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A new species of coral-feeding nudibranch (Mollusca: Gastropoda) from the Gulf of Thailand

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Abstract

The validity and position of the Indo Pacific genus *Phestilla* Bergh, 1874 (Fionoidea: Trinchesiidae) have been subject of some controversy as a result of several recent studies, which have sequentially synonymized or re-established it. At present, the genus includes eight valid species, the most of them described in the nineteenth and twentieth centuries, and all but one feeding on scleractinian corals of four genera: *Porites* Link, 1807 (Poritidae), *Tubastraea* Lesson, 1830, *Dendrophyllia* Blainville, 1830 (Dendrophylliidae) and *Montipora* Blainville, 1830 (Acroporidae). The discovery of an unknown *Phestilla* species feeding on *Pavona explanulata* (Lamarck, 1816) (Agariciidae) in Koh Tao, Thailand, motivates this work, in which this new species is described providing morphoanatomical and molecular characters. In addition, its systematic position and ecological significance as coral parasite are discussed.

Keywords Fionoidea · Trinchesiidae · Ecto-parasite · *Phestilla* Bergh, 1874 · *Pavona explanulata* (Lamarck, 1816) · Camouflage

Abbreviations

am	Ampulla
bc	Bursa copulatrix
dd	Deferent duct
fmg	Female gland mass
hd	Hermaphroditic duct
ov	Oviduct
p	Penis
pr	Prostate
v	Vagina
MNHN	Muséum National d'Histoire Naturelle, Paris

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Introduction

The Indo Pacific nudibranch genus *Phestilla* Bergh, 1874 (Fionoidea: Trinchesiidae) currently includes eight valid species that were largely described by Rudolph Bergh and William Rudman in the nineteenth and twentieth centuries. Still, several undescribed taxa potentially belonging to the genus have been recorded by other authors (Robertson 1970; Raabe 2006; Gosliner et al. 2018). The genus *Phestilla* includes species that previously have been assigned to the genera: *Aeolidia* Cuvier, 1798 (Ostergaard 1955), *Aeolidiella*

Bergh, 1867 (Gosliner 1979), *Cratena* Bergh, 1864 (Bergh 1870), *Cuthona* Alder & Hancock, 1855 (Rudman 1979), *Tenellia* Costa, 1866 (Ekimova et al. 2019), and *Hermosita* Gosliner & Behrens, 1986 (Ortea et al. 2003).

The validity and position of the genus *Phestilla* have been subject of some controversies as well. Cella et al. (2016) studied the phylogenetic relationships of some families within the superfamily Fionoidea, and after an extensive molecular analysis, concluded that the genus *Phestilla* and several other related genera were to be synonymized with the genus *Tenellia* (Fionidae: Trinchesiidae). Soon after, they were all reinstated by Korshunova et al. (2017), who showed that their morphology, ecology and ontology were not fully considered in this decision. The results of a recent phylogenetic study by Fritts-Penniman et al. (2020) are consistent with those of Cella et al. (2016). These authors consider that the genus *Phestilla* should remain in the synonymy because the alternative would result in the fragmentation of the genus *Cuthona* into multiple genera.

Several species of the genus *Phestilla* have been used as model organisms in a variety of fields ranging from medical pharmaceuticals to evolutionary biology and invertebrate development (Pasquinelli et al. 2000; Kimberly 2003; Ritson-Williams et al. 2009). Recently, the genus has also been of focus for its role in the ecology of reef corals. The genus *Phestilla* is the largest corallivorous clade of nudibranchs known (albeit not the only one), with all its currently included species restricted to the Indo-Pacific Ocean (Robertson 1970; Rudman 1979, 1981, 1982a; Faucci et al. 2007; Goodheart et al. 2017). All but one of the described taxa within the genus have been confirmed to feed on four genera of scleractinian corals, which are not taxonomically related: *Porites* Link, 1807 in the family Poritidae (Rudman 1979, 1981, 1982a), *Tubastraea* Lesson, 1830 and *Dendrophyllia* Blainville, 1830 both in the family Dendrophylliidae (Robertson 1970; Ritson-Williams et al. 2003; Fritts-Penniman et al. 2020), and *Montipora* Blainville, 1830 in the family Acroporidae (Wang et al. 2020). However, some undescribed species supposedly belonging to the genus *Phestilla* have been reported to feed on three other genera of the order Scleractinia (Fritts-Penniman et al. 2020): *Goniopora* Blainville, 1830, also in the family Poritidae (Robertson 1970), *Pavona* Lamarck, 1801 (Wong et al. 2017) and *Gardineroseris* Scheer & Pillai, 1974 (Gosliner et al. 2018), both belonging to the family Agariciidae.

To date, 112 species of nudibranchs have been reported from the Gulf of Thailand (Jensen 1998; Chavanich et al. 2013; Mehrotra and Scott 2016; Martynov et al. 2019). Of these, 72 species (roughly 63%) have thus far been recorded or described from the island of Koh Tao (Mehrotra and Scott 2016; Mehrotra et al. 2017; Korshunova et al. 2019), including the species *Phestilla lugubris* (Bergh, 1870) and *Phestilla melanobrachia* Bergh, 1874. The island of Koh

Tao has also been shown to host a high biodiversity of fish and corals (Scaps and Scott 2014; Scott et al. 2017a; Urgell et al. 2018), despite the occurrence of massive bleaching events in 1998 and 2010, which affected some coral species more than others (Yeemin et al. 2006, 2009; Hoeksema and Matthews 2011, 2015; Hoeksema et al. 2012). Moreover, the coral reefs of the island seem to be highly susceptible to extensive coral predation, in particular due to outbreaks of the corallivorous sea star *Acanthaster* spp. and muricid snails belonging to the genus *Drupella* Thiele, 1925, sometimes following a coral bleaching event (Hoeksema et al. 2013; Scott et al. 2015, 2017b; Moerland et al. 2016). Importantly, it has also been shown that the coral reefs of Koh Tao are undergoing a dramatic shift in community structure with significant reductions in populations of threatened corals (i.e., *Acropora* spp.) and less threatened corals such as *Pavona* spp., the latter of which may make up as much as 20% of the coral cover at Koh Tao, resulting in growing amounts of macroalgae (Scott et al. 2017a).

In this paper, we describe a new species of corallivorous nudibranch belonging to the genus *Phestilla* collected in Koh Tao feeding on *Pavona explanulata* (Lamarck, 1816), discussing its ecological significance as a coral parasite.

Material and methods

Sampling

Surveys were carried out at Koh Tao, Thailand, between January 2018 and March 2019. Specimens were collected by SCUBA diving from coral reef habitats at depths ranging from 7 to 21 m. Individuals were photographed in-situ with an Olympus TG-4 camera with an underwater housing. For preservation for both, molecular and morphological analysis, 95% ethanol was used. Specimens were tentatively determined by the collectors on site or by specialists through in-situ photographs. Identification of species was aided by the use of relevant literature (Rudman 1979, 1981, 1982a) and compared with known species prevalence in Thai waters (Jensen 1998; Nabhitbhata 2009; Chavanich et al. 2013). Additionally, taxon validity for molluscs was confirmed with the most recent literature at hand and assisted with Molluscabase as part of the World Register of Marine Species (WoRMS 2019) and references contained within.

Anatomical studies

An Olympus SZX16 stereomicroscope was used to study the internal anatomy and to prepare glycerin slides for light microscopy of jaws, radula, and penis. For the purposes of comparison, diagrams were made of the reproductive apparatus,

jaws, cutting edge of the jaws, and radula. Cerata (singular = ceras) and dorsal surfaces were also prepared for microscopy to assess presence and state of possible microalgal symbionts. The type specimens are deposited in MNHN.

