Parasites or predators? Gastropod ectoparasites and their scleractinian host corals at Koh Tao, Gulf of Thailand, with the description of a new species

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Abstract

Recent years have seen a rapid increase in the study of coral-associated gastropods. In particular, the description of several new species in conjunction with their host specificity or dietary variability, has raised questions pertaining to their impact on reef health. These corallivores have been labelled as both 'parasite' and 'predator' by different studies, due to the tendency of some species to entirely consume their 'host' corals. Here we present new findings of corallivory and parasitism based on surveys conducted on the reefs of Koh Tao, Gulf of Thailand. A total of 6566 corals were assessed for their tendency to host gastropods of the nudibranch genus *Phestilla* and the caenogastropod family Epitoniidae. Thirteen gastropod species were found to be associated with 20 scleractinian coral species, including six that do not match the original description of previously known taxa. Herein we describe one of them, the first nudibranch proven to be associated with corals of the scleractinian genus *Acropora* and discuss conservation implications of these coral/gastropod relationships. Additionally, we explore the complex topic of defining these relationships as parasitic versus predatory and the merits of using these labels to better understand the ecology of these relationships.

Keywords *Acropora* · Coral-associated gastropods · Corallivory · Epitoniidae · *Phestilla* · Predation

1 Introduction

Parasitism is a consumer strategy whereby smaller organisms, classified as endo- or ectoparasites, obtain energy and other resources from larger hosts, often without directly causing the death of the latter (Hudson et al. 2006). Endoparasites occupy the internal organs or tissues of their hosts, while a large number of ectoparasites can be spotted with the naked eye and collected without sacrificing the host (Demopoulos and Sikkel 2015; Scheifler et al. 2019). Classifying symbionts as parasites or predators has been debated over a long period of time (Raffel et al. 2008). These organisms have historically been placed in either category after making assumptions on the presence or absence of harm or benefit in the hosts. During predation, an organism (the predator) consumes either all or part of another living organism (the prey),

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causing a direct destructive impact on the prey. In contrast, parasitism is a symbiosis wherein one organism (the parasite) causes harm to another (the host), utilizing it as habitat and depending on it for resource acquisition, typically not killing the host directly. More recently, a compelling case was put forward by Raffel et al. (2008) who argued that these labels do not represent opposing ecological functions but instead represent distinct but often overlapping terms pertaining to different ecological functions. Thus, a parasite may indeed also be a predator, but does not imply it, and similarly most predators are not parasitic, but some may be. Nonetheless, definitions of parasites and the delineation of parasitic relationships remain topics of debate among and between different fields within the biological sciences (Rózsa and Garay 2023) reinforcing the need for further study of the drivers and impacts of these relationships.

Among reef-dwelling molluscs, various gastropods are known as predators or parasites of stony corals, which may have impact on coral reef health. These animals have been the topic of the classic revision by Robertson (1970), who did not classify them as either predators or parasites. Gastropods in the family Muricidae Rafinesque, 1815 make up some of the most well-documented coral predators (*Drupella* spp.) and ectoparasites (*Coralliophila* spp.), with species exhibiting both strategies across the Indo-Pacific (Baums et al. 2003; Kaullysing et al. 2019; Simmonds et al. 2020). While the genus *Drupella* Thiele, 1925 has broadly been accepted as a coral predator, records of *Coralliophila* H. Adams & A. Adams, 1853 range from minimal to extensive host damage and mortality depending on the host coral species (Ward 1965; Robertson 1970; Potkamp et al. 2017; Verboom and Hoeksema 2023). Within the muricid subfamily Corralliophilinae, snails of the genera *Leptoconchus* Rüppell, 1835, and *Magilus* Monfort, 1810, are also symbiotic with scleractinian corals (Robertson 1970). They are parasitic by excavating holes in the coral skeleton (Massin 1982; Massin and Dupont 2003; Gittenberger and Gittenberger 2011). The presence of a siphon that protrudes from the coral surface (Hoeksema 2017) suggests that *Leptoconchus* snails do not eat from the host's tissue but may steal some of its food. Recent years have seen substantial increases in the documentation on the biodiversity and ecology of corallivorous gastropods, with growing attention on largely overlooked groups.

The nudibranch genus *Phestilla* Bergh, 1874 (family Trinchesiidae), which presently comprises 11 species (MolluscaBase 2023), has recently seen a rapid increase in the description of new taxa and in the documentation of their ecology (Hu et al. 2020; Mehrotra et al. 2020; Wang et al. 2020) with growing evidence of more undescribed biodiversity (Gosliner et al. 2018; Fritts-Penniman et al. 2020; Mehrotra et al. 2021). At present, members of the genus have been known to feed on corals of the scleractinian

genera *Dendrophyllia* de Blainville, 1830, *Duncanopsammia* Wells, 1936 (as *Turbinaria* Oken, 1815), *Goniopora* de Blainville, 1830, *Montipora* de Blainville, 1839, *Pavona* Lamarck, 1801, *Porites* Link, 1807, *Rhizopsammia* Verril, 1870 and *Tubastraea* Lesson, 1830 (Mehrotra et al. 2020; Yiu et al. 2021). Additionally, the species *Phestilla chaetopterana* (Ekimova et al. 2019) has been associated exclusively with worms belonging to the genus *Chaetopterus* Cuvier, 1830, however, the precise nature of the relationship remains to be explored (Ekimova et al. 2019). Despite the broad range of diet across the genus, most species have shown some prey specificity, aligning closely with the taxonomic relatedness among prey items, with some species possessing a high degree of prey-specificity (Fritts-Penniman et al. 2020; Yiu and Qiu 2022). This variability in diet extends beyond prey selection and includes blurring the lines between the predator-parasite dynamic across the different species. For example, 'outbreaks' of *Phestilla* species in situ and in aquaria have been attributed to colony-wide stress and mortality events (Wang et al. 2020; Knapp et al. 2022). Most *Phestilla* spp. show a minute size and a remarkable camouflage against the background of their host coral. These traits are shared with the monotypic nudibranch genus *Pinufius* Er. Marcus & Ev. Marcus, 1960 (family Pinufiidae), which is composed of corallivores that feed exclusively on *Porites* spp. (Rudman 1981; Fritts-Penniman et al. 2020; Jia et al. 2023).

A similarly diverse group of gastropods consists of coral-associated species belonging to the family Epitoniidae, a highly speciose family, which is largely considered parasitic on a diverse range of cnidarian hosts, with numerous genera such as *Epidendrium* A. Gittenberger & E. Gittenberger, 2005, *Epifungium* A. Gittenberger & E. Gittenberger, 2005, *Epitonium* Röding, 1798 and *Surrepifungium* A. Gittenberger & E. Gittenberger, 2005 associated with scleractinian corals (Gittenberger and Hoeksema 2013). While epitoniid gastropods have long been known to parasitise corals and other anthozoans, such as Actiniaria and Zoantharia (Robertson 1963, 1970; Bosch 1965; Zann 1980; den Hartog 1987; Kokshoorn et al. 2007), a renewed attention on these often-cryptic gastropods has been driven by the works of Gittenberger (2003), Gittenberger et al. (2000), Gittenberger and Gittenberger (2005), and Scott et al. (2017c), among others. Prey genera reported by these authors are: *Tubastraea* (family Dendrophylliidae); *Ctenactis* Verril, 1864, *Cycloseris* Milne Edwards & Haine, 1849, *Danafungia* Wells, 1966, *Fungia* Lamarck, 1801, *Halomitra* Dana, 1846, *Heliofungia* Wells,1966, *Herpolitha* Eschscholtz, 1825, *Lithophyllon* Rehberg, 1892, *Lobactis* Verril, 1864, *Pleuractis* Verril, 1864, *Podabacia* Milne Edwards & Haime, 1849, *Sandalolitha* Quelch, 1884, *Zoopilus* Dana, 1946 (all Fungiidae); and *Plerogyra* Milne Edwards & Haime, 1848 (family Plerogyriidae).

The island of Koh Tao in the Gulf of Thailand has been home to a number of investigations into the diversity and ecology of the corallivorous gastropod *Drupella* (Hoeksema et al. 2013; Moerland et al. 2016; Scott et al. 2017a). The island has seen numerous shifts in reef communities, many of which have been attributed to, or compounded by, threats pertaining to corallivory (Scott et al. 2017a, b). The island has also been found to host a diversity of coral ectoparasites, including *Phestilla* spp. and unidentified epitoniids (Scott et al. 2017c; Mehrotra et al. 2021, 2023), and is also the type locality for a number of recently described nudibranch species (Mehrotra et al. 2017, 2020; Korshunova et al. 2019. In the present study, we survey a large diversity of known and suspected prey scleractinian species of parasitic gastropods from the reefs and soft sediment habitats of the island. These surveys were carried out with the primary goal to document the diversity of symbiotic relationships between host coral and parasite species. In doing so, a number of previously undescribed corallivores were documented, with one such species newly described in this study. Secondly, we explore the range of ecological associations based on observations made on the quantity of gastropods on each host as well as observations of host mortality.

2 Methodology

2.1 Field surveys

Between the months of February 2018 and February 2020, 114 roving diver surveys utilising SCUBA were carried out on the coral reefs and soft-substrate habitats of Koh Tao (Fig. 1), ranging from depths of 2 to 32 m. Surveys did not overlap spatially within any given 6-month period with a concise effort to survey previously unsurveyed sites/depth ranges, or host corals per site. Roving diver surveys were chosen to maximise the area surveyed in any single dive, and overlap was minimised by not having the same host species and site/section of the reef surveyed within a 6-month period. Surveys were largely carried out during the day ($n = 103$) with some surveys being carried out at night ($n = 11$). Surveys involved a close and detailed examination of the external surfaces of coral colonies of species that had been shown to host coral associated gastropods based on previous surveys (Mehrotra et al. 2021). Additionally, several species that were taxonomically related to host corals or species that shared certain morphological or ecological features with known host corals (such as a monostomatous corallum shape or an unattached mode of life) were included. For each solitary or colonial coral (henceforth 'coral') that was completely examined, presence or absence of nudibranch or epitoniid gastropods found feeding or laying egg bundles on living tissue or recently exposed skeleton

was assessed. Surveys were conducted visually and thus only visually evident ectoparasites were included within the survey. In instances where multiple colonies of a given species were in close proximity to one another, colonies were separated based on visual assessment of discontinuity of both tissue and skeleton, thus distinguishing two or more separate colonies.

