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# A New Species of Predatory Nudibranch (Gastropoda: Trinchesiidae) of the Scleractinian Coral *Goniopora*

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Members of the nudibranch genus *Phestilla* are common predators of scleractinian corals, but currently this genus has 10 described species only. Here we describe *Phestilla goniophaga* sp. nov., the first formally named predatory nudibranch species of the stony corals from the genus *Goniopora*. The new species can be distinguished from its congeneric species by the large number of long cerata (up to 16 rows and 23 cerata per row), and white rounded hump on the notum. The hump resembles the mouth of the coral poly, while the cerata resemble the coral tentacles. The egg masses of *P. goniophaga* sp. nov. are unique among *Phestilla* spp. egg masses in being bright orange in color, and forming a coiled ribbon. Analysis of the *COI*, *16S rRNA* and *H3* genes of *P. goniophaga* sp. nov. also showed that this species is distinct from other congeneric species.

**Key words:** Coral, Coral-eating, Corallivory, Mollusca, *Phestilla*.

## BACKGROUND

The genus *Phestilla* Bergh, 1874 is a small group of tergipedid nudibranchs with reduced cephalic tentacles and without ceratal cnidocacs (MolluscaBase 2020). With the exception that *P. chaetopterana* (originally *Tenellia chaetopterana*) lives inside the tube of the polychaete *Chaetopterus* sp. (Ekimova et al. 2017), all *Phestilla* spp. are obligate predators of scleractinian corals. There has been some controversy in the systematics of nudibranchs of the superfamily Fionoidea Nordsieck, 1972 with a total of 317 species including those classified in *Phestilla* Bergh, 1874 (Tergipedidae) (MolluscaBase 2020). Cella et al. (2016) merged the families Calmidae, Eubranchidae, Fionidae and Tergipedidae into a single family Fionidae based on the molecular phylogenetic result that this would make the family monophyletic. In addition, they treated *Phestilla* and several other related genera (*Trinchesia*, *Catriona* and *Cuthona*) as junior synonyms of *Tenellia*. Ekimova et al. (2017) and Fritts-Penniman et al. (2020) supported this classification scheme, and in the latter publication the authors pointed out that otherwise *Cuthona* had to be divided into many genera. But Korshunova et al. (2017) reverted the classification of these families and genera because they thought Cella et al. (2016) did not fully consider the morphological and ontological characteristics when making the decision. Three recent studies (Wang et al. 2019; Hu et al. 2020; Mehrotra et al. 2020) all considered it more appropriate to retain *Phestilla* because this genus is monophyletic (except *P. sibogae*), and all the species except *P. chaetopterana* are obligate corallivores. Due to the inclusion of *P. chaetopterana* and *P. viei* in *Phestilla*, Mehrotra et al. (2020) provided an updated diagnosis of the genus with respect to the morphology of the oral tentacles, oral

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veil, presence of a swollen hump on notum, shape and arrangement of cerata, masticatory processes, radular teeth and penile stylet.

Previous studies have found that corallivorous *Phestilla* spp. are associated with only few genera/species of scleractinican corals. Specifically, *P. lugubris*, *P. minor*, *P. panamica*, and *P. poritophages* are predators of *Porties* (Harris 1975; Rudman 1979 1981 1982; Gosliner et al. 2018). *Phestilla melanobrachia* is a predator of dendrophylliid corals *Tubastraea* spp. and *Dendrophyllia* spp., and the its color changes according the color of the prey (Harris 1968 1975; Salvini-Plawen 1972). *Phestilla subodiosa* feeds on *Montipora* spp., common corals in the aquarium trade (Wang et al. 2020). *Phestilla viei* (Mehrotra et al. 2020) and *P. fuscostriata* (Hu et al. 2020) feeds on *Pavona explanulata* and *Pavona decussata*, respectively. As for *P. sibogae*, it was treated as a junior synonym of *Phestilla lugubris* by Rudman (1981). However, Gosliner et al. (2018) consider that they are different species and *P. sibogae* feeds on hydroids of the genus *Sertularella*.

