoctena</i> var. <i>natalensis</i> Pople, 1960	<i>Cladiella krempfi</i> (Octocorallia)
9c	<i>C. gonoctena</i> var. <i>rosea</i> Dawydoff, 1938	<i>Klyxum</i> (Octocorallia)
10	<i>C. huchonae</i> Alamaru, Brokovich & Loya, 2015	<i>Dendronephthya hemprichi</i> (Octocorallia)
11	<i>C. indica</i> Davansan & Varadarajan, 1942	NA
12	<i>C. komaii</i> Utinomi, 1963	<i>Cladiella digitulata</i> (Octocorallia)
13	<i>C. krusadiensis</i> Devanesen & Varadarajan, 1942	<i>Pentaceros hedemanni</i> (Asteroidea)
14	<i>C. lineolata</i> Fricke, 1970	<i>Sarcophyton</i> (Octocorallia)
15	<i>C. loyai</i> Alamaru & Brokovich, 2015	<i>Herpolitha limax</i> , <i>Ctenactis echinata</i> (Scleractinia)
16	<i>C. mellosa</i> Gershwin, Zeidler & Davie, 2010	<i>Sarcophyton</i> (Octocorallia)
17	<i>C. mesnili</i> Dawydoff, 1938	Planktonic/free living
18	<i>C. meteoris</i> Thiel, 1968	Free living on soft sediments
19	<i>C. metschnikowii</i> Kowalevsky, 1880	<i>Zostera</i> (seagrass)
20	<i>C. mitsukurii</i> Abbott, 1902	<i>Melobesia</i> (red algae) and <i>Sargassum</i> (brown algae)
21	<i>C. perrieri</i> Dawydoff, 1930	<i>Posidonia</i> (seagrass) or free living on rocks
22	<i>C. punctata</i> Fricke, 1970	<i>Sarcophyton</i> (Octocorallia)
23	<i>C. reichelti</i> Gershwin, Zeidler & Davie, 2010	Variety of red and green algae and seagrasses
24	<i>C. scaberiae</i> Matsumoto & Gowlett-Holmes, 1996	<i>Scaberia agardhii</i> (algae)
25	<i>C. sophiae</i> Dawydoff, 1938	<i>Solenocaulon jedanensis</i> (Octocorallia)
26	<i>C. tattersalli</i> Devanesen & Varadarajan, 1942	Planktonic/free living
27	<i>C. thomsoni</i> Matsumoto, 1999	<i>Jania</i> (coralline algae)
28	<i>C. weilli</i> Dawydoff, 1938	<i>Heterocentrotus mamillatus</i> (Echinoidea)
29	<i>C. willeyi</i> Abbott, 1902	<i>Zostera</i> , <i>Caulerpa</i> , <i>Sargassum</i> (seagrass and algae) and <i>Echinothrix diadema</i> , <i>Echinothrix calamaris</i> , <i>Heterocentrotus mamillatus</i> (Echinoidea)
30	<i>C. waltoni</i> Glynn, Bayer & Renegar, 2014	Various species of shallow-water gorgonians from the genera <i>Eunicea</i> , <i>Plexaurella</i> , <i>Muricea</i> , <i>Gorgonia</i> , <i>Pseudoplexaura</i> , <i>Antillologorgia</i> , <i>Plexaura</i> , <i>Muriceopsis</i> (Octocorallia)
31	<i>C. wuennenbergi</i> Fricke, 1970	<i>Sarcophyton</i> (Octocorallia)
32	<i>C. yulianicorum</i> Alamaru, Brokovich & Loya, 2015	<i>Sarcophyton</i> (Octocorallia)
33	<i>Vallicula multiformis</i> Rankin, 1956	Various algae and invertebrates, such as seagrasses, algae, <i>Pearsonothuria graeffei</i> (Holothuroidea)

