

## THE GENUS *Phyllorhiza* (RHIZOSTOMEAE: MASTIGIIDAE) IN COASTAL WATERS OF THE ANDAMAN SEA AND THE GULF OF THAILAND

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**ABSTRACT:** Jellyfish belonging to the genus *Phyllorhiza* were gathered during both the northeast monsoon and southwest monsoon periods from the coast of Phang-nga, Phuket, Krabi, Trang, and Satun Provinces, southwestern Thailand, Andaman Sea, during 2009–2018. Additional specimens were collected from Chachoengsao, Phetchaburi, and Chumphon Provinces, the Gulf of Thailand, in 2015 and 2019. Morphological study and DNA analysis revealed that all specimens belong to one species *P. punctata*. This is the first detailed description of the species for this area even if *P. punctata* was previously recorded. The 16S and 18S sequences were deposited in NCBI genebank as KT982716 and KT982748, respectively. Comparative sequence analysis of the 16S rRNA and 18S rRNA gene fragments between our specimens from Thai waters and those in GenBank revealed that our samples matched those available sequences of *P. punctata* from Western Mexico, USA (Gulf of Mexico), Australia, and Eastern Mediterranean, based upon maximum likelihood. However, our clade is separate from *P. pacifica* which is found in the same geographic regions. The morphological analysis of *P. pacifica* requires further study.

**Keywords:** *Phyllorhiza*, Andaman Sea, Gulf of Thailand, morphological characters, molecular study

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### INTRODUCTION

*Phyllorhiza* Agassiz, 1862 are true jellyfish belonging to the class Scyphozoa, order Rhizostomeae, family Mastigiidae. The genus *Phyllorhiza* was first assigned by Agassiz in 1862. The genus is characterized by having 8 broad, leaf-shaped oral arms divided into three-fringed lobes with numerous pendant filaments. Collins *et al.* (2019) recognized 4 species of *Phyllorhiza*, which include *P. punctata* von Lendenfeld, 1884, *P. peronlesueuri* Goy, 1990, *P. luzoni* Mayer, 1915, and *P. pacifica* (Light,

1921). However, the status of *P. luzoni* is *nomen dubium*.

Among the species of *Phyllorhiza*, *P. punctata* is well known with a world-wide distribution. Its common name is the Australian spotted jellyfish or white spotted jellyfish and it was first collected from Port Jackson, Australia (von Lendenfeld 1884; Kramp 1965; 1970). This species is a native species of the Western Pacific (Kramp 1965; 1970). The species is well known as a non-indigenous species (NIS) and has migrated globally, *e.g.*, Mediterranean Sea (Abed-Navandi and Kikinger 2007, Galil *et al.*

2009; Gueroun *et al.* 2015; Deidun *et al.* 2017), the southern Aegean Coast of Turkey (Gülşahin and Tarkan 2012), Mexico (Ocaña-Luna *et al.* 2010), Gulf of Mexico, Caribbean Sea, Hawaii (Larsen and Perry [https://gcrf.usm.edu/fisheries\\_center/docs/brochure.sea.jellies.MS.sound.pdf](https://gcrf.usm.edu/fisheries_center/docs/brochure.sea.jellies.MS.sound.pdf)), Southern Brazil (Haddad and Noqueira-Junior 2006), and North East Brazil (Morandini *et al.* 2006).

In South East Asia, *P. punctata*, was reported in the coastal waters of Malaysia (Maghsoudlou *et al.* 2016; Low 2017). In Thai waters, *P. punctata* has been recorded from both the Gulf of Thailand and the Andaman Sea (Aungtonya and Chanachon 2012; Department of Marine and Coastal Resources 2017). While the DNA sequence of *P. pacifica* from the Andaman Sea, Phang-nga and Phuket Provinces, was clarified by Daglio and Dawson (2017), no detailed descriptions of *P. punctata* and *P. pacifica* accompany the noted occurrence of those two species.

The aims of this study are to describe, illustrate, and analyze the DNA sequence of *Phyllorhiza* from the Andaman Sea and the Gulf of Thailand as part of the continuing effort to understand the genetic diversity and DNA barcoding of jellyfish in Thai waters.