There have been several records of nudibranchs feeding on *Goniopora* corals in Indo-Pacific locations (Gosliner et al. 2018) including Singapore (Robertson 1970), Papua New Guinea (Gosliner 1992; Gosliner et al. 1996), and Guam and Palau (Ritson-Williams et al. 2003; Faucci et al. 2007). Nevertheless, no formal description of these nudibranchs is available. Ritson-Williams et al. (2003 2007 2009) reported *Phestilla* sp. 2 as a specialist predator of the scleractinian genus *Goniopora* (Poritidae) and studied its dietary breadth and larval development in Guam. They found that, when *Porities cylindrica*, *Goniopora fruticosa*, *G. minor*, *G. lobata* and *G. eclipsensis* were offered to the nudribranch, it showed higher preference for *G. fruticosa*, followed by *G. minor* and *G. lobata* (Ritson-Williams et al. 2003). Its larval development took 5 days after which the larvae would undergo metamorphosis in response to the cues from its favorite coral *G. fruticosa* (Ritson-Williams et al. 2007). Moreover, water-soluble cues from *G. fruticosa* caused a higher percentage of competent larvae of *Phestilla* sp. 2 to undergo metamorphosis than those cues from *Porites annae*, *P. Cylindrica*, *Psammocora contigua*, *G. fruticosa*, *G. tenuidens*, *G. eclipsensis*, *G. minor*, and *G. lobata* (Ritson-Williams et al. 2009). This series of experiments show that, although *Phestilla* sp. 2 can feed on multiple species of *Goniopora*, *G. fruticosa* is its most favorite species in terms of diet and settlement substrate.

During surveys of coral communities in Hong Kong in 2019, we discovered a species of *Phestilla* feeding on *Goniopora* spp. and laying eggs on the skeleton of this genus of corals (Fig. 1A). In this paper, we provide morphological description of this species,

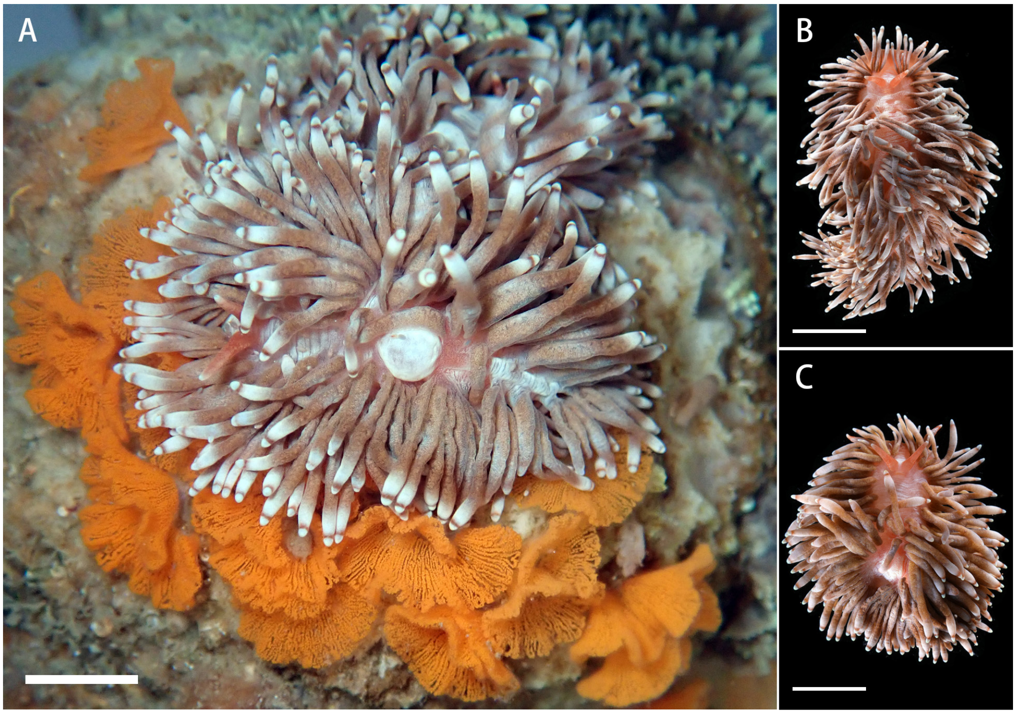

**Fig. 1.** *Phestilla goniophaga* sp. nov. A, A colony of *Goniopora* sp. with two adults of *P. goniophaga* sp. nov. and their coiled egg ribbons. B, Holotype (BU-Mol-20-001). C, Paratype (BU-Mol-20-002). Scale bars: A–C = 10 mm. All photographs were taken when the nudibranchs were alive.

and report a molecular phylogenetic analysis of its relationship with other congeneric species.

## MATERIALS AND METHODS

### Sample collection

Samples of the *Phestilla goniophaga* sp. nov. were collected by SCUBA diving from Sharp Island (22°21'32.9"N 114°17'47.8"E, water depth ~2 m) and Chek Chau (22°30'04"N 114°21'32"E, water depth ~ 2 m) in June 2019 and June 2020, respectively. The specimens were preserved either in 95% ethanol for molecular analysis or in 4% formaldehyde in seawater for morphological analysis. All specimens examined in this study are deposited in Hong Kong Baptist University (BU-Mol-20-001 to BU-Mol-20-006).