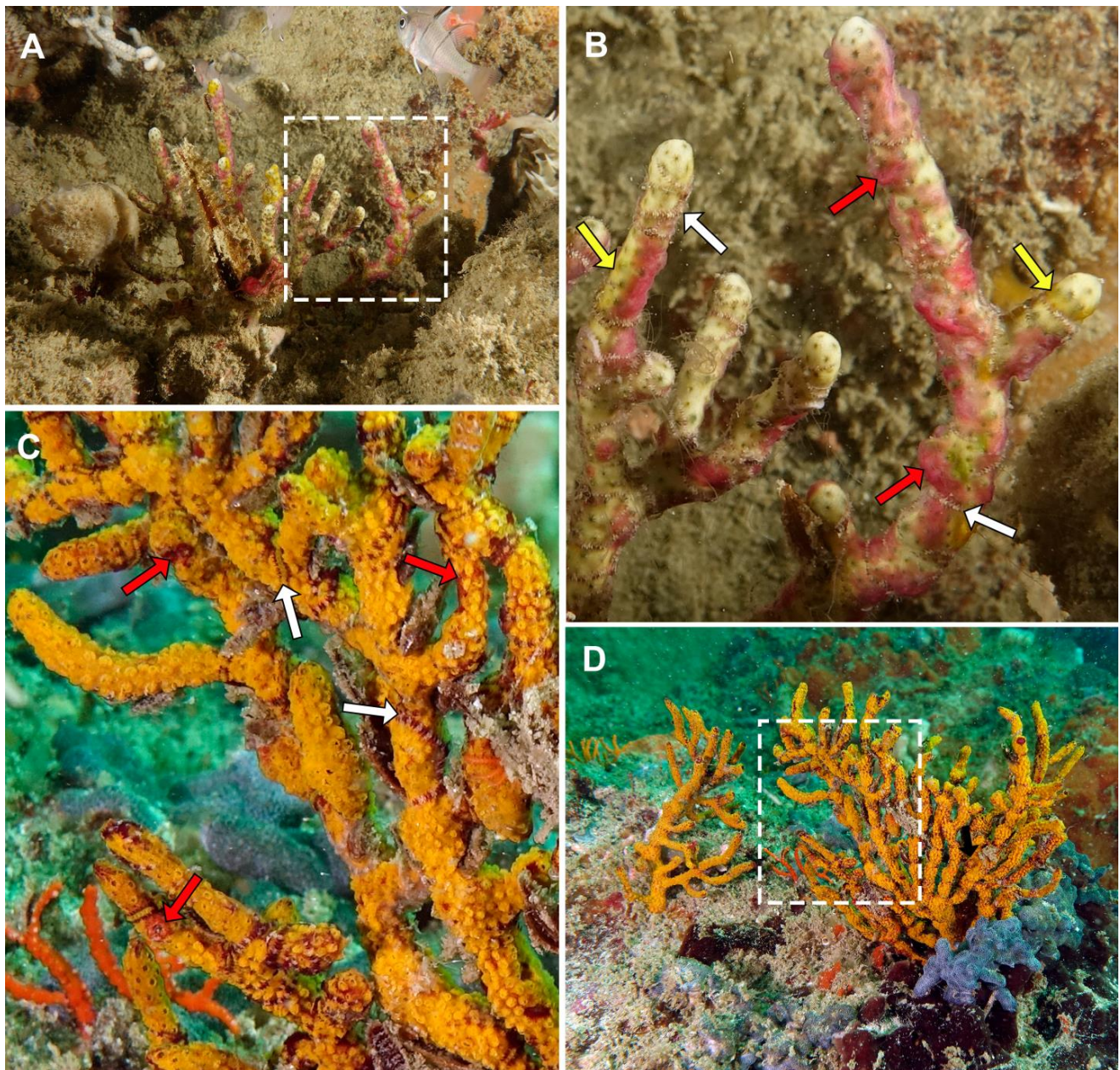


Figure 2. Aggregations of *Coeloplana* sp. on gorgonians around Masirah Island, Oman. (A,B) Colony of *Euplexaura* sp. at 18 m depth (BOMAN-13166) covered with both colour morphotypes of *Coeloplana* (red and yellow arrows), some with extended tentacles. (C,D) Colony of *Melithaea* sp. (BOMAN-13152) at 7 m depth. *Coeloplana* individuals occur in both colours in this species; however, it is very difficult to see them underwater. Note the concurrent presence of the ophiuroid *O. mirabilis* in both gorgonians (white arrows). All observations were made during the day (Photo credit: K. Samimi-Namin).