DNA extraction, amplification, and sequencing

Tissue was taken from the ventral region of the foot of each specimen and DNA extracted using Quiagen 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′-GGTCAACAAATCAT AAAGATATTGG-3′) and HC02198 (5′-TAAA CTTCAGGGTGACCAAAAAATCA-3′). Partial sequences of the 16S rRNA region were amplified using primers from Palumbi et al. (1991) using the pairs 16Sar-L (5′-CGCC TGTTTATCAAAAACAT-3′) and 16Sbr-H (5′-CCGG TCTGAACTCAGATCACGT-3′). Due to reduced clarity of sequences for some specimens, a new reverse primer was designed to solve this issue. The reverse primer 16s-xH (5′-CCGGTYTGAAMYYAGATCACGTAGG-3′) proved effective for all samples. Primers for the histone 3 region were taken from Colgan et al. (2000) using the primers H3F (5′-ATGGCTCGTACCAAGCAGACVGC-3′) and H3R (5′-ATATCCTTRGGCATRATRGTGAC-3′). To assess the identity of dinoflagellate symbionts (see "Results"), tissue was also taken from several cerata which was followed by the same DNA extraction protocol. Primer pairs SymITSFP (5′-CTCAGCTCTGGACGTTGYGTT-GG-3′) and SymITSb (5′-GCGGGTTCATTGTCTGACT-3′) were sourced from van Oppen et al. (2001) for the region comprising the genes ITS1-5.8s-ITS2-28S.

PCR was carried out using BioRads MJ Mini™ Personal Thermal Cycler 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. The same protocol was used for both 16S primer combinations. For the genes ITS1-5.8s-ITS2-28S, the protocol included an initial denaturing step at 95 °C for 5 min; 30 cycles of denaturing at 95 °C for 30 s, annealing at 50 °C for 1 min 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.

Molecular analysis

Consensus sequences were generated from raw reads using Geneious (Kearse et al. 2012). A total of 107 sequences of the genes cytochrome c oxidase subunit I (COI), mitochondrial 16S structural rRNA subunit (16S), and nuclear histone 3 (H3) of various Trinchesiidae spp. (Table 1) were accessed from NCBI's GenBank (Clark et al. 2016). GUIDANCE-2 (Sela et al. 2015) was employed to identify offending sequences in alignments. Sequences were aligned and trimmed using MEGA X (Kumar et al. 2018), resulting in sequences 659 bp, 454 bp, and 327 bp in length respectively. Hypervariable indel-rich regions of the 16s gene were not removed (Cella et al. 2016). Four independent phylogenetic analyses were performed: a COI only dataset using both maximum likelihood (ML) and Bayesian inference (BI) estimation methods, and a concatenated dataset (COI + 16S + H3) with both ML and BI estimation methods.

The ML phylogenetic hypothesis was inferred using IQ-TREE (Nguyen et al. 2018) with 1500 bootstrap pseudoreplicates. The concatenated analysis was performed with a partitioned model (Chernomor et al. 2016). IQ-Tree's ModelFinder (Kalyaanamoorthy et al. 2017) tool invoked full tree searches to determine optimal models for each partition. The BI phylogenetic hypothesis was inferred using MrBayes (Ronquist et al. 2012) with the GTR + I + G model. Two simultaneous runs with three hot (temperature = 0.1) and one cold Metropolis-coupled Monte Carlo Markov chains (MCMCMC) for 6,000,000 generations with a flat Dirichlet prior. Cold chains were sampled every 6000 generations and diagnostics were calculated every 1000 generations with a 25% burn-in. While models chosen for ML and BI analysis were different, the search space of the models used for ML (TVM and TIM2) are subsets of the search space of the GTR model and, furthermore, the model selection step may not be necessary for phylogenetic analyses in general (Abadi et al. 2019). Raw Newick and Tree Nexus were visualized, re-rooted, and exported in FigTree (Rambaut 2018).

Species delimitation

Two further versions of the COI dataset were created to calculate uncorrected pairwise distances (p-distance) within MEGA X (Kumar et al. 2018) and to conduct automatic barcode gap discovery (ABGD) analysis (Puillandre et al. 2012). Both had included all individuals but the outgroup, except the dataset p-distance included two species from closely related genera (Catriona gymnota (Couthouy, 1838), Tenellia adspersa (Nordmann, 1845)). 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,

Table 1 Sequences used for species delimitation, phylogeny reconstruction and species identification. Specimens sequenced as part of the present work are indicated with * and all other sequences were sourced from the NCBI

Nudibranch species	COI	16S	H3
Phestilla viei sp. nov.	MN239112	MN257606	MN257608
Phestilla viei sp. nov.	MN239113	MN257607	MN257609
Phestilla minor	DQ417304	–	–
Phestilla minor	DQ417303	–	–
Phestilla minor	DQ417314	–	–
Phestilla minor	DQ417310	–	–
Phestilla minor	DQ417320	–	–
Phestilla minor	DQ417318	–	–
Phestilla minor	DQ417311	–	–
Phestilla minor	DQ417312	–	–
Phestilla poritophages	KY128968	KY128759	KY128554
Phestilla poritophages	KY128969	–	–
Phestilla sp. A	KY128992	–	–
Phestilla melanobrachia	DQ417282	–	–
Phestilla melanobrachia	KY129077	KY128868	KY128662
Phestilla sp. 2	DQ417284	–	–
Phestilla sp. 2	DQ417283	–	–
Phestilla sp. 2	DQ417286	–	–
Phestilla sp. 3	KY129080	–	–
Phestilla lugubris	KJ522463	–	–
Phestilla lugubris	DQ417294	–	–
Phestilla lugubris	DQ417300	–	–
Phestilla lugubris	DQ417289	–	–
Phestilla lugubris	DQ417299	–	–
Phestilla lugubris	KY129075	KY128866	KY128660
Phestilla sp.	KU971244	–	–
Phestilla sp.	KU971239	–	–
Phestilla sp.	KU971241	–	–
Phestilla sp.	KY129074	–	–
Phestilla subodiosa	MN255477	MN255475	MN255482
Phestilla chaetopterana	MF458314	MF458308	MF458310
Phestilla chaetopterana	MF458313	–	–
Catriona aurantia	KY985467	MF523458	MG386404
Catriona columbiana	KY128906	KY128698	KY128493
Catriona gymnota	KY128908	KY128700	KY128495
Diaphoreolis lagunae	KY128956	KY128749	KY128543
Diaphoreolis viridis	KY129104	KY128898	KY128690
Diaphoreolis flavovulta	KY128950	KY128745	KY128538
Fiona pinnata	KY129047	KY128838	KY128486
Tenellia adspersa	KY129085	KY128876	KY128668
Tergipes teripes	KJ434068	KJ434053	KJ434083
Tergiposacca longicerata	KY129086	KY128877	KY128669
Trinchesia foliata	KY128912	KY128704	KY128499
Trinchesia lenkae	KY129093	KY128884	KY128676
Trinchesia speciosa	KY128998	KY128790	KY128585
Rubramoena amoena	KY128904	KY128696	KY128491
Rubramoena rubescens	KY128916	KY128710	KY128503
Samla bicolor	MF523383	MF523436	MF523308
Zelentia cf. *pustulata*	KY128891	KY128891	KY128683
Zelentia pustulata	KY952184	MH614971	MH614992
Zelentia roginskae	MH614983	MH614974	MH614994
Zelentia nepunicea	MH614985	MH614976	MH614996
Zelentia fulgens	KY128952	KY128747	KY128540
Zelentia willowsi	MH614987	MH614978	MH614998
Zelentia ninel	KY952180	MH614967	MH614980
Dinoflagellate species	**Region spanning ITS1-5.8s-ITS2-28S**		
Durusdinium sp.	MN299374		

Pmax = 0.2, Steps = 10, X = 1, Nb bins = 20. An amino acid substitution type was used in conjunction with the Poisson model. Rates among sites were assumed to be uniform and homogeneous. Gaps and missing data were considered pairwise. Variance was estimated with 10,000 pseudoreplicate bootstraps.

Results

Systematics

Order Nudibranchia Cuvier, 1814 (in Blainville 1814).
    Superfamily Fionoidea Gray, 1857.
    Family Trinchesiidae Nordsieck, 1972.
    Genus *Phestilla* Bergh, 1874.