### Morphological analysis

The external morphological characteristics were examined under a Motic SMZ-171 stereomicroscope, and photos were taken using a Canon Mark IV camera. The veligers were examined under a Motic BA210 compound microscope. To extract the radula and the jaws, the buccal masses from two specimens were soaked in 10% bleach solution for 10 min at room temperature (~22°C) to dissolve soft tissues, and then rinsed in deionized water four times to remove the bleach. The radula and jaws were dried in an oven, gold-plated, mounted on a stub, and examined under a LEO 1530 FESEM scanning electron microscope (SEM). Specimens BU-Mol-20-002 and BU-Mol-20-005 were also dissected under the stereomicroscope to examine the reproductive system.

### Molecular analysis

Foot tissues of three specimens (BU-Mol-20-001 to BU-Mol-20-003) were used for molecular analyses. Genomic DNA was extracted using the TaKaRa MiniBEST Agarose Gel DNA Extraction Kit Ver.4.0 (TaKaRa Biotechnology, Dalian, China). Concentration and purity of the DNA samples were determined using a NanoDrop ND-1000 spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA), and DNA integrity was checked using electrophoresis on 1.0% agarose gel. Polymerase chain reaction (PCR) reactions were then conducted using the extracted DNA as templates to amplify the *COI*, *16S rRNA* and *H3* genes. The primers used were identical to those adopted by Ekimova et al. (2017): HCO2198 and LCO1498 (Folmer et al. 1994), 16SarL (Palumbi et al. 1991), 16SR (Puslednik and Serb 2008), H3AF and H3AR (Colgan et al. 1998). PCR programs were identical to those in Wang et al. (2019) and Hu et al. (2020). PCR products were sent to BGI Hong Kong for sequencing on an ABI 310 Genetic Analyzer. All new sequences were deposited in GenBank (Table S1).

To understand the phylogenetic relationship between the new species and other related species, fragments of *COI*, *16S rRNA* and *H3* genes from 28 nudibranch species belonging to 11 genera (MolluscaBase 2020) were downloaded from GenBank (Table S1). The species names used in this paper conformed to those adopted in WORMS (MolluscaBase 2020). In some cases, informal names used in previous studies such as *Phestilla* sp. 2 (Faucci et al. 2007) were also used in this study. The *COI*, *16S rRNA* and *H3* sequences were aligned separately using MUSCLE v.3.8.31 (Edgar 2004) under default settings. For each species, the sequences of the three genes were concatenated using SequenceMatrix v.1.7.8 (Vaidya et al. 2011). Phylogenetic analyses were conducted using the Maximum Likelihood (ML) method and the Bayesian inference (BI) method based on the concatenated dataset. The ML analysis was conducted using raxmlGUI v.1.3.1 (Silvestro and Michalak 2012) with bootstrap supports estimated from analyses of 1000 pseudoreplicates. The GTR+I+G nucleotide-substitution model was selected using jModelTest v. 2.1.1 (Darriba et al. 2012) as the best model for the phylogenetic analysis, based on Akaike information criteria (AIC). The BI analysis was conducted using MrBayes v 3.2 (Ronquist and Huelsenbeck 2003) with random starting trees and 1x $10^7$ generations. Diagnostics were calculated every 1000 generations with a 25% burn-in to calculate posterior Probability (PP). Phylogenetic trees were rendered using FigTree 1.4.0., edited and annotated by Adobe Illustrator CC 2019 (Adobe, USA).

## RESULTS

### Morphology and Life-history Characteristics
### Class GASTRAPODA
### Order NUDIBRANCHIA
### Family Trinchesiidae F. Nordsieck, 1972

### *Phestilla goniophaga* sp. nov.

(Figs. 1–4)
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*Type material*: Holotype BU-Mol-20-001, live specimen 30 mm in length, ethanol preserved specimen 20 mm in length. ParatypesBU-Mol-20-002 to BU-

Mol-20-006, live specimens 8–15 mm in length, ethanol preserved specimens 7–17 mm in length. BU-Mol-20-001 to BU-Mol-20-004 were collected from Sharp Island in June 2019. Specimens BU-Mol-20-005 to BU-Mol-20-006 were collected from Chek Chau in June 2020.

*Type locality*: Eastern Hong Kong waters.

*Etymology*: The species epithet *goniophaga*, composed of parts of the Latin genus name "*Goniopora*" and "*phaga*" (eat), describes the predator-prey relationship between this new species and corals from the genus *Goniopora*.

*Geographical distribution*: The type specimens were collected from eastern Hong Kong waters including Sharp Island and Chek Chau. It has been found at Tung Ping Chau Marine Park and Wui Pai in north east waters and Bluff Island in eastern waters in our recent surveys, therefore should be a widely distributed species in Hong Kong. Comparing the *COI* sequences (with query cover of 90.0% and percent identity of 100.0%) deposited in NCBI shows that it is conspecific to *Phestilla* sp. 2 in Palau (Faucci et al. 2007). Thus, *P. goniophaga* sp. nov is expected to be widely distributed in the Indo-Pacific region where *Goniopora* spp. are found.