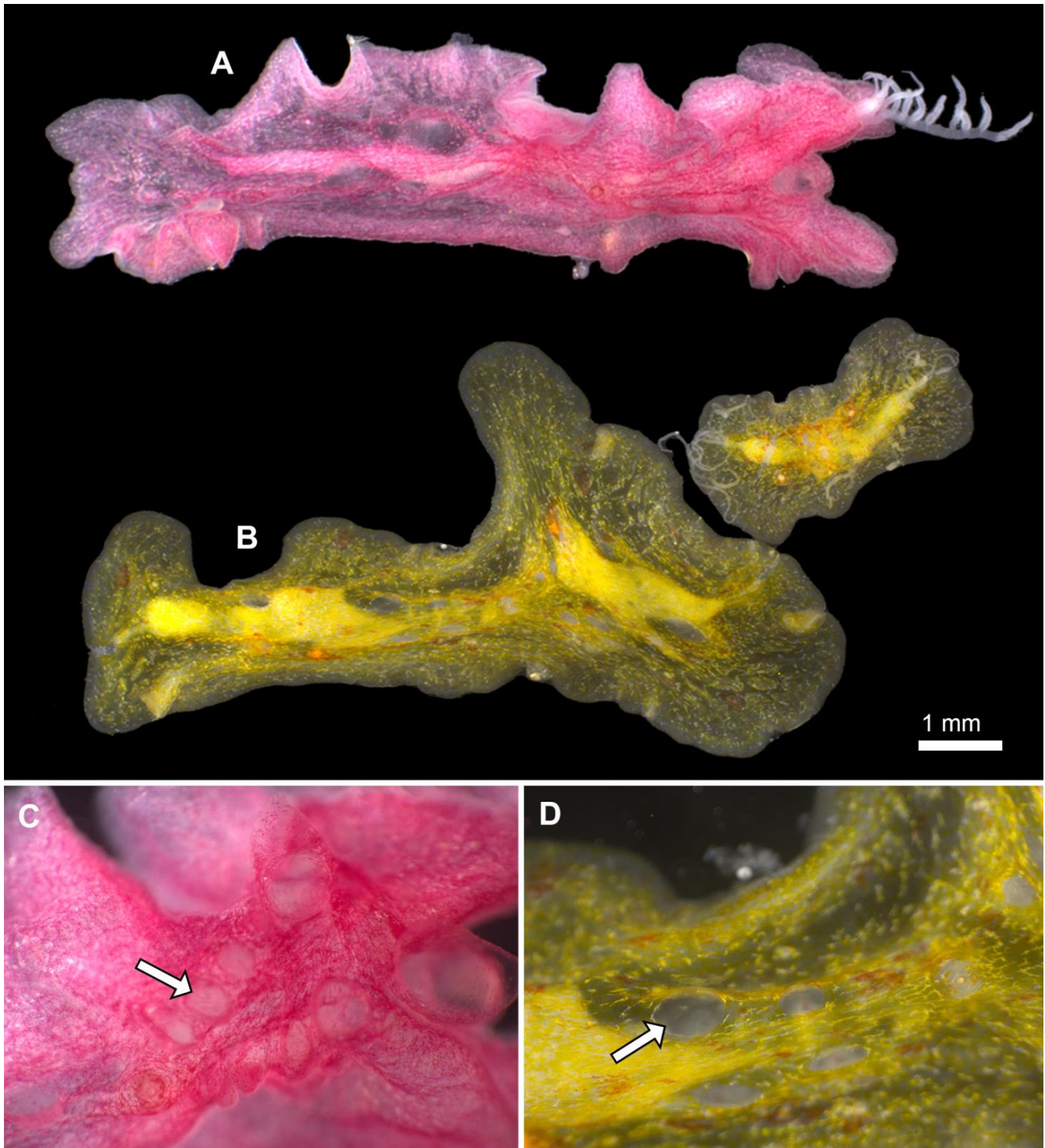


Figure 3. (A,B) Photographs of the two colour morphs of *Coeloplana* sp. (C,D) Close-ups of the aboral papillae (white arrow) (Photo credit: G. Paulay).