For corals on which corallivorous gastropods were found, the number of individuals on each host coral was further quantified. The overall health (outside of complete mortality), depth, size and growth form of associated corals were not individually quantified, with an emphasis instead put on maximising dive time to survey a greater number of corals. Maximum diameter of 20 randomly selected corals per host species was however recorded for size ratio comparisons (Online Resource 1). Additional photographs were taken in situ and ex situ for specimens or associations deemed to be of particular interest. Corals were identified in situ based on corallite structure, septal structure (where visible/possible) and growth form, among other features, with identifications being aided by relevant taxonomic literature (i.e., Hoeksema 1989; Veron 2000; Cairns 2001; Arrigoni et al. 2014; Mehrotra et al. 2023). The exception was with regard to the species *Porites lutea* Milne Edwards & Haime, 1851 and *P. lobata* Dana, 1846, which were not always distinguishable in situ and thus were grouped together in an effort to again provide emphasis on surveying a greater number of corals in situ. Gastropod parasites were identified with relevant available literature (i.e., Rudman 1981; Gittenberger and Gittenberger 2005; Gittenberger and Hoeksema 2013; Mehrotra et al. 2020) or in cases where specimens did not match any known species description, they were grouped by external morphological (and conchological) traits. In the case of epitoniid gastropods, external morphology alone may be insufficient to confirm identity. Molecular techniques, which herein are used solely for the delimitation of the species belonging to the genus *Phestilla*, may be needed to aid in the identification of epitoniid species (Gittenberger and Gittenberger 2005).

2.2 Sample collection and morphology

Specimens of parasitic gastropods on corals belonging to the genus *Acropora* Oken, 1815 were collected by SCUBA diving from coral reef habitats at depths ranging from 3 to 8 m. Individuals were photographed in situ with an Olympus TG-4 camera (Tokyo, Japan) with an underwater housing. For preservation for both molecular and morphological analyses, 95% ethanol was used. Specimens were determined by the collectors on site through in-situ photographs. An Olympus SZX16 stereomicroscope (Tokyo, Japan) was used to study the internal anatomy and to prepare glycerin slides for light microscopy of jaws, radula, and penis. For the purpose

Fig. 1 Map of surveyed sites around Koh Tao, with localities for *Phestilla arnoldi* Mehrotra & Caballer sp. nov. indicated in red. Shark Bay: type locality (holotype, paratypes). Tao Tong: locality of additional paratypes
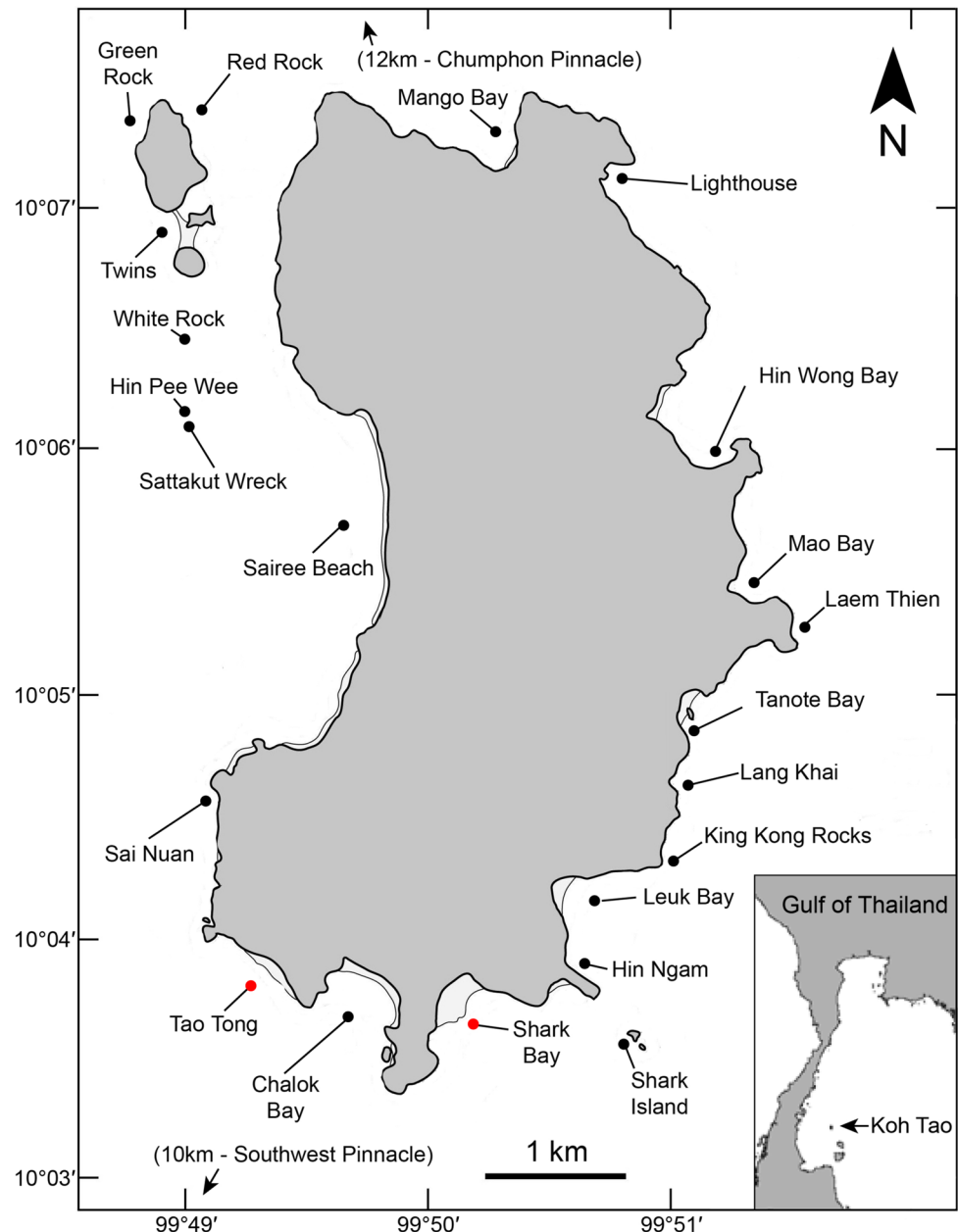
of comparison, diagrams were made of the jaws, cutting edge of the jaws, and radula. The dorsal surfaces were also prepared for microscopy to assess presence and state of possible microalgal symbionts. The holotype and paratype are deposited at the Muséum national d'Histoire naturelle (MNHN), Paris, France and the rest of the paratypes are deposited at the Eastern Marine and Coastal Resources Research Center (EMCOR), Rayong Province, Thailand.

2.3 DNA extraction, amplification, and sequencing

Tissue was taken from the ventral region of the foot of each specimen and DNA extracted using Qiagen DNeasy Tissue Kits. Primer sequences for partial sequences of cytochrome c oxidase subunit I (COI) were sourced from Folmer et al. (1994) using pairs LCO1490 (5′-GGTCAACAAATCATA AAGATATTGG-3′) and HC02198 (5′-TAAACTTCAGGG TGACCAAAAAATCA-3′). Partial sequences of the 16S rRNA region were amplified using primers from Palumbi et al. (1991) using the pairs 16Sar-L (5′-CGCCTGTTTATC AAAAACAT-3′) and reverse primer 16 s-xH (5′-CCGGTY TGAAMYYAGATCACGTAGG3′) from Mehrotra et al. (2020). Primers for the Histone 3 region were taken from Colgan et al. (2000) using the primers H3F (5′-ATGGCT CGTACCAAGCAGACVGC-3′) and H3R (5′-ATATCC TTRGGCATRATRGTGAC-3′). PCR was carried out using

ProFlex™ 3×32-well PCR System with a reaction volume of 20 µl. PCR protocol for the COI region was as follows: an initial denaturing step at 94 °C for 3 min; 40 cycles of denaturing at 94 °C for 30 s, annealing at 45 °C for 30 s, an extension at 72 °C for 1 min, followed by a final extension at 72 °C for 10 min. PCR protocol for the partial 16S region and the nuclear H3 region was: an initial denaturing step at 94 °C for 3 min; 40 cycles of denaturing at 94 °C for 30 s, annealing at 53 °C for 30 s, an extension at 72 °C for 1 min, followed by a final extension at 72 °C for 10 min. Electrophoresis was carried out using 0.5% TBE agarose gel. Purified aliquots were sent to Macrogen (Macrogen Sequencing Services: http://dna.macrogen.com/eng/) for sequencing.

2.4 Molecular analysis

Available sequences for multiple species of *Phestilla* were used for phylogenetic analyses, with the addition of several other species of the family Trinchesiidae and other additional related families used as outgroups. In addition to the two specimens of *Acropora*-feeding nudibranch sequenced for this study, sequences of other specimens were acquired from GenBank based on previous studies, with accession numbers available as supplementary data (Online Resource 2). All sequence metadata such as sample identifier and location were verified based on published material as primary quality control. Sequence alignment was carried out using BioEdit 7.2.5 (Hall 1999) and then reviewed manually. Phylogenetic analyses were carried out by performing both Maximum Likelihood (ML) analysis using MEGA X (Kumar et al. 2018), and Bayesian Inference (BI) using MrBayes 3.2 (Ronquist et al. 2012). An initial analysis was carried out using COI sequences only, followed by a second analysis of concatenated sequences of the COI, 16S and H3 regions. Optimum evolutionary models were selected using the model test feature within MEGA X. The optimum model used for analyses of COI and concatenated sequences was GTR+G+I. Analysis was conducted with 1000 bootstrap replicates and random starting trees. Bayesian inference analysis was conducted with 50,000,000 generations and four Markov chains that were sampled every 1000 generations. The first 25% generations were removed as burn-in with the rest being used to produce the 50% consensus tree.

2.5 Species delimitation

The pairwise distances for COI gene were calculated using the Kimura 2 parameters model implemented in MEGA X. We applied a 9% threshold to suggest a possible species delimitation criterion. Automatic Barcode Gap Discovery (ABGD) analyses (Puillandre et al. 2012) were conducted on the complete COI dataset without the outgroup. Three different ABGD analyses were performed to delineate species within the COI dataset. Each analysis was run using a different nucleotide substitution model, JC69, K80 2.0, and Simple Distance, with the settings Pmin=0.001, Pmax=0.1, Steps=10, X=1, Nb bins=20.

3 Results

3.1 Reef surveys

A total of 6566 corals (colonies or solitary individuals) belonging to 27 species were examined to host nudibranch or epitoniid gastropods. Of these, 283 corals (4.3%) were found to act as relevant hosts (Table 1), with seven of the 27 species not found to host gastropod ectoparasites. Of the 20 coral species with documented associations, the proportion of infected corals ranged from 0.5% of *Tubastraea micranthus* (Ehrenberg, 1834) colonies to 23.2% of *Turbinaria mesenterina* (Lamarck, 1816) colonies. A total of 13 species of ectoparasites were documented across the 283 affected corals, including nine species of *Phestilla* (Fig. 2) and four species of Epitoniidae (Fig. 3). Among the nudibranchs, two previously undescribed species were recorded, and also the species *P. poritophages*, which is here recorded for the first time from Thai waters. Only one of the four species of Epitoniidae was found to match an already described species, with the mushroom coral-associated species neither matching the descriptions of any known *Epifungium* or *Surrepifungium* species. Across the 283 infested corals, a total of 474 relevant gastropod individuals were recorded (Table 2). All gastropods documented were found in direct contact with living coral tissue or recently killed coral skeleton.