Phestilla viei Mehrotra, Caballer & Chavanich sp. nov.
http://zoobank.org/8FDBE04D-484F-4359-B1AE-C95B493D2975

    Phestilla sp.: Fritts-Penniman 2016: 116, Fig. 3.1 E.
    Phestilla sp. 2: Gosliner et al. 2008: 372; Gosliner et al. 2015: 357.
    Tenellia sp. 83: Gosliner et al. 2018: 300.
    ?*Tenellia* D4: Fritts-Penniman et al. 2020: Fig. 1G.

Type material

Holotype: adult, 14 mm long alive, 9 mm long preserved, collected from the surface of host coral *Pavona explanulata* at 9 m depth, Lighthouse Bay (type locality), 10° 7′ 14.95″ N–99° 50′ 36.06″ E, Koh Tao, Thailand, March 6, 2019, deposited in MNHN (IM-2000-28508).

Complementary observations

More than 20 specimens, ranging between 7 and 28 mm, observed (and not collected) in regular diving surveys between 2017 to 2019, Green Rock (10° 7′ 31.24″ N, 99° 48′ 49.57″ E); Mao Bay (10° 5′ 32.95″ N, 99° 51′ 9.29″ E); Hin Fai (10° 6′ 43.42″ N, 99° 49′ 7.18″ E); Laem Thien (10° 5′ 19.13″ N, 99° 51′ 17.64″ E); Koh Tao, Thailand.

Derivatio nominis

Phestilla viei Mehrotra, Caballer & Chavanich sp. nov. is named in honor of Mr. Vie Panyarachun for his years of facilitating citizen science and contributions in curating records of sea slug diversity in Thai waters, and his continued efforts as a marine naturalist.

Diagnosis

Body translucent white to pale yellow dorsally, pale brown laterally. Rhinophores translucent white, smooth, relatively short. Oral tentacles translucent white with brown markings, smooth, 1.5 times the length of rhinophores. Foot corners broad, tapering gently. Pericardium with a distinctive bulbous "hump," sometimes repeated at regular intervals along the dorsum. Firsts rows of cerata joining together in a wide pedunculate base. First ceras of each row held more upright.

Cerata translucent white with brown pigmentation caused by aggregations of unicellular dinoflagellate (*Durusdinium* sp.), held laterally giving a very flattened appearance. Gonopore on the right side below the first ceratal pedunculate row. Anal papilla between first and second postcardiac ceratal rows. Jaws with smooth cutting edges. Radular formula: 19 × 0.1.0. Teeth broad, lacking central cusp, with 8–12 denticles on each side of the median area, the central and lateral ones smaller. Penis 800 µm long, lacking stylet. Feeding on *Pavona explanulata* (for descriptions and illustrations see, e.g., Veron 2000; Waheed et al. 2015).

Description

Length alive up to 28 mm. Body elongate, slightly widened, with ceras arranged in rows, densely packed together, mostly held laterally giving a very flattened appearance (Fig. 1a–d). Rhinophores smooth and relatively short, held close together, tapering gradually towards rounded apices. Oral tentacles smooth, approximately 1.5 times the length of the rhinophores, usually pointing outwards or forwards, giving the anterior margin of the head a well-defined curve (Fig. 2a). A clear oral veil separates the rhinophores from the oral tentacles and anterior margin. A very small eye is visible behind and to the outside of each rhinophore. Foot corners are broad and extended, tapering gently (Fig. 2a). A distinctive bulbous "hump" is visible over the pericardium. In some specimens, particularly larger individuals, this bulbous feature is repeated in regular intervals along the dorsum resulting in 5–7 smaller humps reducing in size towards the tail (Fig. 1a, c). This feature is notably reduced in smaller individuals which may at most have 1–2 humps behind the pericardium. Foot sole smooth and broad, though rarely extending beyond the body wall, tapering to a point at the tail. Rows of cerata joining together in a wide pedunculate base, except in last ones (Fig. 2a). First ceras (most anterodorsal) of each row held more upright, giving a horn-like appearance at regular intervals. Cerata smooth, not widening noticeably, held either S-shaped or bend at right angles away from the body, and have swollen tips, though this is not apparent in all cerata. Digestive glands inside cerata filled with unicellular dinoflagellate *Durusdinium* sp. (Fig. 1e), with between 400 and 1200 individuals per mm of each ceras (Fig. 1f, g). Algal cells appear to be arranged in either short rows or more evenly dispersed. Some of the dinoflagellate's intact cells are also observed under the dorsal surface of the body; however, these appear to be in far lower densities than in the cerata. Gonopore on the right side below the first ceratal pedunculate row. Anal papilla between first and second postcardiac ceratal rows (Fig. 2a).