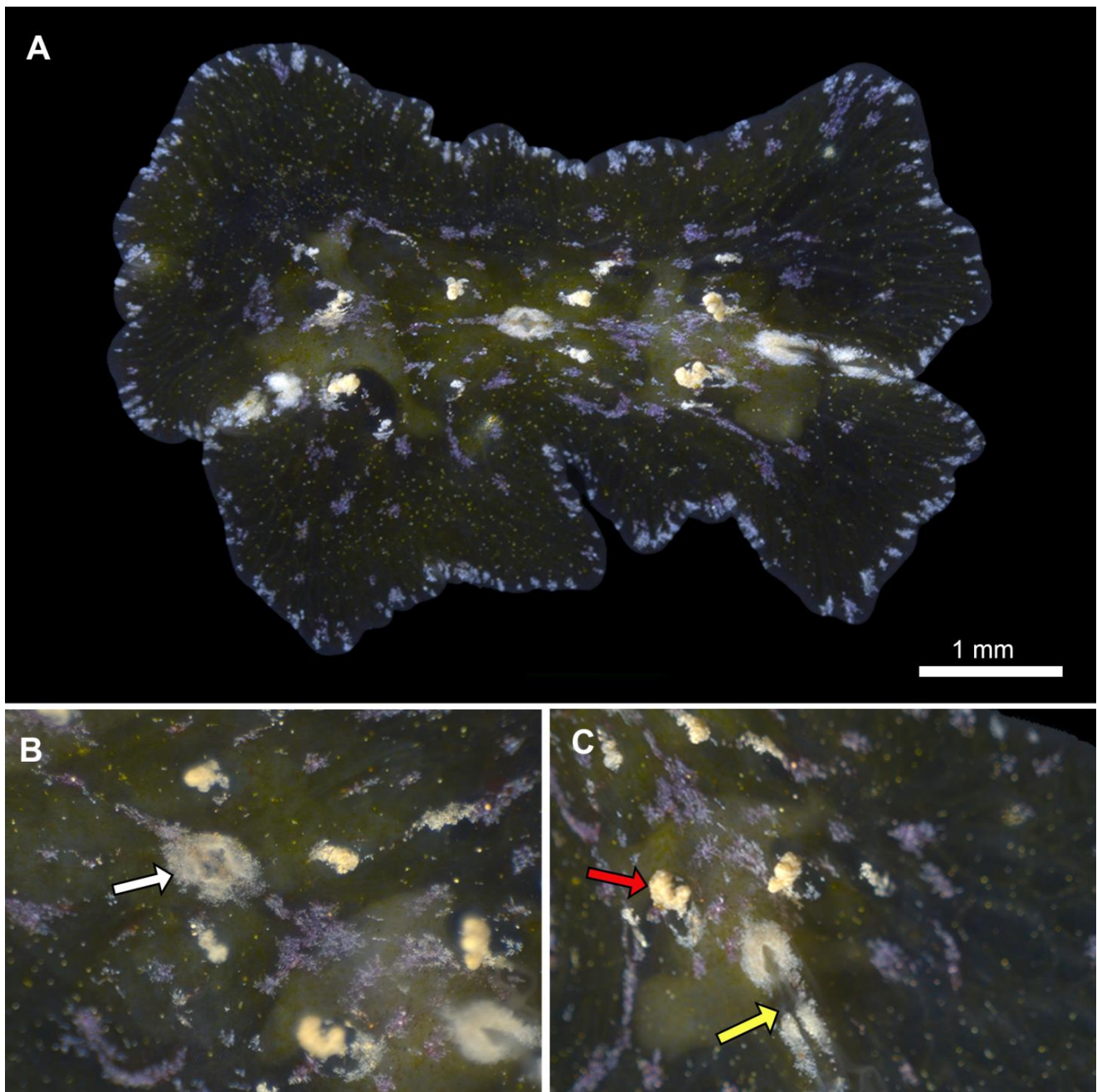


Figure 4. (A–C) Photographs of *Vallicula multiformis* from Oman (BOMAN-10006). (B,C) Close-ups of the same specimen showing the aboral sense organ (white arrow), papillae (red arrow), and the extension of the oral groove to the tentacle sheath (yellow arrow) (Photo credit: G. Paulay).