Among acroporid corals, the one hosting the highest number of ectoparasites was found to be *Acropora muricata* with 4% of 297 colonies assessed found with *Phestilla* sp. specimens (described below). Only one specimen was found among the remaining 215 colonies of three other coral species. The agariciid *Gardineroseris planulata* (Dana, 1846) was not found to host ectoparasites, while both assessed species of *Pavona* (also Agariciidae) shared remarkably similar proportions at 7.6% and 7.2% for *P. decussata* (Dana, 1846) and *P. explanulata* (Lamarck, 1816), respectively. The most intensively surveyed coral family was the Dendrophylliidae with ten assessed species and 3510 specimens, also hosting the greatest proportion of ectoparasitic gastropod individuals for a given host species. While more than 1000 colonies across four species of *Tubastraea* yielded a total of 10 infested corals, the 252 colonies of *Turbinaria* across three species revealed 40 colonies acting as host. Interestingly, both species of *Heteropsammia* Milne Edwards & Haime, 1848 showed differing trends with 6.5% of the 925 *H. cochlea* (Spengler, 1781) corals hosting a previously unidentified epitoniid
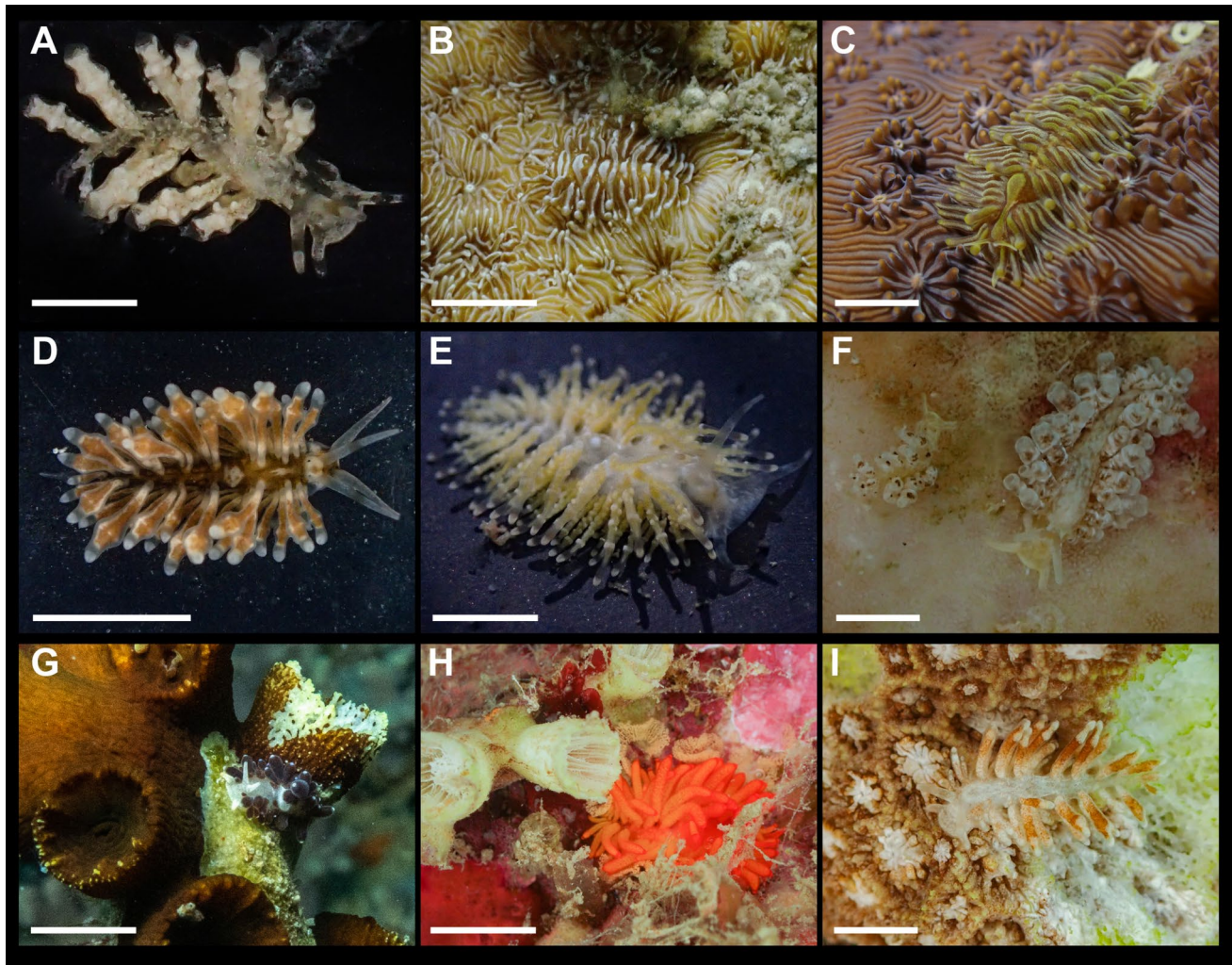
Table 1 Total number of corals (species-wise) surveyed for nudibranch and epitoniid parasitism, with the corresponding number of host coral colonies per *Phestilla* and epitoniid species encountered. Corals surveyed were colonies or solitary

Species	Total corals surveyed	Total Number of Corals hosting gastropods	% of Surveyed Colonies with Parasites	Number of host corals per *Phestilla* species									Number of host corals per epitoniid species			
				P. arnoldi Mehrotra & Caballer sp. nov.	*P. subodiosus*	*P. viei*	*P. fuscostriata*	*P. melanobrachia*	*Phestilla* sp.	*P. cf. minor*	*P. lugubris*	*P. poritophages*	Epitoniidae sp. 1	Epitoniidae sp. 2	*Epidendrium aureum*	Epitoniidae sp. 3
Acropora muricata	297	12	4.04	12	0	0	0	0	0	0	0	0	0	0	0	0
Acropora millepora	33	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0
Acropora florida	12	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0
Montipora aequituberculata	170	1	0.59	0	1	0	0	0	0	0	0	0	0	0	0	0
Pavona decussata	105	8	7.62	0	0	0	8	0	0	0	0	0	0	0	0	0
Pavona explanulata	461	33	7.16	0	0	33	0	0	0	0	0	0	0	0	0	0
Gardineroseris planulata	195	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0
Tubastraea micranthus	771	4	0.52	0	0	0	0	4	0	0	0	0	0	0	0	0
Cladopsammia gracilis	803	47	5.85	0	0	0	0	2	0	0	0	0	0	0	45	0
Tubastraea stimpsoni	46	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0
Tubastraea diaphana	103	2	1.94	0	0	0	0	2	0	0	0	0	0	0	0	0
Tubastraea coccinea	160	12	7.50	0	0	0	0	4	0	0	0	0	0	0	8	0
Turbinaria mesenterina	95	22	23.16	0	0	0	0	0	0	0	0	0	0	22	0	0
Duncanopsammia peltata	52	9	17.31	0	0	0	0	0	0	0	0	0	0	9	0	0
Turbinaria stellulata	105	9	8.57	0	0	0	0	0	0	0	0	0	0	9	0	0
Heteropsammia cochlea	925	60	6.49	0	0	0	0	0	0	0	0	0	60	0	0	0
Heteropsammia moretonensis	450	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0
Goniopora fruticosa	55	4	7.27	0	0	0	0	0	4	0	0	0	0	0	0	0
Goniopora stokesi	174	7	4.02	0	0	0	0	0	7	0	0	0	0	0	0	0
Porites lutea/lobata	405	41	10.12	0	0	0	0	0	0	21	19	1	0	0	0	0
Porites rus	136	3	2.21	0	0	0	0	0	0	2	1	0	0	0	0	0
Heterocyathus aequicostatus	221	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0
Paracyathus rotundatus	49	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungia fungites	312	6	1.92	0	0	0	0	0	0	0	0	0	0	0	0	6
Danafungia scruposa	145	1	0.69	0	0	0	0	0	0	0	0	0	0	0	0	1
Pleuractis moluccensis	64	6	9.38	0	0	0	0	0	0	0	0	0	0	0	0	6
Pleuractis paumotensis	222	4	1.80	0	0	0	0	0	0	0	0	0	0	0	0	4
Total	**6566**	**283**	**–**	**12**	**1**	**33**	**8**	**12**	**11**	**23**	**20**	**1**	**60**	**40**	**53**	**17**

Fig. 2 *Phestilla* spp. found in the present study (SB = scale bar). **A**: *P. subodiosa* (SB: 2 mm); **B**: *P. fuscostriata* Hu, Zhang, Xie & Qiu, 2020 (SB: 4 mm); **C**: *P. viei* (SB: 5 mm); **D**: *P. poritophages* (SB: 10 mm); **E**: *P. lugubris* (SB: 10 mm); **F**: *P.* cf. *minor* (SB: 5 mm); **G–H**: *P. melanobrachia* (SB: 6 mm and 10 mm, respectively); **I**: *Phestilla* sp. (SB: 5 mm)

parasite, while 450 of the smaller *H. moretonensis* Wells, 1964, which lives largely sympatrically with its congener, were found to host none. All surveyed species of Poritidae (or species pair in the case of *Porites lutea* and *P. lobata*) were found to host some ectoparasitic gastropods. In contrast, neither of genera of the family Caryophylliidae were found to host gastropod ectoparasites, which includes *Heterocyathus* Milne Edwards & Haime, 1848, found abundantly alongside its look-alike genus *Heteropsammia*.

The surveys yielded records of three previously undescribed *Phestilla* species (one of which is described in the present study), three seemingly undescribed species of epitoniid snail and the first record for *P. poritophages* in Thai waters. Among the ectoparasites, *Phestilla* spp. were found to have a greater degree of host specificity than epitoniid snails. Only three species of the genus were found to feed on multiple prey species, of which *P. lugubris* and *P.* cf.

minor were found on one and three colonies of *Porites rus* (Forskål, 1775), respectively, with the remaining host corals being *P. lutea/lobata*. The largest gastropod of the study, *Phestilla melanobrachia*, had the broadest range of hosts among all studied nudibranchs, including three species of *Tubastraea*, and the related species *Cladopsammia gracilis*, representing a new host record. Meanwhile, three of the four epitoniids were found to feed on multiple coral species, with Epitoniidae sp. 2 found on *Duncanopsammia peltata* (Esper, 1790) and both surveyed species of *Turbinaria*. Similarly, *Epidendrium aureum* was recorded feeding on *C. gracilis* and *Tubastraea coccinea*, and Epitoniidae sp. 3 was found associated with multiple species of Fungiidae in the genera *Fungia*, *Danafungia* and *Pleuractis*.