    Jaws translucent, flexible, coriaceous, non-calcified, and 820 µm long in the holotype (Fig. 2b). Cutting edge smooth but formed by the union of irregular blocks that
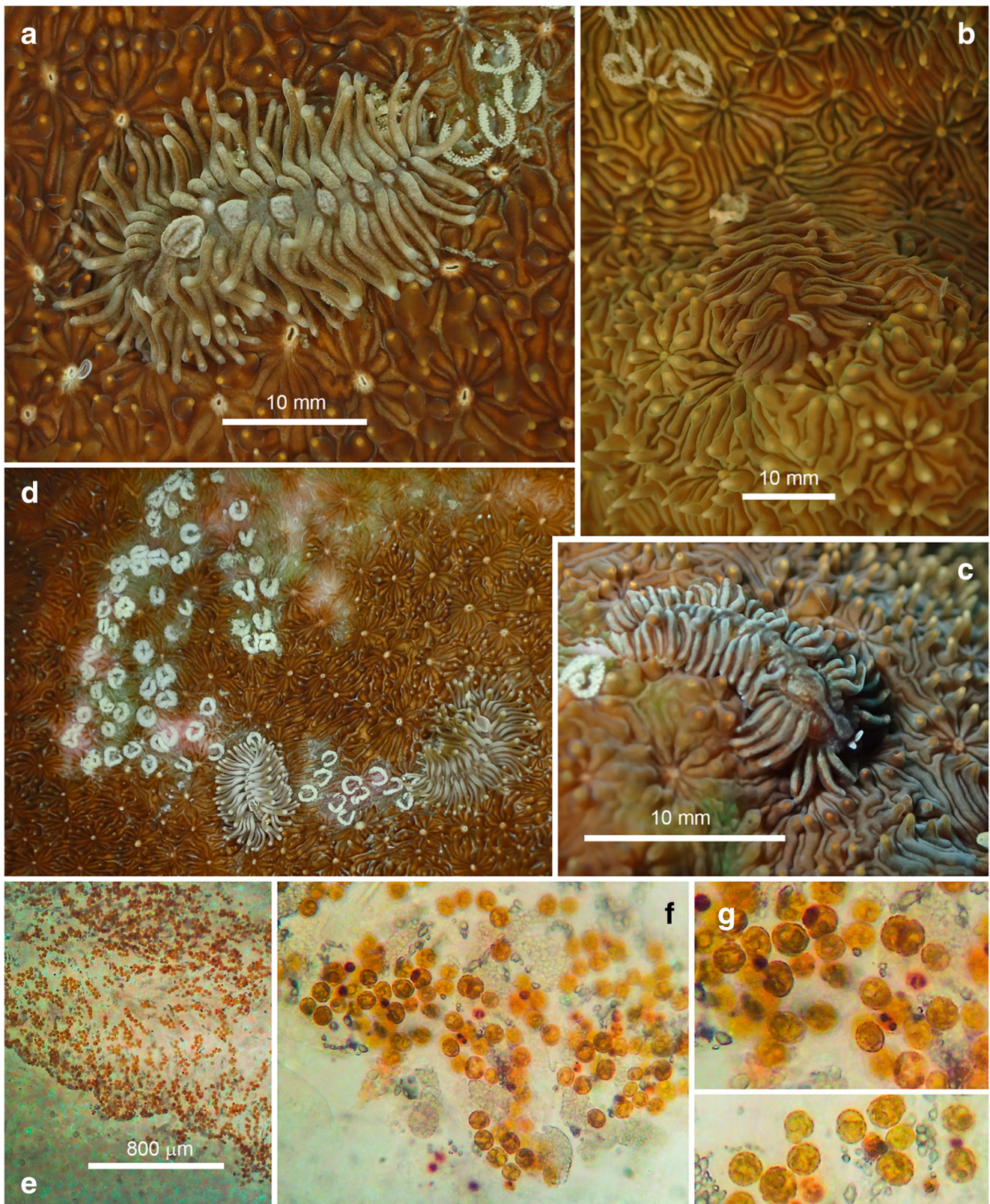
Fig. 1 *Phestilla viei* Mehrotra, Caballer & Chavanich sp. nov. on *Pavona explanulata*. **a** Living specimen (28 mm long) in dorso-lateral view with low symbiont density; **b** Specimen (23 mm long) camouflaged among the coral; **c** Living specimen (17 mm long) in lateral view; **d** Two specimens with low symbiont density with their egg masses. *Durusdinium* sp. associated to *Phestilla viei* Mehrotra, Caballer & Chavanich sp. nov; **e** General view of a section of a single ceras; **f** *Durusdinium* sp. in the ceras matrix; **g** Details of the symbiont cells
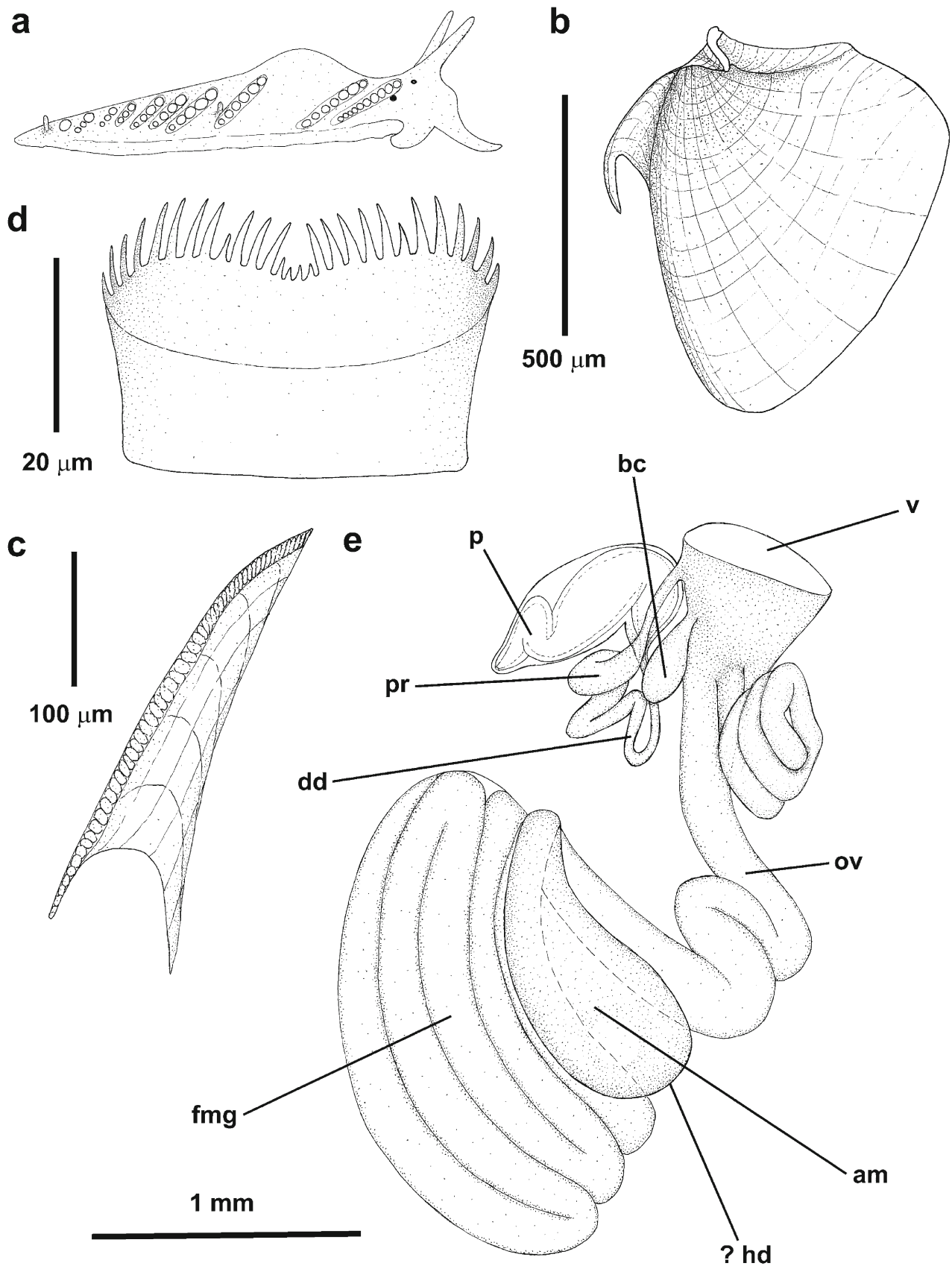
Fig. 2 *Phestilla viei* Mehrotra, Caballer & Chavanich sp. nov., holotype; **a** Scheme of the animal in lateral view, showing the disposition of the cerata; **b** Jaws; **c** Cutting edge of the jaws; **d** Radular tooth (the fourth in the row); **e** Scheme of the genital apparatus

resemble bricks, and that do not seem smooth at first observation (Fig. 2c).

Radular formula: $19 \times 0.1.0$ (holotype). Teeth broad, translucent, flexible and bent forward on the sides, lacking central cusp, with 8–12 denticles on each side of the median area (Fig. 2d). Central and lateral denticles smaller. Penis covered by a sheath, lacking stylet, about 800 μm long preserved (Fig. 2e). Prostate slightly wider than deferent duct, connected to vagina. Female gland mass about 2 mm long, containing wide convoluted ducts. Ampulla sac-like, long, connected to female gland mass and to oviduct. Oviduct wide and convoluted, ends in the vagina. Bursa copulatrix ovoid-elongate, about 400 μm long, also connected to the vagina.

Coloration

Body coloration overall translucent white to pale yellow. This coloration predominantly visible over the pericardium and along the median line on the dorsum where it enlarges and contracts repeatedly throughout the length of the animal, with each enlargement coinciding with a small hump. On either side of these humps there is pale brown pigmentation reaching laterally along the body wall and between rows of cerata. Foot very translucent with internal organs clearly visible, and foot margins white to pale yellow. Oral veil and oral tentacles translucent white with brown markings extending between ¼ to ¾ the length of the oral tentacles, and submarginally along the anterior edge. These markings may be a reticulated network of lines or a thick continuous line, which stretch backwards on the outside of each rhinophore before combining with the brown pigment along the dorsum. A noticeable patch of the oral veil is devoid of pigment, usually reaching to the rhinophores, which may or may not have brown pigment surrounding the base. Rhinophores translucent white throughout. Cerata translucent white with brown cores. Brown pigmentation much more prominent along the ventral region with the dorsal coloration variable based on dinoflagellate's cells density within. Apices colorless but opaque, sometimes with a yellowish hue.

Biology

All animals were observed year-round at different locations around the island, exclusively on their host coral *Pavona explanulata* in coral reef habitats at Koh Tao (Fig. 1a–d). Animals found at depths from 7 to 21 m with no indication of seasonal variation. No observations were made from soft sediment habitats nor on any other substrate other than that of the coral *P. explanulata*, on which it is extremely cryptic. Most easily observed at the head of the distinctive linear trail of egg masses (up to 70 have been observed over the corals at the time of spawning) on freshly consumed coral tissue (Fig. 1d). The spawn is a translucent coil of 0.5–1.5 turns, and it is most regularly crescent shaped forming a distinctive C-shape, though with some larger egg masses arching to form a "paper-clip" (Fig. 1a, d), containing 80–120 eggs each. Eggs strongly contrasted with the dense zooxanthellate coral tissue, range from white to extremely pale yellow. Living animals acquire much of their coloration due to dense aggregations of zooxanthellae in their tissues taken from their coral host (see "Discussion"). Animals rarely consumed more than an estimated 10% of the surface of the coral colony, instead consuming short linear "trails" of tissue, however the total number of polyps or proportional surface area was not measured.