*Habitat*: 2–5 m water depth, associated with colonies of *Goniopora* spp., including *G. columna*, *G. djiboutiensis* and *G. lobata*.

*External morphology of holotype*: Mature live specimen length up to 3 cm (Fig. 1B). Body color brownish to pale reddish. Body excluding cerata elongate, dorsoventrally flattened. Notum with transverse wrinkles. Foot broad with rounded edge.

Oral veil rounded, extending about 1/3 to 1/2 of the length of oral tentacles. Oral tentacles and rhinophores smooth, digitiform. New born individuals with digitiform cerata, older ones terminally more oblate. Ceras cylindrical, each with a subterminal constriction. Cerata arranged in transverse rows with each row being situated on top of a ridge. Numbers of cerata on left and right sides not always identical. Cerata 16 rows, each row with 4 to 23 cerata; anterior and posterior rows with fewer and shorter cerata than mid-body rows. Length of cerata 1 to 8 mm. From eighth row to posterior, distance of lateral rows progressively smaller. Behind eighth row, pericardium forms a white rounded hump, almost halfway down the body (Fig. 1A).

Anus and reproductive opening both on right side of body. Anus acleioproctic, located between sixth and seventh rows of cerata. Reproductive opening located between fourth and fifth rows of cerata.

*Variations in external morphology*: Body length of live and ethanol preserved paratypes vary from about 16 mm to 30 mm, and 8 mm to 17 mm, respectively. There are 10 to 14 rows of cerata and up to 9 to 20 cerata per row. The maximum number of cerata occurs in the seventh and eighth row near the hump. The longest cerata appear in the eighth row, about 9 mm in length. Less rows of cerata and fewer number of cerata per row present in juvenile specimen (Fig. 2B).

*Internal morphology of holotype*: Body color of preserved specimen quite opaque. Digestive gland extending into cerata (Figs. 1B–1C, 3A). Color of cerata

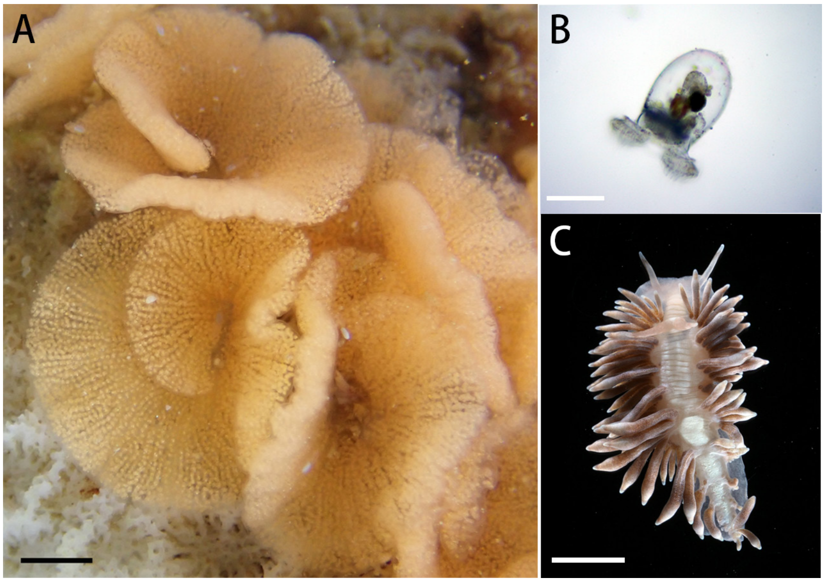

**Fig. 2.** *Phestilla goniophaga* sp. nov. A, Egg masses. B, Veliger with well-developed velum. C, Juvenile with under-developed cerata (paratype BU-Mol-20-003). Scale bars: A = 4 mm, B = 50 µm, C = 5 mm.

and digestive gland identical to that of the dinoflagellate *Cladocpium* sp. (Fig. 3B) in its host coral (Zhang et al. 2019). Glandular region without nematocysts (Fig. 3A).

A pair of jaws present in buccal mass, with a radula folded inside. Jaws thin and triangular, without denticles along masticatory edge (Fig. 3C). Radula formula 35 × 0.1.0. Each tooth with a strong central cusp tapering to a tip, six or seven primary denticles on each side, long and slender, slightly different in length (Fig. 3D). Base of central cusp and primary denticles with small secondary denticles.

Reproductive system diaulic with both female and male ducts (Fig. 3E). Ovotestis large, consisting of a number of lobules located posterior in coelom. Penial bulb elongated. Penis simple, with a small stylet inside penial sac. Prostate spherical, connecting to a swollen, carrot-like ampulla. Female gland big. Hermaphroditic duct connects to ovotestis. Vas deference narrow and winding. Bursa copulatrix spherical, connecting to vagina.