The gastropods that were found with the highest density on host corals (Table 2) were *Phestilla* sp. 2 on *Goniopora stokesi* Milne Edwards & Haime, 1851 with an average of

Fig. 3 Epitoniidae spp. found in the present study (SB = scale bar). **A**: Epitoniidae sp. 1 on host *Heteropsammia cochlea* (SB: 5 mm); **B**: Epitoniidae sp. 1 separated from host (SB: 2 mm); **C**: Epitoniidae sp. 2 on host *Turbinaria stellulata* (SB: 25 mm); **D**: Epitoniidae sp. 2 separated from host (SB: 2 mm); **E**: Epitoniidae sp. 3 on host *Pleuractis moluccensis* (Van der Horst, 1919) (SB: 7 mm); **F**: Epitoniidae sp. 3 separated from host (SB: 2 mm); **G**: *Epidendrium aureum* Gittenberger & Gittenberger, 2005 on host *Cladopsammia gracilis* (Milne Edwards & Haime, 1848) (SB: 7 mm)
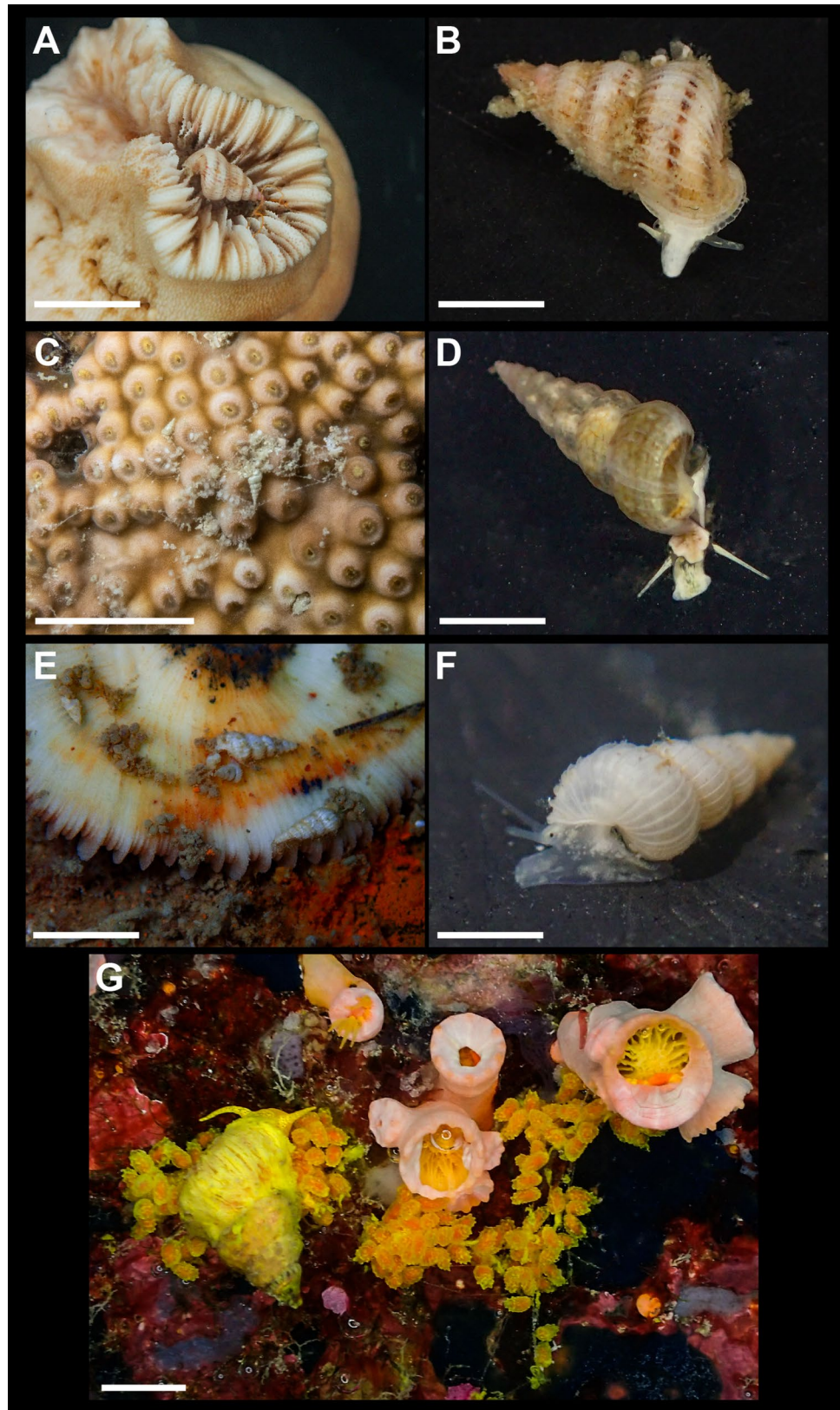
Table 2 Total number of corals (species-wise) surveyed for nudibranch and epitoniid parasitism, with the corresponding number of associated gastropods per host colony

Species	Total colonies surveyed	Mean no. of gastropods per infected host	Total number of individual gastropods per prey coral species									Total number of associated gastropods per host colony			
			P. arnoldi Mehrotra & Caballer sp. nov.	P. subodiosus	P. viei	P. fuscostriata	P. melanobrachia	Phestilla sp.	P. cf. minor	P. lugubris	P. poritophages	Epitoniidae sp. 1	Epitoniidae sp. 2	Epidendrium aureum	Epitoniidae sp. 3
Acropora muricata	297	3.50	42	0	0	0	0	0	0	0	0	0	0	0	0
Acropora millepora	33	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0
Acropora florida	12	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0
Montipora aequituberculata	170	1.00	0	1	0	0	0	0	0	0	0	0	0	0	0
Pavona decussata	105	4.13	0	0	0	33	0	0	0	0	0	0	0	0	0
Pavona explanulata	461	1.64	0	0	54	0	0	0	0	0	0	0	0	0	0
Gardineroseris planulata	195	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0
Tubastraea micranthus	771	1.00	0	0	0	0	4	0	0	0	0	0	0	0	0
Cladopsammia gracilis	803	1.02	0	0	0	0	2	0	0	0	0	0	0	46	0
Tubastraea stimpsoni	46	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0
Tubastraea diaphana	103	1.00	0	0	0	0	2	0	0	0	0	0	0	0	0
Tubastraea coccinea	160	1.00	0	0	0	0	4	0	0	0	0	0	0	8	0
Turbinaria mesenterina	95	1.86	0	0	0	0	0	0	0	0	0	0	41	0	0
Duncanopsammia peltata	52	1.00	0	0	0	0	0	0	0	0	0	0	9	0	0
Turbinaria stellulata	105	1.33	0	0	0	0	0	0	0	0	0	0	12	0	0
Heteropsammia cochlea	925	1.05	0	0	0	0	0	0	0	0	0	63	0	0	0
Heteropsammia moretonensis	450	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0
Goniopora fruticosa	55	1.25	0	0	0	0	0	5	0	0	0	0	0	0	0
Goniopora stokesi	174	5.14	0	0	0	0	0	36	0	0	0	0	0	0	0
Porites lutea/lobata	405	1.88	0	0	0	0	0	0	47	29	1	0	0	0	0
Porites rus	136	1.33	0	0	0	0	0	0	3	1	0	0	0	0	0
Heterocyathus aequicostatus	221	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0
Paracyathus rotundatus	49	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungia fungites	312	1.83	0	0	0	0	0	0	0	0	0	0	0	0	11
Danafungia scruposa	145	2.00	0	0	0	0	0	0	0	0	0	0	0	0	2
Pleuractis moluccensis	64	2.33	0	0	0	0	0	0	0	0	0	0	0	0	14
Pleuractis paumotensis	222	1.00	0	0	0	0	0	0	0	0	0	0	0	0	4
Total	**6566**	**–**	**42**	**1**	**54**	**33**	**12**	**41**	**50**	**30**	**1**	**63**	**62**	**54**	**31**

5.1 individuals per host, and *P. fuscostriata* with an average of 4.1 individuals per host. Most host corals were found to survive presence of associated gastropods, however, a number of associations revealed numerous host corals to have their tissue mostly or completely consumed. The nudibranch *P. melanobrachia* was found to completely consume between 5 and 50% of the host corals on which they were found (Online Resource 1), with all other nudibranchs resulting in <5% of hosts being consumed completely. Similarly, the epitoniid snail *Epidendrium aureum* was found to consume between 5 and 50% of its host corals, and Epitoniidae sp. 1 was found to consume over 5% of its *Heteropsammia cochlea* hosts. The remaining snails were not observed to completely consume their hosts.

3.2 Molecular results

Two specimens of *Phestilla* sp. (described below as a new species) found on *Acropora* corals were successfully sequenced for COI, 16S and H3 regions. The total COI dataset used for the phylogenetic inference, p-distance calculations and ABGD analyses included 48 sequences and was 603 bp in length, while the total concatenated dataset used in phylogenetic analysis included 135 sequences representing 45 specimens and was 1400 bp in length. The tree generated from the COI dataset was found to be well resolved with ML (Fig. 4), with strong support values for most species. The BI analysis resulted in well supported species-level groups but poorly resolved most major clades as polytomies. The concatenated dataset however, provided almost identical topologies in ML and BI analyses (Fig. 5), with some differences in position of outgroups. In all four analyses (ML and BI with COI only and concatenated), *Phestilla arnoldi* Mehrotra & Caballer sp. nov. was strongly supported as distinct from all other presently sequenced species, forming a well-supported clade with *Phestilla subodiosa* Wang et al., 2020. Additionally, the genus *Phestilla* was recovered as a monophyletic group with strong support in the BI analyses (PP = 1), however, with weak support in ML (BS = 0.42). As with other recent analyses, *P. minor* was found to be a complex of species, alongside *Phestilla* sp. 1, and *P. chaetopeterana* (Ekimova et al. 2019) was found to be the earliest diverging species of the presently described taxa. Uncorrected pairwise distance analysis of the COI dataset found *P. subodiosa* to have lowest distance values to *P. arnoldi* Mehrotra & Caballer sp. nov., ranging from 9% - 10%, with all other *Phestilla* species ranging from 12% to 20%. ABGD analyses revealed 18 different partitions, with *P. arnoldi* Mehrotra & Caballer sp. nov. consistently resulting as distinct from all other species.