Distribution

Indonesia (Fritts-Penniman 2016), Madagascar, Papua New Guinea, and the Philippines (Gosliner et al. 2008: as *Phestilla* sp. 2). Thailand (this paper). Gosliner et al. 2015 (as *Phestilla* sp. 2) and Gosliner et al. 2018 (as *Tenellia* sp. 83) widely record the species from the Indian and Western Pacific Oceans.

Remarks

The first record of a species of the genus *Phestilla* (or any nudibranch) feeding on corals belonging to the genus *Pavona* was made by Gosliner et al. (2008, 2015). Fritts-Penniman (2016) reported two *Phestilla* species that were found on *P. explanulata* and *P. decussata* (Dana 1846), which were afterwards documented by Gosliner et al. (2018). Wong et al. (2017) also observed a species of the genus *Phestilla* (determined as "*Tenellia* nudibranchs") feeding on *P. decussata*. At last, Fritts-Penniman et al. (2020) reported *Tenellia* D2-D4 from Indonesia and the Philippines feeding on several species of the genus *Pavona*: *Pavona* sp., *P. decussata* and *Pavona* cf. *explanulata*. *Phestilla viei* sp. nov. is the first species of the genus *Phestilla* described that is known to be an obligate associate of some Indo-Pacific species of the scleractinian family Agariciidae. Considering its camouflage, mimicking the surface area of the genus *Pavona* corals, it is unlikely to have hosts in other scleractinian families. Therefore, the ecology of *P. viei* sp. nov. is a very useful and simple character to easily distinguish it from its congeners.

Phestilla viei sp. nov. is also unique by its behavior: the specimens hold their cerata in a characteristic S-shape or at right angles, which maximize their cryptic ability on the host coral. In addition, the only two other species that have smooth cerata without bulbous extensions are *P. melanobrachia* and *Phestilla chaetopterana* (Ekimova, Deart & Schepetov, 2017). The latter belongs to a genus that is closely related

Table 2 Diagnostic characters of the species belonging to the genus *Phestilla*

Species	Radula	Jaws	Reproductive comparison	Penial stylet
P. chaetopterana	18 teeth, small central cusp with 5–7 long thin denticles on either side. Denticles 3–4 times longer than cusp. Sometimes 2–3 small minor denticles on either side of central cusp	Thin, masticatory process with single row of well-developed denticles	No penial gland or bulb	Small, apical
P. rebus comb. nov.	22 teeth with a prominent central cusp and up to 8 thin denticles on either side, approximately half as long. Minor denticles between these, approximately one third length of major denticles.	Cutting edge with bifurcate denticle tips, with recurved "hooks."	–	–
P. lugubris	33–39 teeth, each with long central cusp and 6–7 denticles on either side. Outside largest getting smaller towards middle, recurved towards tip. In between each are 2–3 small minor denticles	Roughly ovate with a distinctive dorsal indentation. The ventral side is almost straight. Small specimens with sharp denticles on cutting edge	Rudman (1981) described the reproductive apparatus as "typical." Very similar to *P. panamica*. The only difference is that in *P. lugubris* the penial sac is twice the size of the penial bulb	Present. (chitonous tip)
P. melanobrachia	35 teeth, each with long central cusp and 7 denticles on either side. Outside largest getting smaller towards middle, recurved towards tip. In between each are small minor denticles, shorter than *P. lugubris*, looking more like serration near central cusp	Similar to *P. lugubris*, with a pronounced dorsal indentation giving the plate a bilobed appearance. The masticatory process is triangular with a smooth cutting edge	Differentiated by having the penial bulb opening halfway down the penis sheath. It is very similar to other species of *Phestilla* in all other ways	Seemingly absent but see remarks
P. minor	25–32 teeth, each with long central cusp and 4 denticles on either side, approx. each half the size of central. In between each are up to 4 small minor denticles	Similar in shape to those of *P. lugubris* but the cutting edge has a row of fine denticles	Very similar to *P. lugubris*. The epithelium of the penial bulb, however, differs from that of *P. lugubris* in consisting of irregularly shaped cells which suggests a secretory function	Present. (chitonous tip)
P. panamica	46–52 teeth, each with broad but shorter central cusp and 10 long thin recurved denticles on either side. In between each are smaller minor denticles	Elongate and bilobed very similar in shape to those of *P. lugubris*, and the cutting edge is smooth, as in large *P. lugubris* specimens	Very similar to *P. lugubris*. The only difference is that in *P. panamica* the penial bulb is twice the size of the penial sac	Seemingly absent but see remarks
P. poritophages	18 teeth, each with long central cusp and 8–9 denticles on either side. In between each are 2–3 smaller minor denticles. Outside largest getting smaller towards middle	Bearing a single row of denticles along the cutting edge	Two distinct openings, one to penial sac, other to vagina	Absent
P. subodiosa	12 teeth with a central cusp and 5–7 lateral denticles. Central cusp slightly longer than denticles, denticles of similar length to each other	Thin and translucent	Penile bulb curved, short prostate. Female gland mass 1.5x larger than penile bulb. No vas deferens	–
P. viei sp. nov.	19 broad, flexible teeth. No central cusp and 8–12 denticles on either side of median. Central and outermost denticles smaller than others	Translucent, flexible, with a smooth cutting edge made up of irregular blocks	No penial gland or bulb Penis covered in a sheath	No stylet observed in dissection

and also included in the comparison because of the results of the phylogenetic analysis by Fritts-Penniman et al. (2020) and in this study. However, the cerata of *P. melanobrachia* are typically larger and more swollen with small, narrow apices, while those of *P. chaetopterana* are distinctively separated due to only a single ceras being found per row. Both species also hold their cerata differently, with the former typically carrying their cerata upwards and outwards, and the latter hold their cerata flattened dorsoventrally. Furthermore, *P. viei* sp. nov. has some characteristics in common with *Phestilla panamica* Rudman, 1982a, such as cylindrical cerata with bulbous tips and a generally flattened shape, but it is clearly distinguished from the Panamanian species by the irregular nodules and different coloration of its cerata, and by its ecology. The rhinophores in *P. viei* sp. nov. are also short compared to the size of the oral tentacles, which in other species are proportionally larger or of similar size to each other.

The color variation in *P. viei* sp. nov. has been largely attributed to variations in the dinoflagellate density, causing the specimens to appear pale brownish-yellow dorsally when fewer cells are held. In general terms, the coloration of *P. viei* sp. nov. is most similar to some morphs of *Phestilla poritophages* (Rudman, 1979) and *Phestilla minor* Rudman, 1981, both of which have been spotted bearing a dark brown or golden-brown coloration, with individuals of *P. poritophages* even showing distinctive white markings down the dorsal mid-line, similar to that of *P. viei* sp. nov. However, their distinct ceratal morphologies clearly separates these species.

There are two other species belonging to the genus *Phestilla* that, as *P. viei* sp. nov., have a smooth cutting edge on their jaws, *P. panamica* and *P. melanobrachia*. But both of them show a different coloration, external anatomy, prey, and behavior regarding the position of the cerata. The unique radular morphology for *P. viei* sp. nov. allows it to be most easily separated from all other species of the genus *Phestilla*. While all but one species described thus far have a prominent central cusp, this is entirely lacking in *P. viei* sp. nov., which instead shows longer lateral denticles, decreasing in size towards the center and outside edges. The most similar structure to this is found in *P. chaetopterana*, which also has elongated lateral denticles, reaching several times the length of a clear central cusp.