Eggs, egg masses and larvae: The newly laid eggs are orange in color. The developing embryos are light orange. The egg masses are ribbon-shaped, coiled, each ~1 cm in diameter (Fig. 2A). Inside the egg mass, eggs

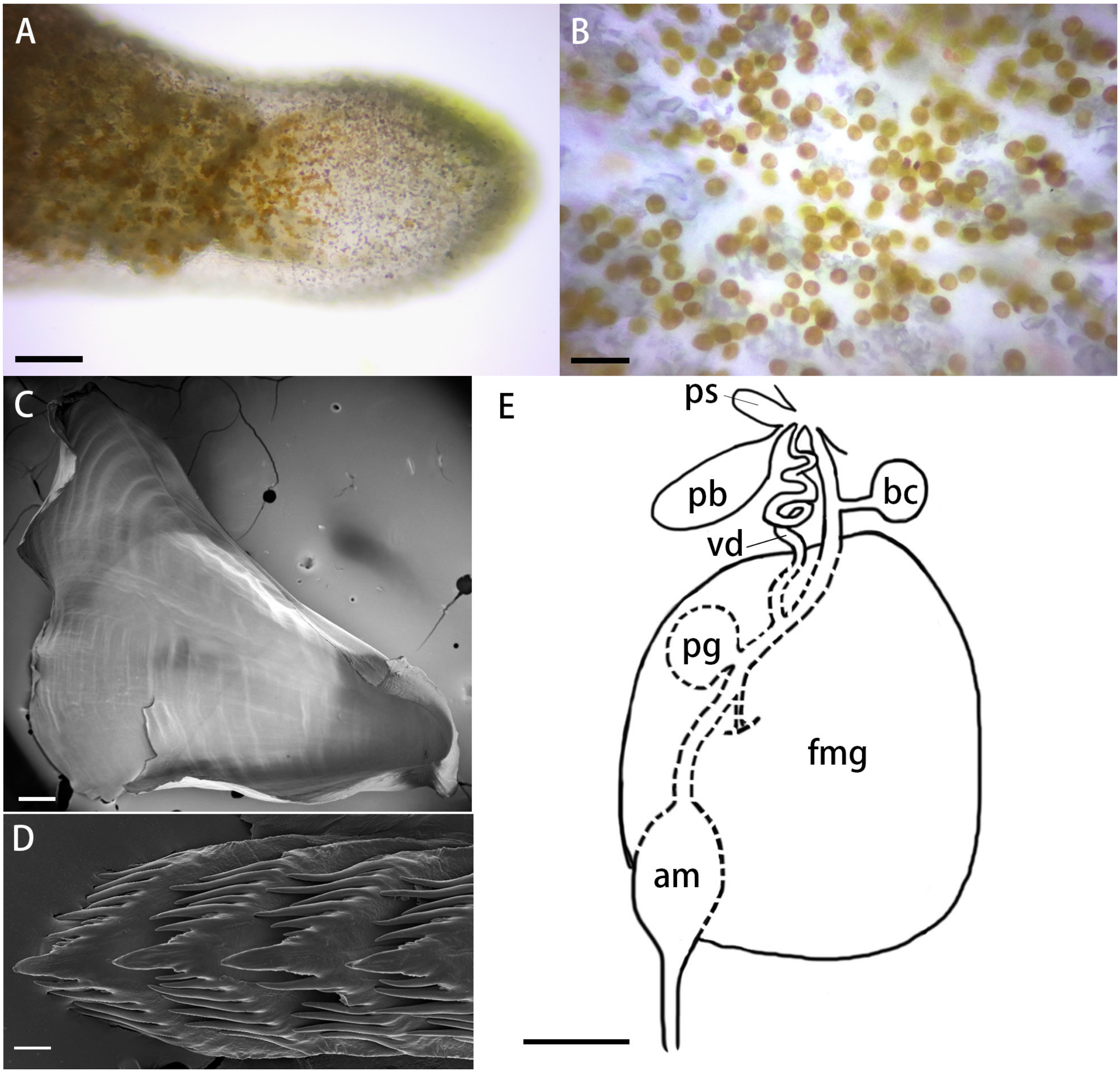

**Fig. 3.** Internal structures of *Phestilla goniophaga* sp. nov. A, Glandular region in the tip of a ceras. B, An enlarged part of ceras showing some intact *Cladocpium* sp. cells. C, A SEM micrograph of the jaw (lateral view). D, Radula. E, Reproductive system. am, ampulla; bc, bursa copulatrix; fgm, female gland mass; pb, penial bulb; pg, penial gland; ps, penial sac; vd, vas deferens. Scale bars: A = 100 µm; B = 10 µm; C = 200 µm; D = 20 µm; E = 5 mm.

are arranged in a radical pattern. Each egg mass has thousands of eggs (> 6000) coated with a translucent membrane (Fig. 2A). Development from egg to planktonic veligers with a well-developed swimming velum (Fig. 2B) takes approximately five days.