3.3 Systematics

Order Nudibranchia Cuvier, 1817
Superfamily Fionoidea Gray, 1857
Family Trinchesiidae Nordsieck, 1972
Genus *Phestilla* Bergh, 1874
Phestilla arnoldi Mehrotra & Caballer sp. nov.
http://zoobank.org/AD8395CC-A780-4D0F-B8AA-DF058311C6AF

Phestilla sp. 2: Mehrotra et al. 2021: Fig. 21G.

Holotype: adult, 4 mm long alive, 2.5 mm long after preservation, collected from the surface of host coral *Acropora muricata* (Linnaeus, 1758) at 5 m depth, in Shark Bay (type locality), 10°3'39.75"N, 99°50'4.43"E, Koh Tao, Thailand, June 4, 2019, deposited in MNHN (MNHN-IM-2000-38763). Paratype 1: adult, 3.5 mm long alive, 2 mm long after preservation, collected from the surface of host coral *A. muricata* at 4 m depth, in Tao Tong, 10°3'58.13"N, 99°49'4.76"E, Koh Tao, Thailand, March 6, 2019, deposited in MNHN (MNHN-IM-2000-38764). Paratype 2: adult, 4 mm long alive, 2 mm long after preservation, collected from the surface of host coral *A. muricata* at 7 m depth, in Shark Bay (type locality), 10°3'39.75"N, 99°50'4.43"E, Koh Tao, Thailand, August 27, 2019, deposited in EMCOR (ATMEC23S01). Paratype 3: adult, 4 mm long alive, 2 mm long after preservation, collected from the surface of host coral *A. muricata* at 7 m depth, in Shark Bay (type locality), 10°3'39.75"N, 99°50'4.43"E, Koh Tao, Thailand, June 4, 2019, deposited in EMCOR (ATMEC23S02).

3.3.1 Complementary observations

Precisely 38 specimens, ranging between 1 and 4 mm (alive), observed (and not collected) as part of the present surveys, all from the type locality (Shark Bay, 10°3'39.75"N, 99°50'4.43"E) or the locality where paratype 1 was collected (Tao Tong, 10°3'58.13"N, 99°49'4.76"E) at Koh Tao, Thailand.

3.3.2 Etymology

Phestilla arnoldi Mehrotra & Caballer sp. nov. is named in honour of Mr. Spencer Arnold for his discovery of this highly cryptic species at Koh Tao, alongside contributing significantly to ectoparasite observations and records at Koh Tao during the survey period. In addition, Mr. Arnold has supported marine biology education and research, and has played an important role in biodiversity monitoring at Koh Tao and elsewhere.

Fig. 4 Phylogeny reconstruction for the genus *Phestilla* based on sequences of the cytochrome oxidase 1 (COI) gene, with prey/host families of specimens highlighted. Bootstrap support values for maximum likelihood analysis (ML) and posterior probabilities for Bayesian inference (BI) shown as ML/BI. Support values <0.75 are not shown. All sequences except those of *Phestilla arnoldi* Mehrotra & Caballer sp. nov. were sourced from GenBank
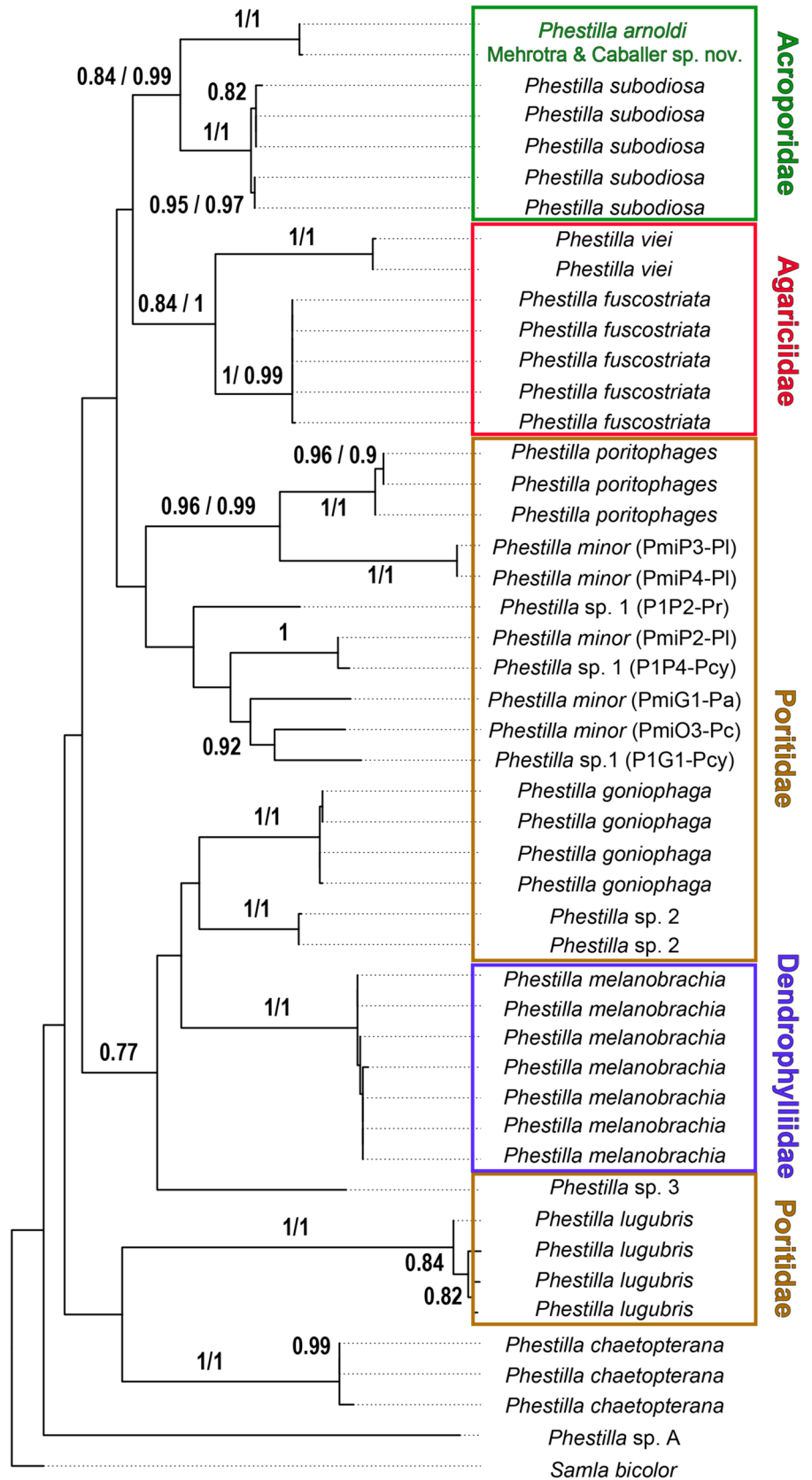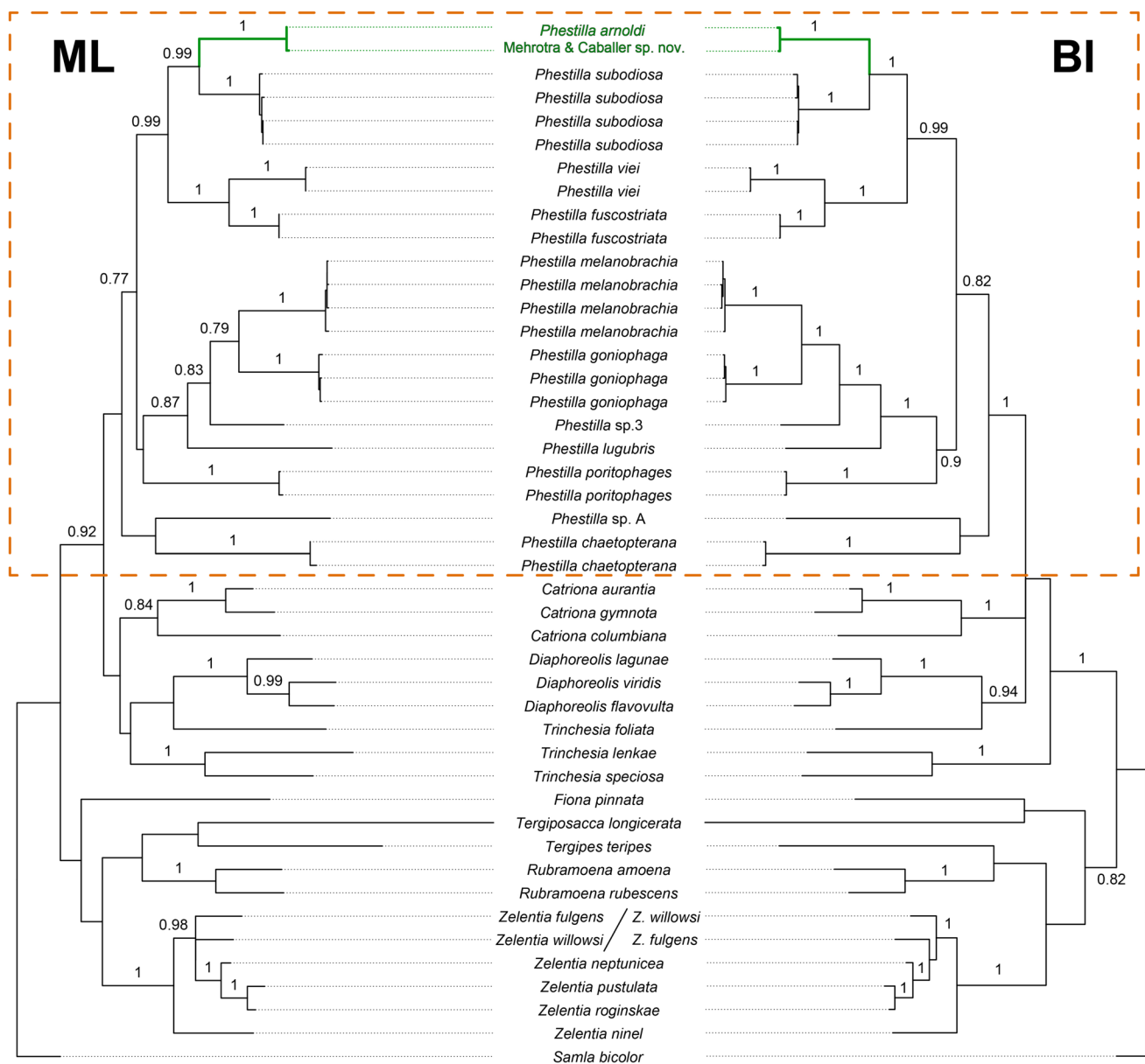
Fig. 5 Phylogenetic trees including the genus *Phestilla* and other related taxa based on concatenated sequences of COI, 16S and H3 regions. *Phestilla* is delineated by a dashed orange line. Bootstrap support values for maximum likelihood analysis (ML) on the left and posterior probabilities for Bayesian inference (BI) shown on the right. Support values <0.75 are not shown. Topological differences on branch placement between ML and BI for *Zelentia fulgens* and *Z. willowsi* marked with a slash. All sequences except those of *Phestilla arnoldi* Mehrotra & Caballer sp. nov. were sourced from GenBank

3.3.3 Diagnosis

Body translucent white with opaque white to yellowish spots. Oral tentacles more than half the length of the rhinophores, both bearing two wide white bands. Snout covered by a characteristic opaque white rectangular patch. Anterior end of the foot rounded. Cerata arranged in rows, the first two separated from the posterior ones. Cerata elongated and slender, with a big distal groove and two smaller ones: one subapical and another basal, each marked with an opaque white ring. Gonopore on the right side below first row of cerata. Anal papilla surrounded by an opaque white line, ahead of first cerata of the third right row. Radular formula: $17 \times 0.1.0$. Radular teeth long and narrow, with a prominent central cusp and 3–6 smaller narrow denticles on each side. Feeding on *Acropora muricata* (Linneaus, 1758).