No penial stylet has been observed in *P. viei* sp. nov., but Rudman (1982a) pointed out the fact that, among the species of the genus *Phestilla*, the penial stylet was only observed after serial sectioning and not observed under dissection alone. However, this character groups again *P. viei* sp. nov. with *P. panamica* and *P. melanobrachia*, which are the other two species bearing jaws with a smooth cutting edge. Future phylogenetic studies might prove this as a synapomorphy if these species branch together. The third species lacking a

penial stylet is *P. poritophages*, a smaller species from East Africa, which has an external morphology much closer to that of a member of the family Cuthonidae Odhner, 1934. A summarized comparison of morphological traits for *Phestilla* spp. species is shown in Table 2.

Molecular analysis results

Six sequences were obtained from two specimens belonging to *P. viei* sp. nov. (Table 1). GUIDANCE2 identified no offending sequences within the alignment, thus the final dataset for both COI and the concatenation were the same as those initially begun with. The COI dataset was 659 bp in length, and the concatenated dataset was 1440 bp.

The trees generated from both, ML and BI, using the COI dataset had mostly consistent topologies and most branches had high support values (Fig. 3). Both inferences resolved *P. viei* sp. nov. to form a strongly supported clade (PP = 100, BS = 82) with another undescribed species of the genus *Phestilla*. Sequences of *P. chaetopterana* resolved as the earliest diverging species within this dataset. Most sub-clades within the genus *Phestilla* resolved agreeably with the current published literature, with the exception of *P. minor*, composed of several supported branches forming a complex which includes *P. poritophages*. Several polytomies were found in the BI tree, possibly due to limited taxon sampling which could contribute to the appearance of long-branch attraction.

The trees generated with the concatenated dataset were agreeable with the current published literature and had no polytomies (Fig. 4). The only difference was that *P. chaetopterana* resolved as the earliest diverging species within the ML tree, while it formed a sub-clade with *P. viei* sp. nov. and an undescribed species in the BI tree. This is likely due to the model selection step and require further research to determine which model should be utilized in future nudibranch phylogenetic studies (Wang et al. 2020).

All three ABGD analyses outputted consistent results, revealing 17 different partitions within our dataset. *P. minor* resolved as a complex with six different species within our analysis. *P. viei* sp. nov. resolved as distinct species to the other species of the genus *Phestilla*.

Uncorrected pairwise distances for all three genes were calculated further allowing a clear distinction between *P. viei* sp. nov. and its congeners, with minimum distances of 11%, 10%, and 4% for COI, 16S, and H3, respectively. It was noted however that COI sequences were highly variable with several species of the genus *Phestilla* having lower distance values with species in other genera including *Catriona* Winckworth, 1841, *Rubramoena* Cella et al., 2016, and *Zelentia* Korshunova, Martynov & Picton, 2017, than with congeners.
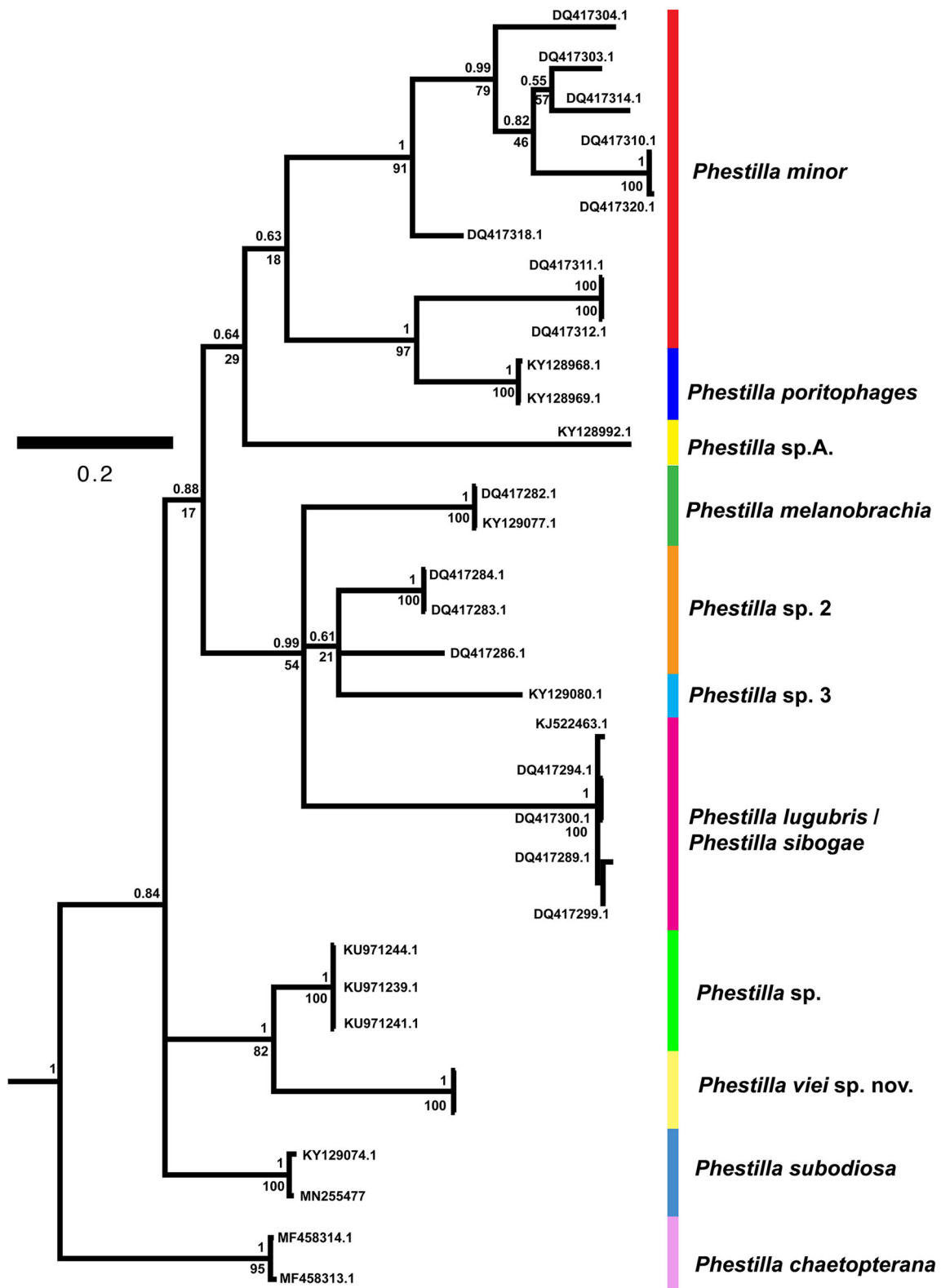
Fig. 3 Phylogenetic hypothesis of *Phestilla* from only COI. Tree topology obtained from Bayesian Inference. Support values above and below nodes indicate PP and BS, respectively. The tree was rooted on *Samla bicolor* (not shown)