*Ecology*: Like other species from the genus *Phestilla*, *Phestilla goniophaga* sp. nov. possess cerata that mimic the color and shape of *Goniopora* spp. tentacles (Fig. 1A–1C). It is among the largest species of *Phestilla*. Individuals of this species together with their orange egg masses are usually found under *Goniopora* spp. colonies.

This new species has been observed to feed on *Goniopora columna*, *G. djiboutiensis* and *G. lobata*, but has not been found to associate with any other genus of corals in Hong Kong. Two to several individuals are often found to live on the same coral colony. During the productive season, they produce up to 20 egg masses on one coral colony, and the egg ribbons are glued tightly on the coral skeleton.

## Molecular Analysis

Nine gene sequences were obtained from three specimens of *P. goniophaga* sp. nov.

Removing the low-quality sites resulted in a 613-bp *COI* fragment, a 410-bp *16S rRNA* fragment and a 306-bp *H3* fragment. The concatenated DNA sequences of the three genes were used for phylogenetic analysis based on both the Maximum Likelihood (ML) method and the Bayesian inference (BI) method (Fig. 4). The topology of the two analyses were almost identical and most branches had high support values, except with several polytomies where the support values are quite low (ML < 50, PP < 0.9). All the *Phestilla* species with available sequences except *P. sibogae* formed a

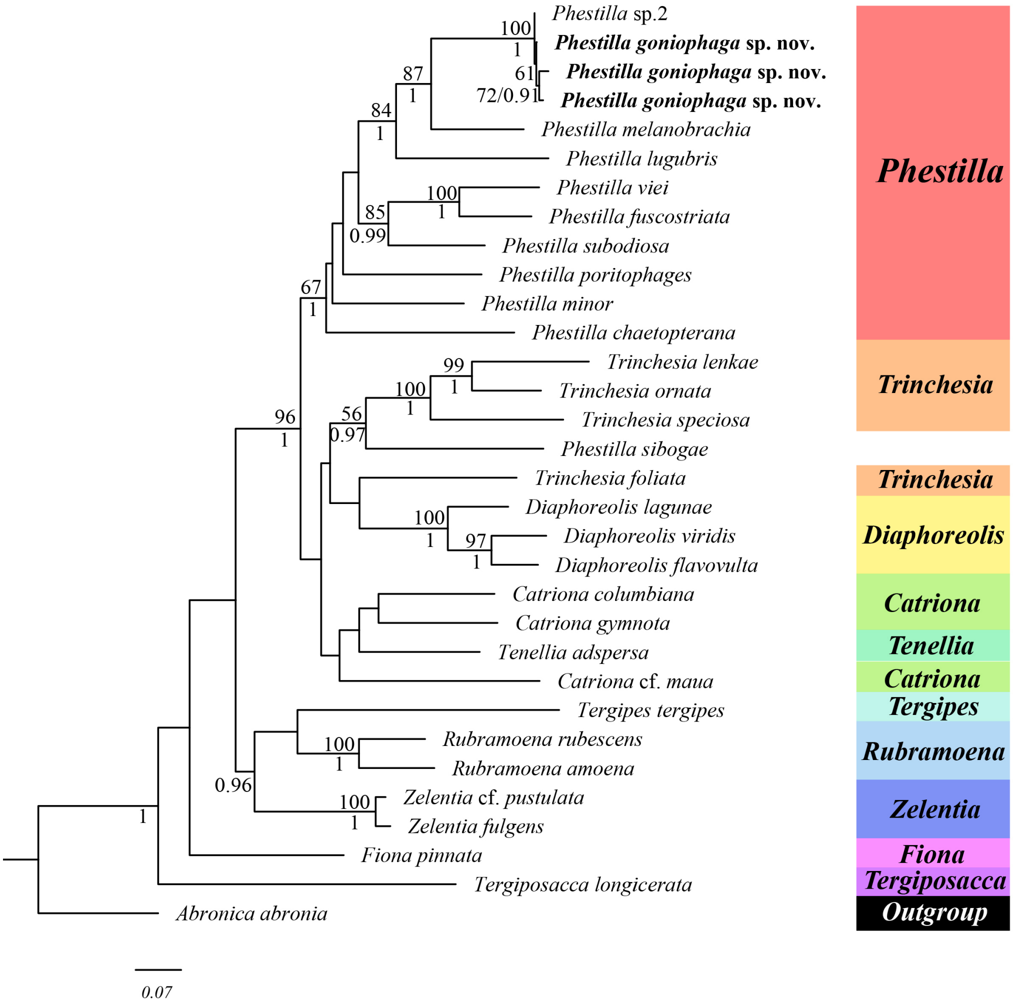

**Fig. 4.** Phylogenetic tree of nudibranchs from the family Trinchesiidae constructed based on the concatenated sequences of *COI*, *16S rRNA* and *H3* genes, inferred by Maximum Likelihood (ML) analysis and Bayesian Inference (BI) analysis. Only ML bootstrap values > 50 and PP value > 0.9 are shown.