3.3.4 Description

Length alive up to 4 mm, most specimens found smaller. Body elongate, not slender, slightly widened (Fig. 6). Rhinophores smooth, conical, long, held separated in "V", tapering gradually towards more or less rounded apices. Oral tentacles smooth, more than half the length of the rhinophores, usually pointing outwards. Eyes black, moderately big, visible behind and to the outside of each rhinophore. Anterior end of foot rounded. Foot sole smooth and moderately broad, sometimes extending beyond the body wall, tapering to a point at the tail. Tail long and narrow, representing almost one third of the total length. Cerata arranged in four rows, the first two notably separated from the posterior ones, with a fifth row emerging in large specimens. Each row composed of 3; 3; 3; 2; and 1 cerata (Fig. 7A). Cerata elongated and slender, with a large, sometimes flattened, bulge in the upper end followed by a second smaller subapical bulge which is globose and conspicuous. Cerata with a smooth surface, possessing a single big distal groove and two smaller ones: one subapical and another basal (Fig. 7B: cerata after preservation). Pericardium indistinct, between first and second rows of cerata. Digestive glands inside cerata not ramified. Penial papilla very small, rounded, wide and short, on the right side, below first row of cerata (Fig. 7A). Anal papilla short, ahead of the first cerata of the third right row (Fig. 7A).

Jaws translucent amber, flexible, coriaceous, non-calcified, 390 µm long, 260 µm wide in the holotype (Fig. 7C). Cutting edge with a row of 12-13 simple conical teeth that occupy 41 µm of the total length (Fig. 7D). Radular formula: $17 \times 0.1.0$ (holotype). Radular teeth long and narrow, 46 µm long, 26 µm wide in the holotype, with a prominent central cusp and 3-6 narrow denticles on each side, usually 5 (Fig. 7E). Denticles bigger the closer they are to the central cusp, which sometimes has some small denticles surrounding it.

3.3.5 Coloration

Body translucent white with opaque white to yellowish spots, which may aggregate to form lines and bands (Fig. 6A-C). Foot sides transparent with small patches of opaque white spots. Rhinophores and oral tentacles translucent white at the basal half and translucent reddish orange at the apical half, though reddish orange pigment is largely absent in smaller specimens. Translucent rhinophores further separated by two wide white bands formed by opaque white spots: one medial and the other one sub apical or apical. Snout covered by a characteristic opaque white rectangular patch connecting both rhinophores and both tentacles with straight lines and the rhinophore and the palp on each side with curved lines. Dorsum and sides

of the body covered with irregular patches of spots. Sides of the body may show a white line connecting the base of the cerata and the anal papilla, and a triangular path on each side of the snout. Cerata translucent white with two rings of opaque white to yellowish spots coinciding with each bulge. Digestive glands inside cerata range from white to bright green to brown/reddish brown depending on the density of symbiodiniacean endosymbiont cells. This same pigmentation, based on endosymbiont density, is seen as a distinctive band running from beneath the outside of each rhinophore, under each eye before ramifying into the digestive gland of each ceras.

3.3.6 Biology

All animals were observed between March and September during survey years at one of two locations, Shark Bay or Tao Tong, Koh Tao, exclusively on their host coral *Acropora muricata* (Fig. 6D, E). Animals found at depths from 3 to 8 m predominantly on parts of colonies that appeared to show stress (localised bleaching or tissue loss) though always with some healthy tissue in within a centimetre of the nudibranch. No observations were made from soft-sediment habitats nor on any other substrate other than that of the coral *Acropora muricata*, on which it is extremely cryptic. The spawn capsules (Fig. 6E) are amorphous to oblate spheroid structures between 0.5 and 1 mm, containing 12–22 white to pale yellow eggs each. Capsules appear to be placed haphazardly on recently killed coral skeletons and rarely exceed 4 in number at any given time. Eggs highly cryptic on the white of coral skeletons. Living animals acquire most of their limited coloration due to dense aggregations of zooxanthellae in their tissues taken from their host coral.

3.3.7 Distribution

Presently only known from its type locality, Koh Tao, Gulf of Thailand.

3.3.8 Remarks

Phestilla arnoldi Mehrotra & Caballer sp. nov. is the smallest known *Phestilla* species (and among the smallest known nudibranchs) to date, with most adult specimens found approximately 3 mm in length. The external morphology of *P. arnoldi* Mehrotra & Caballer sp. nov. resembles that of a member of the genus *Eubranchus* Forbes, 1838 (family Eubranchiidae), but the internal anatomy and the genetic evidence indicate otherwise, placing it in the genus *Phestilla*. All currently known species of *Phestilla* are readily distinguished from *P. arnoldi* Mehrotra & Caballer sp. nov. based on their radulae, cerata and size. Most presently
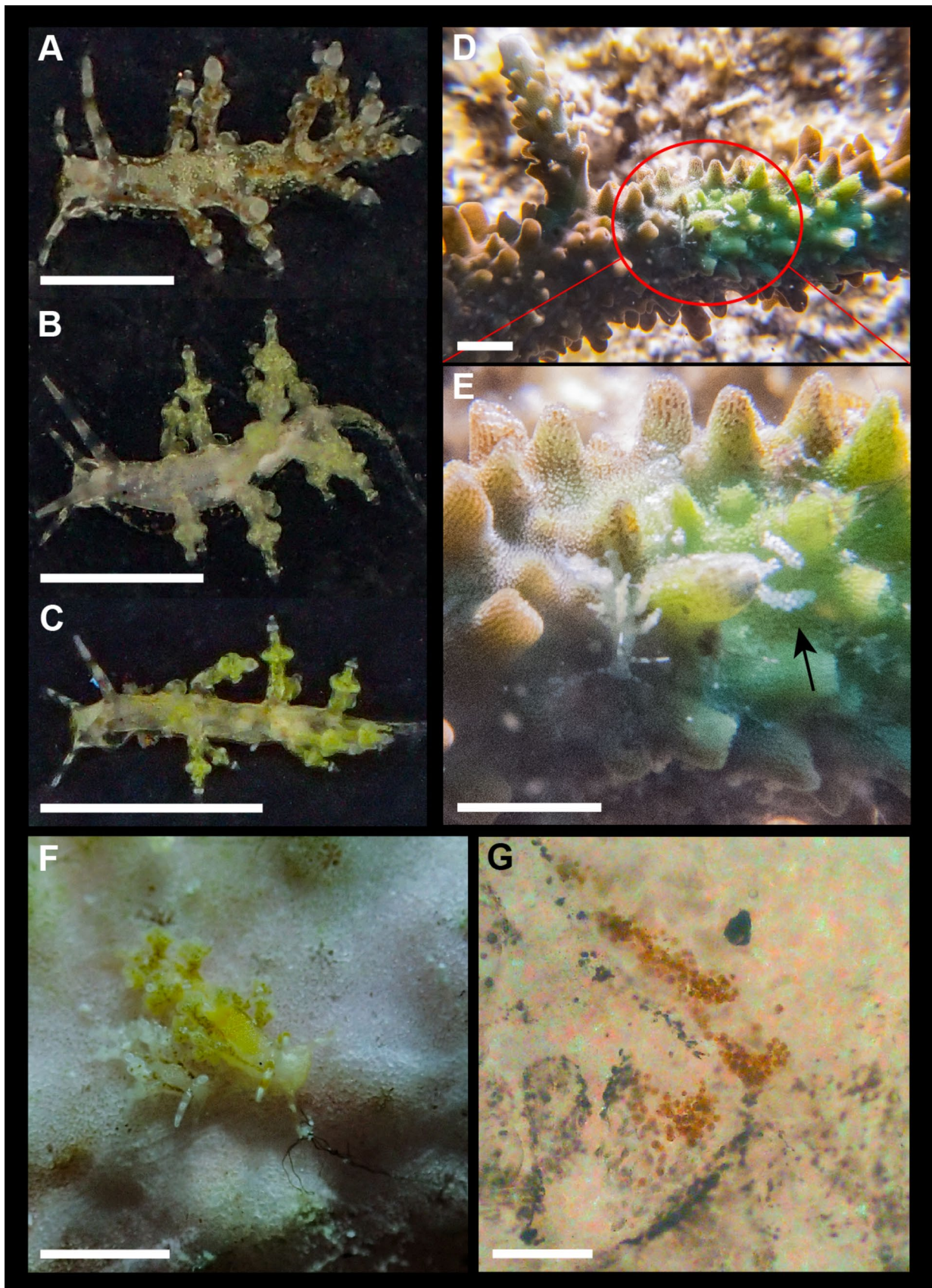
◄**Fig. 6** *Phestilla arnoldi* Mehrotra & Caballer sp. nov. **A**–**C**: Pigmentation differences as mediated by recent feeding and the relative presence of endosymbiotic Symbiodiniaceae. **D**–**F**: Specimens in situ on their *Acropora* host, egg bundles indicated by black arrow. **G**: Right-anterior of a specimen under light microscopy with living Symbiodiniaceae cells along lateral digestive ducts, with an eye visible in the top right. Scale bars: **A**, **B** = 1 mm; **C** = 2 mm; **D**, **E** = 4 mm; **F** = 2 mm; **G** = 0.1 mm

described species of *Phestilla* either have radulae with teeth bearing long lateral denticles decreasing in size towards the central cusp (*P. lugubris* (Bergh, 1870), *P. melanobrachia* Bergh, 1874 and *P. poritophages* (Rudman, 1979)) or a distinctly shortened or absent central cusp (*P. fusostriata* Hu, Zhang, Xie & Qiu, 2020 and *P. viei* Mehrotra, Caballer & Chavanich, 2020). All non-*Pavona*-feeding species (*P. chaetopterana, P. melanobrachia, P. goniophaga* Hu, Zhang, Xie & Qiu, 2020, *P. rebus* Er. Marcus & Ev. Marcus, 1960, *P. lugubris, P. minor* Rudman, 1981 s. str., *P. panamica* Rudman, 1982 and *P. poritophages*) further possess recurved lateral denticles or minor denticles between major denticles on either side of the central cusp, features which are not found in *P. arnoldi* Mehrotra & Caballer sp. nov. Furthermore, all other known species of *Phestilla* possess longer bodies in adults with more rows of cerata, which in several species are held laterally giving a dorsoventrally flattened appearance.