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15101060/s1>, Video S1. *Coeloplana* sp. yellow colour morph from Oman, Video S2. *Coeloplana* sp. red colour morph from Oman. Video S3. *Vallicula multiformis* from Oman.

Author Contributions: Conceptualization, K.S.-N. and G.P.; methodology, K.S.-N., N.B., M.R.C., B.W.H., C.S.M., N.B. and G.P.; software, K.S.-N.; validation, K.S.-N., N.B., M.R.C., B.W.H., C.S.M., N.B. and G.P.; investigation, K.S.-N., N.B., M.R.C., B.W.H., C.S.M., N.B. and G.P.; resources, G.P., C.S.M. and K.S.-N.; data curation, G.P., C.S.M. and K.S.-N.; writing—original draft preparation, K.S.-N., N.B., M.R.C., B.W.H., C.S.M. and G.P.; writing—review and editing, K.S.-N., N.B., M.R.C., B.W.H., C.S.M.,

N.B. and G.P.; visualization, K.S.-N. and G.P. All authors have read and agreed to the published version of the manuscript.

Funding: The research is supported by grants by NSF DEB-1457817 to G.P. and C.S.M., and the Richard Lounsbery Foundation to K.S.-N.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: The Environment Authority of Oman is acknowledged for granting the collection permits. We are thankful to S. Dobretsov (Sultan Qaboos University, Oman), S. Wilson, and O. Taylor (Five Oceans Environmental Services LLC) for their support. J.H. Ausubel (Rockefeller University) and L. Brown (Lounsbery Foundation), are greatly appreciated for their continued support and encouragement to K. S.-N. Three anonymous reviewers are appreciated for their constructive comments and suggestions, which helped improve the manuscript.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