Maximum Likelihood

Bayesian Inference
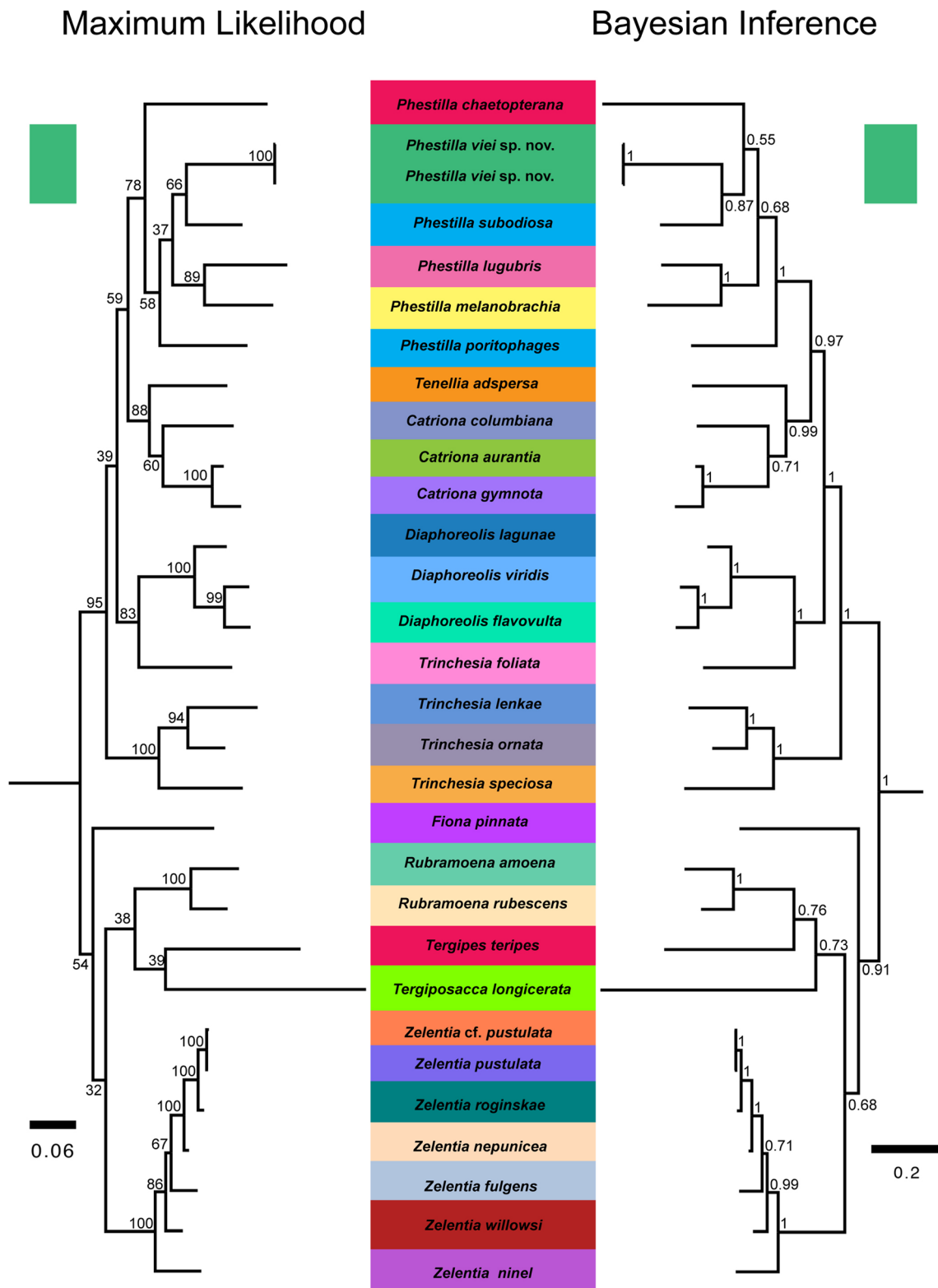
Fig. 4 Phylogenetic hypotheses of Fionidea from the concatenated dataset (COI + 16S + H3). Left and right tree topologies obtained using Maximum Likelihood and Bayesian Inference respectively, and support values indicate PP and BS, respectively. The tree was rooted on *Samla bicolor* (not shown)

Discussion

The superfamily Fionoidea has included a large number of genera along its taxonomic history. Many of them were pruned using morphological data (Miller 1977; Williams and Gosliner 1979), but still the validity of some names has been contested by several authors (Burn 1973; Miller 1977; Williams and Gosliner 1979; Brown 1980; Miller 2004).

The synonymy of the genus *Phestilla* with *Tenellia* has recently been revalidated by Fritts-Penniman et al. (2020). These authors justify this decision based on their results that "support the previous work by Cella et al. (2016) … as this clade (*Phestilla*) is nested within a much larger clade, the members of which have been synonymized with *Tenellia*". Fritts-Penniman et al. (2020) point out that this is the simplest solution, because the alternative would be to divide the specious genus *Cuthona* in many genera.

On the other hand, Fritts-Penniman et al. (2020) recognize the existence of a well-supported monophyletic group including all the species of the genus *Phestilla*, *P. chaetopterana* and *Pinufius rebus* Marcus & Marcus, 1960 that they call "*Phestilla* clade". The taxonomic decision of synonymizing the genus *Phestilla* is just the simplest solution that Cella et al. (2016) and Fritts-Penniman et al. (2020) find with their molecular results, but despite the support of these results, they discuss valid alternatives that would not imply the invalidation of the genus *Phestilla*. Additionally, we agree with Korshunova et al. (2017), in which there are other characters beyond molecular data that have not been adequately pondered.

Despite the quality of the studies performed by Cella et al. (2016) and Fritts-Penniman et al. (2020), from the taxonomic point of view it is simpler to maintain the genus *Phestilla* because it forms a monophyletic group of species that can be recognized by common morphological and ecological traits, until an integrative study is tackled that provides answers that can be rationally applied to the classification.

With regard to species that are already classified within the genus *Phestilla*, or should be transferred to the genus, we make the following considerations: Fritts-Penniman et al. (2020) transferred *Pinufius rebus* to the genus *Tenellia* based on the results of their phylogenetic analyses. Nonetheless, this species makes part of the "*Phestilla* clade" of the genus *Tenellia* (Fritts-Penniman et al. 2020), therefore, we herein transfer it to the genus *Phestilla*. We also note that the specific epithet of *Phestilla subodiosus* Wang et al., 2020 does not follow ICZN Article 34.2 and should be changed to *Phestilla subodiosa* to establish the correct gender of the epithet.

Our phylogenetic analysis results are consistent with these of Fritts-Penniman et al. (2020) and Wang et al. (2020), and *P. chaetopterana* resolved either as the earliest diverging species (ML tree) of the *Phestilla* clade or formed a sub-clade with *P. viei* sp. nov. and an undescribed species (BI tree). This ML-BI difference can be attributed to the limited taxon sampling of each species or perhaps to the different models utilized. While the search spaces of the models used for ML are subsets of the search space of the one used by GTR, it is possible that the species tree was near the model perimeter boundaries of the ML analysis. This hypothesis is sustained by the lower support values of the ML tree. Nevertheless, *Phestilla* formed a strongly supported clade with *P. chaetopterana* within each tree (PP = 100, ML = 78), these results support Wang et al.'s (2020) decision to place *P. chaetopterana* within *Phestilla*. In addition, the radular morphology of *P. viei* sp. nov. atypical for a species of the genus *Phestilla* and closer to that of *P. chaetopterana* strongly supports the reassignment of the latter species.

Fritts-Penniman et al. (2020) synonymize *Phestilla sibogae* Bergh, 1905 in the same paragraph where they decide to retain the name *T. sibogae* for a non-corallivorous species from Philippines that, in their concatenated trees, falls out of the "*Phestilla* clade". The validity of this taxonomic act is doubtful under the rules of the International Code of Zoological Nomenclature, especially if we consider that the specimens they used were collected by other authors (Faucci et al. 2007; Cella et al. 2016) in isolated oceanic islands 3000 to almost 10,000 km away from the type locality of *P. sibogae*: Pepela Bay, Timor. Faucci et al. (2007) and Cella et al. (2016) did not provide descriptions nor illustrations of the specimens they determined as *P. sibogae*. Fritts-Penniman et al. (2020) did not find genetic differences between their sequences and these of *P. lugubris* because they were most probably only working with *P. lugubris*. There is no evidence proving that they have used sequences of *P. sibogae*, and therefore, there is no basis for the synonymy of *P. sibogae* that should be re-instated.

Fritts-Penniman et al. (2020) also suggest that *P. panamica* is a junior synonym of *P. lugubris*, because the specimens they "are not genetically distinct", but, again, their samples come from isolated islands far away from the coast of Mexico, and thousands of kilometers away from the type locality of *P. panamica*, Saboga Island, Panama. Until more detailed studies are performed with material coming from the type locality (or at least close), we prefer to retain the name *P. panamica*.

Therefore, ten species should be included in the list of valid taxa belonging to the genus *Phestilla*: *P. lugubris*, *P. melanobrachia*, *P. sibogae*, *P. rebus* comb. nov., *P. poritophages*, *P. minor*, *P. panamica*, *P. subodiosa*, *P. chaetopterana*, and *P. viei* sp. nov. (this study).