Phestilla subodiosa is the sister species of *P. arnoldi* Mehrotra & Caballer sp. nov. and the one that most closely resembles it, sharing a diminutive size of up to 5 mm (Yiu and Qiu 2022) and zooxanthellae-derived pigmentation. However, both species are distinguished by their rhinophores, cerata and radulae. The rhinophores in *P. arnoldi* Mehrotra & Caballer sp. nov. are twice the length of the oral tentacles and possess distinctive white bands, whereas *P. subodiosa* possesses proportionally shorter rhinophores, similar in size to the oral tentacles, with a single brown median band. Furthermore, *P. arnoldi* Mehrotra & Caballer sp. nov. possesses four rows of cerata with a vestigial fifth row only in the largest specimens (>3.5 mm), each ceras possessing grooves and with the largest of the two bulges often reaching twice the diameter of the rest of the ceras. In comparison, *P. subodiosa* has up to five or six distinct rows of cerata, with each ceras bearing a pair of tapered bulges that are less prominent than those of *P. arnoldi* Mehrotra & Caballer sp. nov.. Internal differences between the species include the radulae, with the teeth of *P. arnoldi* Mehrotra & Caballer sp. nov. having a prominent central cusp and lateral denticles reducing in size from the cusp. In comparison *P. subodiosa* possesses teeth with a central cusp much more similar in size to the lateral denticles, which do not reduce in size considerably further from the cusp. The jaws of *P. arnoldi* Mehrotra & Caballer sp. nov. appear to be elongated with a distinct cutting edge, whereas *P. subodiosa* has wider and seemingly more

rounded jaws, with nothing yet known of its cutting edge. By far the most reliable distinguishing feature between the two species (or with any other *Phestilla*) is their ecology, with both species preying exclusively on different acroporid genera, with *P. subodiosa* being associated with *Montipora peltiformis* Bernard, 1897 (Wang et al. 2020; Yiu and Qiu 2022).

The nudibranch *Phyllidia bourgini* Risbec, 1928, a junior synonym of *Phyllidiella rosans* (Bergh, 1873), is another nudibranch that has been recorded as consuming *Acropora* (Vicente 1966; Salvini-Plawen 1972), but this is based on a single, doubtful observation (Robertson 1970). Species of the genera *Phyllidia* Cuvier, 1797 and *Phyllidiella* Bergh, 1869 are well-known as sponge eaters on Indo-Pacific reefs (van Alphen et al. 2011; Papu et al. 2020).

4 Discussion

4.1 On the ecology of parasites and predators

The presently described species, *Phestilla arnoldi* Mehrotra & Caballer sp. nov. bears considerable similarity to its sister species, *P. subodiosa*, which is perhaps unsurprising given the relatedness of prey species and the prevailing hypotheses regarding diversification within the genus. The extent of host specificity, the resulting morphological and developmental variability, and thus the evolutionary implications in *Phestilla* nudibranchs have been investigated with increasing frequency in recent decades (Rudman 1981; Ritson-Williams et al. 2003; Faucci et al. 2007; Fritts-Penniman et al. 2020; Yiu et al. 2021; Yiu and Qiu 2023). This wealth of information has allowed for a deeper understanding in the complex relationships between *Phestilla* spp. and their prey. For example, some species appear to be highly host-specific, such as *Phestilla fuscostriata* and *P. viei*, which each appear to prey only on a single species of *Pavona*, whereas others, such as *P. melanobrachia*, may feed on corals representing multiple related genera within a single family. It should be noted that we did not observe any individuals of *P. melanobrachia* feeding on *Duncanopsammia* corals, despite recent findings (Yiu et al. 2021) and their abundance in our surveys, which may add further evidence to indicate that prey specificity is influenced by biogeography in addition to prey availability. Furthermore, larval metamorphosis and settlement appear to be triggered by the presence of highly specific prey types (Faucci et al. 2007; Yiu and Qiu 2022), and radular morphology appears to vary consistently with prey type (i.e., reduced/absent central cusp in *Pavona* feeders). The growing body of evidence showing that *Phestilla* diversification is strongly mediated by host shifting from one coral to another, combined with the recent discovery of various new species (Mehrotra et al. 2020; Hu et al. 2020; Wang et al. 2020), may
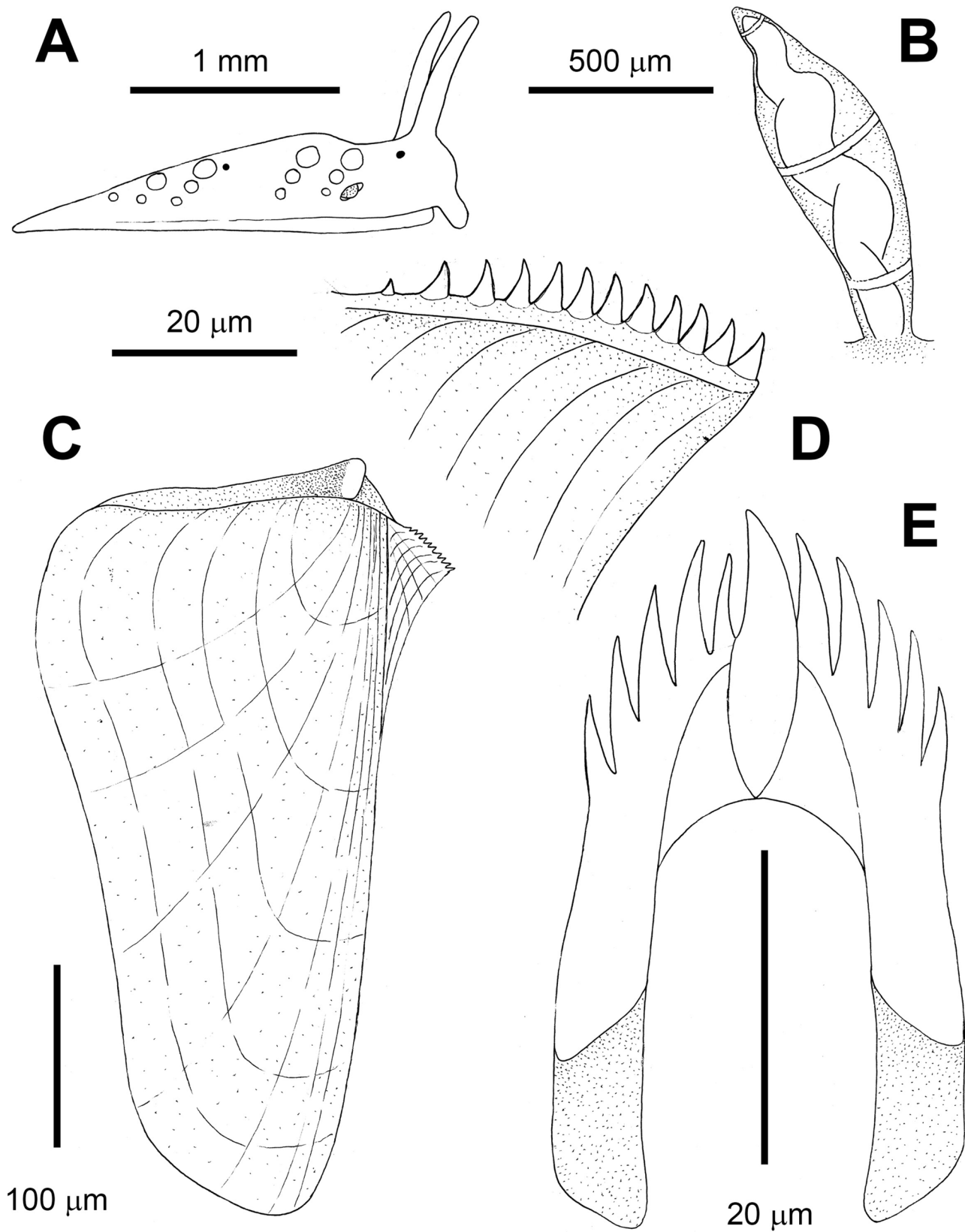
Fig. 7 *Phestilla arnoldi* Mehrotra & Caballer sp. nov., holotype. **A**: Scheme of the animal in lateral view, showing position of cerata. **B**: Cerata showing lateral grooves. **C**: Jaws. **D**: Cutting edge of jaws. **E**: Radular tooth

indicate a wealth of coral associated nudibranchs yet to be found. It is thus pertinent to explore further the ecological role of these and other coral-associated gastropods.

Historically, Scleractinia-associated Epitoniidae and nudibranchs have been considered as corallivorous ectoparasites (Gittenberger and Hoeksema 2013). Classifying and separating organisms between 'parasite' and 'predator' serves the purpose of attributing certain ecological assumptions to a given role with respect to its prey (Hassel 1966; Hatcher et al. 2006; Thieltges et al. 2013). Several ectoparasite species surveyed in the present study were found most often in direct association with stressed or damaged host-coral tissue (*P. arnoldi* Mehrotra & Caballer sp. nov., *P. subodiosa*, *P. lugubris*, *P. fuscostriata*, and *P.* cf. *minor*) whereas other species (*P. viei*, *P. melanobrachia*, and Epitoniidae spp.) were typically found with visible feeding scars on otherwise healthy (when not largely consumed) corals. The direct tissue damage caused by ectoparasites, being less than larger predators, may result in less noticeable adverse effects such as reduction in host fitness, coral microbiome dysbiosis, compromised reproduction, and diseases (Hudson et al. 2006; Rotjan and Lewis 2008; Clements et al. 2020). Corallivores have been increasingly found to be associated with the proliferation in coral disease (Nicolet et al. 2018; Montano et al. 2022; Renzi et al. 2022). While studies have been limited, the genus *Phestilla* too has been conclusively shown to act as a vector for coral pathogens and contribute to the spread of disease under ex-situ conditions (Dalton and Godwin 2006).