monophyletic clade (posterior probabilities [PP] = 1). *Phestilla sibogae* is nested inside a clade of several *Trinchesia* species, rather than with other species of *Phestilla*. These results are congruent with the results of several previous studies (Cella et al. 2016; Ekimova et al. 2017; Mehrotra et al. 2020; Wang et al. 2020). The three specimens of *P. goniophaga* sp. nov. form a monophyletic clade with *Phestilla* sp. 2 from Palau (Faucci et al. 2007) and were deeply nested within the *Phestilla* clade. *Phestilla goniophaga* sp. nov. was sister to *P. melanobrachia*, a predator of corals from the genus *Tubastraea* (Harris 1968 1975; Salvini-Plawen 1972). *Phestilla lugubris*, together with the former mentioned species formed a clade that was sister to a clade consisting of *P. subodiosa*, *P. viei* and *P. fuscostriata*. *Phestilla poritophages*, *P. minor* and *P. chaetopterana* were progressively more distantly related to the clade.

Uncorrected minimum *p*-distance among the three individuals of *P. goniophaga* sp. nov. was small – only 0.3% for *COI*, 0.8% for *16S rRNA* and 0.0% for *H3*. However, the distances between the new species and its most closely related species *P. melanobrachia* are much larger – 14.3% for *COI*, 5.9% for *16S rRNA* and 3.9% for *H3* (Table S2).

## DISCUSSION

Our analyses showed that the divergence in *COI*, *16S rRNA* and *H3* sequences between *Phestilla goniophaga* sp. nov. and other *Phestilla* species ranged from 14.3 to 22.6%, 5.9 to 15.5% and 3.9 to 9.7%, respectively (Table S2). These values are much higher than the intraspecific sequence divergences in most molluscan species (*i.e.*, < 2% in *COI*, Layton et al. 2014), which supports the recognition of the new species. Phylogenetic analyses showed that *P. goniophaga* sp. nov. is nested within a clade that contains *P. melanobrachia*, *P. lugubris*, *P. minor* and *P. poritophages*, as well as an undescribed species *Tenellia* sp. 3 (Cella et al. 2016). Among these species, *P. goniophaga* sp. nov. is sister to *P. melanobrachia*. This clade is sister to a clade comprising of *P. subodiosa*, *P. viei*, *P. fuscostriata* and *P. chaetopterana*.

Among *Phestilla* spp., *P. melanobrachia* has been known to form obligate association with the scleractinian coral *Tubastraea* Lesson, 1830 and *Dendrophyllia* Blainville, 1830 (Harris 1975; Robertson 1970; Ritson-Williams et al. 2003; Fritts-Penniman et al. 2020), while *P. lugubris*, *P. panamica*, *P. minor* and *P. poritophages* are associated with corals from the genus *Porites* Link, 1807 (Rudman 1979 1981 1982). *Phestilla fuscostriata* (Metrotra et al. 2020) and *Phestilla subodiosa* (Hu et al. 2020) is a predator of *Pavona explanulata* (Lamarck, 1816) and *Pavona decussata* (Dana, 1846), respectively. *Phestilla viei* is a predator of *Montipora* Blainville, 1830 (Wang et al. 2020). Therefore, our phylogenetic analysis support the hypothesis that this host-specificity together with the monophyly of *Phestilla* support the conclusion of previous studies indicating corallivory in these nudibranchs has evolved only once, consisting with that in previous studies (Cella et al. 2016; Fritts-Penniman et al. 2020), although since then there has been host shift from one genera to another (Faucci et al. 2007).

There has been some confusion in the taxonomy history and diet of *Phestilla sibogae.* This species was originally described as a predator of *Porites*. However, Rudman (1981) considered it to be identical with *P. lugubris*. Gosliner et al. (2018) found that this species (as *Tellelia sibogae*) is a predator of hydroides from the genus *Sertularella*. The sequence of *P. sibogae* we used was taken from Cella et al. (2016), who found it to be a predator of hydroids (as *Tenellia sibogae*) by Gosliner et al. 2018. In the phylogenetic tree, it was nested with *Trinchesia* species which are known to feed on hydroids, outside the *Phestilla* clade. Our results therefore indicate that the sequence of *P. sibogae* used by Cella et al. (2016) was not likely from *P. sibogae* or *P. lugubris*, but a species of *Trinchesia.*

Although no *Goniopora*-eating nudibranch species was formally named prior to this study, our analysis showed that *Phestilla* sp. 2 collected from *Goniopora* in Palau (Faucci et al. 2007) should be conspecific of *P. goniophaga* sp. nov. based on their high similarity in *COI* (100%) and *16S rRNA* (99.75%) sequences. As such, we believe that *P. goniophaga* sp. nov. is widely distributed in the tropical and subtropical Indo-Pacific together with its host coral *Goniopora* (Veron 2000).