References

1. Ryan, J.F.; Pang, K.; Schnitzler, C.E.; Nguyen, A.D.; Moreland, R.T.; Simmons, D.K.; Koch, B.J.; Francis, W.R.; Havlak, P.; Smith, S.A.; et al. The genome of the ctenophore *Mnemiopsis leidyi* and its implications for cell type evolution. *Science* **2013**, *342*, 1242592. [CrossRef] [PubMed]
2. Schultz, D.T.; Haddock, S.H.D.; Bredeson, J.V.; Green, R.E.; Simakov, O.; Rokhsar, D.S. Ancient gene linkages support ctenophores as sister to other animals. *Nature* **2023**, *618*, 110–117. [CrossRef] [PubMed]
3. Whelan, N.V.; Kocot, K.M.; Moroz, T.P.; Mukherjee, K.; Williams, P.; Paulay, G.; Moroz, L.L.; Halanych, K.M. Ctenophore relationships and their placement as the sister group to all other animals. *Nat. Ecol. Evol.* **2017**, *1*, 1737–1746. [CrossRef]
4. Lindsay, D.J.; Miyake, H. A novel benthopelagic ctenophore from 7217m depth in the Ryukyu Trench, Japan, with notes on the taxonomy of deep sea cydippids. *Plankton Benthos Res.* **2007**, *2*, 98–102. [CrossRef]
5. Rankin, J.J. The structure and biology of *Vallicula multiformis*, gen. et sp. nov., a platyctenid ctenophore. *Zool. J. Linn. Soc.* **1956**, *43*, 55–71. [CrossRef]
6. Alamaru, A.; Brokovich, E.; Loya, Y. Four new species and three new records of benthic ctenophores (Family: Coeloplanidae) from the Red Sea. *Mar. Biodivers.* **2016**, *46*, 261–279. [CrossRef]
7. Glynn, P.W.; Bayer, F.M.; Renegar, D.A. *Coeloplana waltoni*, a new species of minute benthic ctenophore (Ctenophora: Platyctenida) from south Florida. *Proc. Biol. Soc. Wash.* **2014**, *127*, 423–436. [CrossRef]
8. Glynn, P.W.; Coffman, B.; Primov, K.D.; Moorhead, S.G.; Vanderwoude, J.; Barrales, R.N.; Williams, M.K.; Roemer, R.P. Benthic ctenophores (Platyctenida: Coeloplanidae) in South Florida: Predator–prey interactions. *Invertebr. Biol.* **2018**, *137*, 133–150. [CrossRef]
9. Hoeksema, B.W.; Waheed, Z.; Alamaru, A. Out of sight: Aggregations of epizoid comb jellies underneath mushroom corals. *Coral Reefs* **2013**, *32*, 1065. [CrossRef]
10. Alamaru, A.; Hoeksema, B.W.; van der Meij, S.E.T.; Huchon, D. Molecular diversity of benthic ctenophores (Coeloplanidae). *Sci. Rep.* **2017**, *7*, 6365. [CrossRef]
11. Galt, C.P. Natural history of the benthic ctenophore *Vallicula multiformis* in Kaneohe Bay, Hawaii. (Abstr.). *Am. Zool.* **1998**, *38*, 181a.
12. Glynn, P.W.; Coffman, B.; Primov, K.; Renegar, D.A.; Gross, J.; Blackwelder, P.; Martinez, N.; Dominguez, J.; Vanderwoude, J.; Riegl, B.M. Benthic ctenophore (Order Platyctenida) reproduction, recruitment, and seasonality in south Florida. *Invertebr. Biol.* **2019**, *138*, e12256. [CrossRef]
13. Coleman, N. *Nudibranchs Encyclopedia: Catalogue of Asia/Indo-Pacific Sea Slugs*; Neville Coleman’s Underwater Geographic: Springwood, Australia, 2008.
14. Gosliner, T. Six new species of aglajid opisthobranch mollusks from the tropical Indo-Pacific. *Zootaxa* **2011**, *2751*, 1–24. [CrossRef]
15. Mills, C. Phylum Ctenophora: List of All Valid Species Names. Available online: <http://faculty.washington.edu/cemills/Ctenolist.html> (accessed on 15 January 2023).
16. Giraldez, B.W. The first record of the Indo-Pacific benthic ctenophore *Coeloplana (Benthoplana) meteoris* (Ctenophora: Coeloplanidae) in the Arabian-Persian Gulf. *J. Asia Pac. Biodivers.* **2019**, *12*, 467–469. [CrossRef]
17. Thiel, H. *Coeloplana meteoris* nov. spec. (Ctenophora, Platyctenea): Beschreibung und systematische Stellung mit einem Vergleich der Gastrovascularsysteme in dieser Ordnung. *Meteor Forsch. Reihe D Biol.* **1968**, *3*, 1–13.
18. Arafat, H.; Alamaru, A.; Gissi, C.; Huchon, D. Extensive mitochondrial gene rearrangements in Ctenophora: Insights from benthic Platyctenida. *BMC Evol. Biol.* **2018**, *18*, 65. [CrossRef]

19. Matsumoto, G.I.; Gowlett-Holmes, K.L. A new benthic ctenophore (Ctenophora: Coeloplanidae) from south Australia. *Rec. S. Aus. Mus.* **1996**, *29*, 33–40.
20. Glynn, P.W.; Coffman, B.; Vanderwoude, J.; Martinez, N.; Dominguez, J.H.; Gross, J.M.; Renegar, D.A. Antipredatory escape behaviors of two benthic ctenophores in South Florida. *Ecology* **2019**, *100*, e02497. [[CrossRef](#)]
21. Dawydoff, C. Les coeloplanides Indochinoises. *Arch. Zool. Exp. Gen.* **1938**, *80*, 125–162.
22. Dawydoff, C. *Coeloplana dubosqui* nov. sp., Coeloplanide provenant du Golfe de Siam, commensale des Pennatules. *Arch. Zool. Exp. Gen.* **1930**, *70*, 87–90.
23. Bayer, F.M. The shallow-water Octocorallia of the West Indian region. A manual for marine biologists. *Stud. Fauna Curacao Carib. Is.* **1961**, *12*, 1–373.
24. Glynn, P.W.; Coffman, B.; Dettloff, K.; Dominguez, J.; Gillette, P.R.; Martinez, N.; Jones, N.P.; Riegl, B.M. Non-native brittle star interactions with native octocoral epizoots: An endemic benthic ctenophore in peril? *Mar. Biol.* **2021**, *168*, 142. [[CrossRef](#)]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.