Additionally, marine gastropods may also act as vectors for other parasites when they move between hosts (Mouritsen and Jensen 1997). The prevalence of ectoparasites on damaged and stressed tissue in our study reinforces the hypothesis raised by others that such a behaviour may further contribute to the spread of pathogens and stressors (Dehnert et al. 2022; Renzi et al. 2022). Therefore, while the ecology and direct impact of ectoparasites may differ from predators in general, their ability to significantly influence life strategies of corals may be distinct from but just as important as those of non-parasitic predators (Mikheev et al. 2020). In addition, metabolic implications of parasitism include parasites stealing food from the host, as suggested by the presence of an epitoniid living inside the gastric cavity of a sea anemone (den Hartog 1987). A similar kleptoparasitic relationship has also been suggested as feeding mechanism for *Phestilla chaetopterana* (Ekimova et al. 2019). A recent variation of kleptoparisitism, termed 'kleptopredation' has been documented by the nudibranch *Cratena peregrina* (Gmelin, 1791) with regard to its relationship with its hydrozoan prey/hosts (Willis et al. 2017). Ectoparasitic snails are not known to cause damage to the host coral's skeleton,

in contrast to endoparasitic gastropods that do not feed on their host's soft tissue but reside inside their skeleton, either inside galls, such as *Leptoconchus* spp. (Hoeksema and Gittenberger 2008; Gittenberger and Gittenberger 2011), or partially embedded and wounding the host's upper surface, such as some vermetid worm snails (Hoeksema et al. 2022; Bieler et al. 2023).

Discussions on the merits or challenges of studying mollusc parasites and predators as corallivores have been carried out for decades (Hassell 1966; Raffel et al. 2008), however, such discussions are notably sparse in the literature (Gittenberger and Hoeksema 2013). Broadly, our findings reinforce the assertions by Raffel et al. (2008) that state that a single organism may be identified as both a parasite and a predator, however one does not preclude the other. Thus, while the gastropods discussed in the present study were found to be corallivorous, based on the observations of active feeding, we noted that the impact on the 'host' coral appeared to vary considerably. For example, our observations found that snails of *P. melanobrachia* and *E. aureum* were able to completely consume multiple colonies of their prey corals, which were notably among the smallest of prey colonies hosting among the largest of the studied gastropods. These prey items were the species *Cladopsammia gracilis*, *Heteropsammia cochlea*, *Tubastraea coccinea* and *T. diaphana*, and were the only species consumed entirely in the present study. An example of soft tissue consumption of a small colony of *T. coccinea* being entirely eaten by *Epidendrium billeeanum* (DuShane & Bratcher, 1965) has been reported from the East Pacific (Rodríguez-Villalobos et al. 2016). This would then indicate that both *P. melanobrachia* and *Epidendrium* spp. may occasionally be considered to be predators, but not parasites, as by consuming the prey they are unable to influence the coral in many of the ways typically associated with parasites. Furthermore, this suggests that the size ratio between host and gastropod may determine the probability that a given host may be entirely consumed or not (Online Resource 1). Interestingly, the gastropod associated with *H. cochlea*, Epitoniidae sp. 1, was smaller than many other gastropod ectoparasites, however, the host coral was also the smallest of those studied. A single example of *Phestilla lugubris* individuals on an entirely bleached and mostly consumed colony of *Porites lutea/lobata* was also recorded, however, it is unclear whether this was caused by the gastropod. Nonetheless, these cases indicate that all corallivorous gastropods at Koh Tao may be considered varying degrees of parasitic potential, ranging from none (i.e. *Drupella* spp.), to some (i.e. *P. melanobrachia* and *E. aureum*) to considerable (i.e. *Phestilla viei*) based on their capacity to entirely consume their host.

A second possible contributing factor is the proportion of gastropods on a single host. Several species were

regularly found in small groups on a single host, such as *Phestilla arnoldi* Mehrotra & Caballer sp. nov., *Phestilla fuscostriata*, *Phestilla* sp., *Phestilla* cf. *minor*, Epitoniidae sp. 2 and Epitoniidae sp. 3, which may contribute to the risk of host corals to be consumed. While our findings suggest that larger gastropods were more likely to consume hosts entirely and were more likely occurring alone or in smaller aggregations than smaller gastropods, rapid population increases have been found to lead to mortality of coral hosts under ex situ conditions. While widespread infestation and coral-health impacts in situ by associated gastropods remains rare, records show a growing number of cases of significant coral loss in aquaria and other ex situ environments (Barton et al. 2020; Wang et al. 2020; Cabrito et al. 2022; Knapp et al. 2022). These cases highlight the potential impact of outbreaks driven by large aggregations of gastropods typically seen feeding on relatively small amounts of coral tissue. Certainly, host mortality driven by a proliferation of parasites is not a novel concept in the study of ecology. Resource-use strategies may differ considerably between obligate and facultative parasites in coral reef communities, with increased host availability reinforcing population growth and thus increasing the potential for population outbreaks (Mikheev et al. 2020). Therefore, the size of a given coral host may determine its capacity to host larger gastropods or larger aggregations of gastropods, and thus may be a useful indicator for the potential of an associated gastropod to shift from a parasite to a predator response to hosts. This may have implications on the potential threat of such gastropods on the survival of juvenile coral recruits or corals which may not grow to form large colonies. A recent example of this documented complete colony loss in small colonies of *Porites rus* due to predation by what appears to be *Phestilla lugubris* at in situ coral nurseries in the Maldives (Dehnert et al. 2022). Similarly, it has been shown that certain epitoniid species, while parasitic on larger anemones, may entirely consume juveniles (Thorson 1957). Typically, the prevailing perspectives suggest that the interaction between a parasite and its host is longer than an interaction between a predator and a prey (Raffel et al. 2008).

To date, little work has been done to evaluate in-situ population control measures on gastropod ectoparasites of corals, however, there is evidence that species of butterflyfish in the genus *Chaetodon* and wrasses in the genus *Thalassoma* may help control populations of *Phestilla* nudibranchs (Gochfeld and Aeby 1997). Wrasses and damselfish too have been found to predate upon exposed epitoniid gastropods associated with mushroom corals (Gittenberger and Hoeksema 2013), though these gastropods have thus far only been recorded under 'upright' mushroom corals at Koh Tao (Scott et al. 2017c).

Additionally, *Thalassoma* wrasses have been documented to opportunistically feed on sea slugs at Koh Tao (Mehrotra et al. 2019), however, predation on coral-associated gastropods was not documented.

4.2 Implications for biodiversity loss and conservation

The impact of extensive corallivory and outbreaks of invertebrate corallivores continue to be topics of concern in modern coral reef studies (Bruckner et al. 2017; Pratchett et al. 2021). In Thailand, the majority of observations and investigations have originated at Koh Tao (Hoeksema et al. 2013; Moerland et al. 2016). Outbreaks and significant coral mortality have been documented by the crown-of-thorns sea star (*Acanthaster* sp.) as well as gastropods in the genus *Drupella* (Scott et al. 2017a). Both groups of predators were found to have broad dietary preferences and the capacity to consume the entirety of multiple coral types. The reefs of Koh Tao have additionally been shown to be threatened by disease (Lamb et al. 2014), epibiosis (Stuij et al. 2023; Allchurch et al. 2022) and the increasing regularity of coral bleaching events (Scott et al. 2017b). Furthermore, there are indications that it is not only the abundance of these reefs that may be threatened, but also their heterogeneity, with shifts in coral community structure reducing biodiversity and habitat complexity (Scott et al. 2017b; Monchanin et al. 2021). The island has seen success in many of its coral conservation efforts (Hein et al. 2020), actions driven by the increasing documentation of coral mortality and threats. With apparent changes in coral community structure occurring and the possibility of extirpation of certain coral types, loss of (and possible proliferation of) an obligate parasite should be considered when considering conservation measures. For example, Schiaparelli et al. (2022) provided records of the rare ectoparasitic gastropod *Heliacus jeffreysianus* (Tiberi, 1867) of family Architectonicidae, which is hosted by the further parasitic zoantharian *Savalia savaglia* Bertoloni, 1819. In their study, the authors contribute important ecological information on the rarely studied association and make a case for an upgraded conservation status for both species. The vast majority of invertebrate taxa have yet to be assessed by the IUCN Red List (Cardoso et al. 2012; IUCN 2023), which continues to be a cause for concern as species discoveries and descriptions may fall behind widespread biodiversity loss in coral reef habitats.

In the Gulf of Thailand, *Acropora* remains one of the most threatened groups of corals (Chankong and Manthachitra 2013; Yeemin et al. 2013), a trend that extends to the reefs of Koh Tao (Scott et al. 2017b), with *Phestilla arnoldi* Mehrotra & Caballer sp. nov. being the only *Acropora*-associated ectoparasite at the island. To date, no other obligate parasite of *Acropora* corals has

been found in Thai waters, however, this is possibly due to the high cryptic nature of known acroporid parasites. For example, one of the most documented obligate parasites of *Acropora* corals is the flatworm *Prosthiostomum acroporae* (Rawlinson et al. 2011), which has a broad geographic range and is a highly cryptic pest on both natural and aquarium corals (Barton et al. 2020), but has yet to be documented in Thai waters. *Acropora* corals can also become infested by acoel flatworms of the genus *Waminoa* Winsor, 1990, which have demonstrated high degrees of speciation and host specifity (Kunihiro et al. 2019), and also have a reputation as negatively impacting coral health (Hoeksema and Farenzena 2012; Ponti et al. 2016; Maggioni et al. 2022). With widespread declines in threatened coral groups in the tropics, as well as reports of long-term declines in parasite populations attributed to changing climates in Puget Sound, USA (Wood et al. 2023), a compelling case for the need of more focus on obligate parasites may be made. However, in regions such as Thailand, policy and management strategies pertaining to coral reef conservation provide little to no mention of ectoparasites, either as a cause of, or subject to conservation concerns. Despite this, due to research surrounding coral predators, government-supported management initiatives surrounding responses to coral predators and predator outbreaks have begun to be introduced at Koh Tao.

If current trends persist and *Acropora* corals continue to decline at Koh Tao, *P. arnoldi* Mehrotra & Caballer sp. nov. may not last indefinitely at its type locality (Weterings 2011; Scott 2014; Scott et al. 2017b), however, presence of the species at other locations is likely. With the rapid rate of change in coral communities occurring across the tropics, it is therefore possible that other similar species may share the same decline as their hosts (Hoeksema 2017; Montano 2020, 2022). The previously undocumented coral associations presented here highlight both the sizeable biodiversity yet to be studied in tropical reefs as well as the need to further study the mechanisms by which specific coral-associated fauna may influence wider reef communities (van der Schoot and Hoeksema 2023). The host dependence of numerous cryptic invertebrates should also be included as criterion in the IUCN Red List assessment of scleractinian species because the presence of associates adds to their biodiversity value (Hoeksema 2017; van der Schoot and Hoeksema 2023).

Declarations

This article is registered in ZooBank under http://zoobank.org/59012 8C6-8A36-4CF7-A644-A99F34ACC8CF.

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

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