Morphologically, *P. goniophaga* sp. nov. can be distinguished from its congeneric species in five aspects. First, with up to 16 rows of cerata and 23 cerata in a single row, this new species has the largest number of cerata. Several species of this genus, such as *P. fuscostriata*, *P. chaetopterana*, *P. viei* and *P. subodiosa* have only a small number of cerata, likely due to paedomorphosis – the retention of larval trait of only few cerata in the adult. Several other *Phestilla* species possess a large number of cerata, but not numerous as in *P. goniophaga* sp. nov. For instance, *P. panamica* has up to 13 rows of cerata, and each row has up to 18 cerata (Rudman 1982). *Phestilla lugubris* has up to 15 rows of cerata, and each row has up to 18 cerata (Rudman 1981). *Phestilla melanobrachia* has up to 15 rows of cerata, and each row has up to 15 cerata (Harris 1968). Second, with the exception of *P. melanobrachia*, species in the clade that includes *P. panamica*, *P. lugubris*, *P. minor* and *P. viei* share a common characteristic that the pericardium forms a swollen hump on the notum (Rudman 1979 1981 1982). In *P. lugubris*, the hump situates at about anterior one-third of the notum (Rudman 1981), but in *P. goniophaga* sp. nov., *P. minor* and *P. panamica*, it is located in roughly the middle of the notum (Rudman 1982). Other species of *Phestilla* do not have an apparent hump on the notum. Third, the radula morphology of *P. goniophaga* sp. nov. is also unique. Among the recognized species of *Phestilla*, only *P. lugubris* and *P. melanobrachia* also possess a radula with a strong central cusp flanked by six to seven long, slender, and pointed primary denticles (Rudman 1981; Korshunova et al. 2017). However, unlike *P. lugubris* whose secondary denticles of the central cusp are quite large (~1/2 length of central cusp), those of *P. goniophaga* sp. nov. are usually very small (~1/5 length of central cusp). Fourth, the reproductive system of *P. goniophaga* sp. nov. resembles that of *P. panamica* and *P. lugubris* to some extent (Rudman 1981 1982), with respect to the shape of the organs and their relative position. However, in *P. melanobrachia*, its closely related species, the shape of ampulla and its relative position to female gland mass are different. Fifth, the color and shape of the egg mass of *P. goniophaga* sp. nov. are unique. No other *Phestilla* species lays orange color and coiled ribbon-shaped egg masses.

## CONCLUSIONS

We report *Phestilla goniophaga* sp. nov. – the first formally named predatory nudibranch of the scleractinian coral *Goniopora* spp. This new species has a white hump on the notum and long cerata that resembles the polyp mouth and tentacles of its host coral, respectively. It can be distinguished from other species of *Phestilla* by the large numbers and rows of cerata, the small secondary denticles on the central cusp of its radula, and the orange colored and coiled egg masses. Analyses of the *COI*, *16S rRNA* and *H3* gene sequences confirmed that *P. goniophaga* sp. nov. is a member of *Phestilla*, and it is distinct from other congeneric species. Although there have been studies in the biodiversity of nudibranchs in the northern South China Sea (Su et al. 2009), little is known about the diversity of coral-eating *Phestilla.* Together with Hu et al. (2020), our present study indicates that coral-eating nudibranchs in this region may have been overlooked in previous field surveys of nudibranchs. Given that their feeding activities may pose a threat to coral heath that is already deteriorating due to various human stressors (Mehrotra et al. 2020; Xie et al. 2020), it is essential to further discover their diversity and experimentally determine their potential ecological impact.

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**Authors' contributions:** JWQ initiated the study. JH conducted the morphological analysis and drafted the manuscript, JH and YZ conducted the molecular analysis, SKFY conducted the ecology survey, YJX first discovered and collected some of the samples. All authors revised the manuscript.

**Competing interests:** JH, YZ, SKFY, YJX and JWQ declare they have no conflict of interest.

**Availability of data and materials:** Nine DNA sequences of *Phestilla goniophaga* sp. nov.—three from the *COI* gene, three from the *16S rRNA* gene and three from the *H3* gene—are deposited in GenBank (accession numbers in Supplementary Material Table S1). The type specimens are deposited in Hong Kong Baptist University (catalog numbers BU-Mol-20-001 to BU-Mol-20-006).

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**Ethics approval consent to participate:** Not applicable.

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## Supplementary materials

**Table S1.** GenBank accession numbers of the sequences used to reconstruct the phylogeny of *Phestilla* spp. and their related genera/species. (download)

**Table S2.** Uncorrected *COI/16S rRNA/H3 p*-distances (%) among all species of described *Phestilla* with available sequences. (download)