The inclusion of *P. viei* sp. nov., *P. rebus* comb. nov., and *P. chaetopterana* in the genus makes it necessary to redescribe the diagnosis of the genus *Phestilla* as follows: Trinchesiid with smooth rounded oral tentacles (except *P. rebus* comb. nov.) and rounded oral veil. Pericardium sometimes forms swollen hump (Rudman 1981). Cerata unbranching and arranged regularly in sloping rows (Rudman 1981; Korshunova et al. 2017), lacking

cnidosacs, which are replaced by large glandular cells (Rudman 1981; Korshunova et al. 2017). Each ceras elongated to club-shaped, bulbous in most of the species, with enlarged ceratal tips. Masticatory processes well defined with denticles (Rudman 1979; Korshunova et al. 2017), irregularly indented (Bergh 1905; Rudman 1981) or smooth (Bergh 1874; Rudman 1982a; this paper). Narrow to wide uniserial radular teeth (Rudman 1981; Korshunova et al. 2017; this paper). Radular teeth typically with a central cusp at the same level as outer denticles, but longer than inner denticles (Korshunova et al. 2017), with cases long, same-sized lateral denticles and short central cusp (Ekimova et al. 2019: *P. chaetopterana*) or absent central cusp (this paper). Very short, straight penile stylet (Rudman 1981; Korshunova et al. 2017) or potentially absent (Rudman 1979, 1982a; this paper). Anus acleioproctic (Korshunova et al. 2017). All species but *P. chaetopterana* feed on scleractinian corals.

Mimicking the color patterns of the host coral is a good strategy to survive for associated species of the genus *Phestilla*, but not all species of corallivorous nudibranchs (or gastropods) show this kind of camouflage. Members of the pleurobranchid species *Berthellina citrina* (Rüppell & Leuckart, 1828) are aposematic by showing a bright yellow or orange coloration, while they can be found feeding on a wide range of prey species, consisting of sponges and scleractinian corals (Willan 1984). Corallivorous parasites of the large, gastropod family Epitoniidae are found on limited numbers of host species, like in the case of the genus *Phestilla*, but instead of hiding themselves by the use of camouflage, they protect themselves by dwelling underneath their host coral (Gittenberger and Hoeksema 2013; Scott et al. 2017c). An exception would be the yellow epitoniids feeding on the genus *Tubastraea* sun corals, which mimic the yellow coloration of their prey's tentacles (Gittenberger and Hoeksema 2013; Rodríguez-Villalobos et al. 2016). It seems logical to assume that mimicry would be most effective if predator and prey have evolved together in an obligate host-specific relationship. In other words, camouflage by host mimicry may result in host specificity in the genus *Phestilla*. Most of the currently described corallivorous species of the genus are host-specific on the zooxanthellate coral genus *Porites*, and the azooxanthellate coral genus *Tubastraea*. All the species of the genus *Phestilla* feeding on the genus *Porites* show some degree of cryptic ability (camouflage) on their hosts (Rudman 1979, 1981, 1982a), though there is considerable morphological variation among them. Similarly, the behavior of *P. melanobrachia* to switch between the differently colored species of the genus *Tubastraea*, results in a drastically different coloration within the nudibranch, promoting a more cryptic morphology (Robertson 1970; Ritson-Williams et al. 2003). Even the annelid-associated nudibranch *P. chaetopterana*, shows variation in the color of the digestive gland due to dietary variability (Ekimova et al. 2019). Thus, it is not surprising for *P. viei* sp. nov. to show remarkable cryptic abilities that allow the species

to camouflage among the polyps of the coral *P. explanulata*. The intricate septacostal arrangement of the coral appears to be closely mimicked by the shape and positioning of cerata, centering around one of the several dorsal "humps" seen on the nudibranch, that we further hypothesise mimic the distinctive and often raised polyp mouth. In our experience, such elaborate and effective camouflage on the genus *Pavona* corals was rare, but a recent observation of the pycnogonid *Endeis* sp. on *Pavona varians* Verrill, 1864 by Montano and Maggioni (2018) has further highlighted the degree of camouflage that some invertebrates may be capable of on agaraciid host corals.

The presence of microalgal cells within *P. viei* sp. nov. was assessed visually, and subsequent molecular evidence confirmed their identity as *Durusdinium* sp. (formerly "Clade D," see LaJeunesse et al. 2018). Different species of nudibranch, including *Phestilla* spp. feeding on corals of the genus *Porites*, have been shown to have considerable variation in their use of host-acquired zooxanthellae (Rudman 1981, 1982b). We suggest that in the present case, these photosynthetic cells are most likely taken directly from the host coral *Pavona explanulata* on which it feeds. The dense collections of these over the dorsal inner surface of the cerata indicate a probable symbiotic relationship between the nudibranch and the dinoflagellate. However, the photosynthetic role within the nudibranch was not confirmed in the present study. It is interesting to note further possible evolutionary adaptations to facilitate this, such as the translucent dorsal surface of the cerata, promoting light penetration, with pigment observed predominantly along the ventral surface. The role of zooxanthellae as a symbiont as opposed to simply part of the diet in many nudibranchs has been assessed in numerous studies (Kempf 1984; Hoegh-Guldberg and Hinde 1986; Wägele and Johnsen 2001; FitzPatrick et al. 2012; Mies et al. 2017) and such a form of "kleptosymbiosis" has already been documented in numerous other nudibranch families such as Aeolidiidae, Pinufiidae, and Tethydidae (Rudman 1982b; Kempf 1984; Burghardt and Wägele 2006).

At present, *P. chaetopterana* is believed to possess a unique ecology, not only within the genus *Phestilla*, but also among all known cladobranchs. Ekimova et al. (2019) suggest that it may feed on the mucus feeding net or the fecal matter of worms belonging to the genus *Chaetopterus*, and that it likely plays some as yet unspecified symbiotic relationship with the worms. All other currently described species in the genus are obligate corallivores and tend to be host-specific to at least the genus level (but see Ritson-Williams et al. 2003). The two genera of hermatypic corals known to host obligate nudibranch parasites, *Pavona* and *Porites*, have both been identified as to contain coral species that are resistant to stresses related to temperature and sedimentation (Marshall and Baird 2000; Guest et al. 2012). At Koh Tao, populations of resistant corals, including these genera, have been shown to be increasing while more vulnerable corals such as *Acropora*, *Montipora* and *Turbinaria* have shown a corresponding decline (Scott

et al. 2017a). However, both resistant and vulnerable corals, especially those belonging to the genera *Pavona*, *Acropora* and *Montipora*, have been found to be prominent prey of the corallivorous muricid snail *Drupella* spp. at Koh Tao (Moerland et al. 2016; Scott et al. 2017b). The broader ecological impacts of ecto-parasitic nudibranchs on coral reef ecosystems requires further study. With numerous host-specific corallivorous nudibranchs yet to be described (Robertson 1970; Faucci et al. 2007; Gosliner et al. 2018), the continued widespread decline of certain coral species (Carpenter et al. 2008) may take with them a wealth of biological information. With the loss of numerous gastropod taxa already underway (Régnier et al. 2015; Cowie et al. 2017), it is vital that research into these threatened ecosystems expands substantially.

Compliance with ethical standards

Conflict of interest   The authors declare that they have no conflict of interest.

Ethical approval   All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies   All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities, through Chulalongkorn University, Thailand. The study is compliant with CBD and Nagoya protocols.

Data availability   The molecular data generated during and/or analyzed during the current study are available in the GenBank repository and can be found using accession numbers provided in Table 1. Specimens used in the present study are deposited in the following museum: MNHN (IM-2000-28508).

Author contribution   RM and MC conceived and designed the study. RM and SC conducted samplings. RM and SA conducted in-field ecological data collection. MC performed anatomical studies. RM and AW did the molecular analysis. All authors analyzed data. RM wrote the first draft of the manuscript. All authors made contributions and approved the final manuscript.

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