## MATERIAL AND METHODS

### Collection of specimens and morphological study

Materials in this study were collected during surveys of venomous jellyfish distribution in the Andaman Sea, a monitoring project carried out during the period 2009 to 2018. Specimens from the Gulf of Thailand were collected from Chachoengsao, Phetchaburi, and Chumphon Provinces in 2015 and 2019 (Fig. 1). The samples were collected from surface water by hand net, and from deeper water ( $\leq 5$  m depth) with a shrimp trammel net. The specimens were fixed and preserved in 3% formalin.

A total of 53 samples in the genus *Phyllorhiza* were gathered during both the northeast monsoon and southwest monsoon from the coast of the

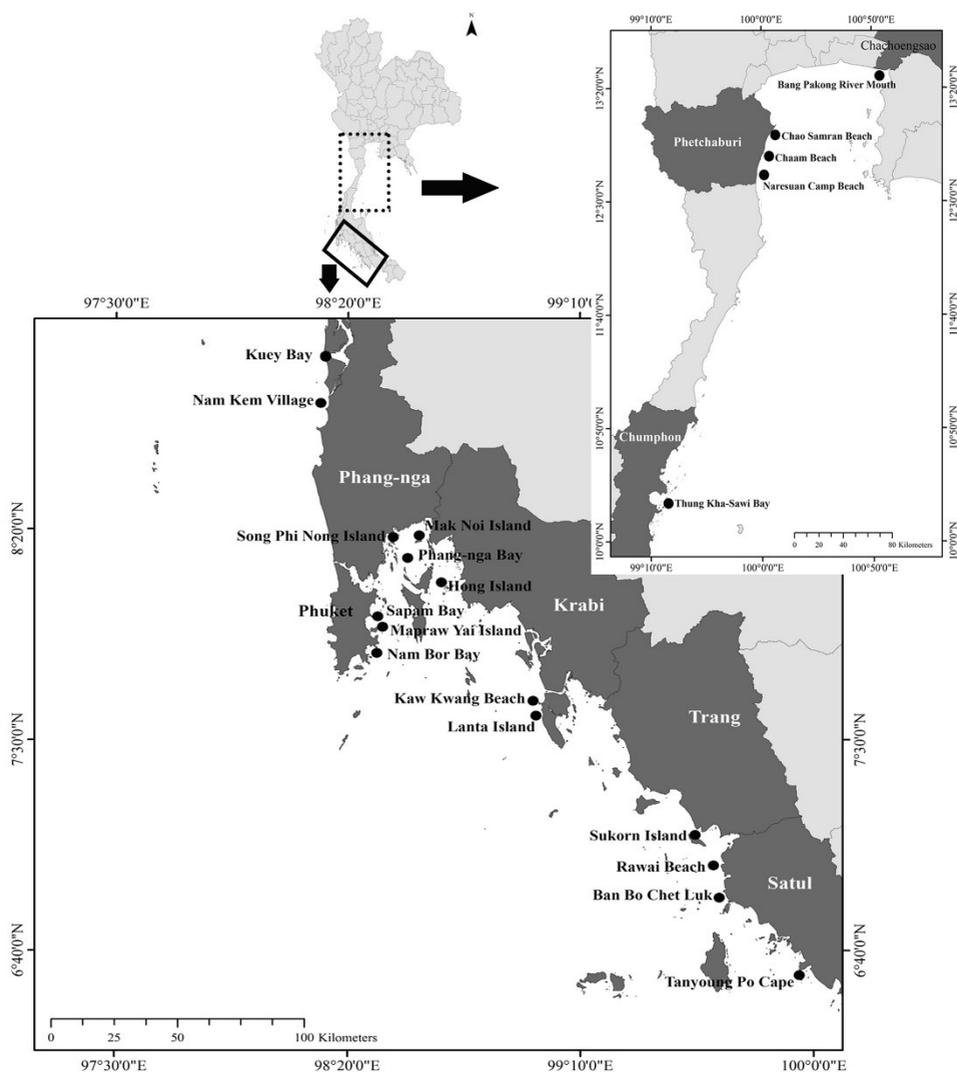
Andaman Sea during 2009–2018 and from the Gulf of Thailand in 2015 and 2019 (Fig. 1). Nearly all specimens were collected from sporadic sighting, except on one occasion when the sampling took place during an aggregation. Twelve specimens were collected from the Gulf of Thailand, Phetchaburi Province. Specimens of *Phyllorhiza* were examined, photographed and the bell diameters of preserved specimens were measured with digital vernier callipers (0.1 cm precision). Identification followed that of Mayer (1910), Kramp (1961), and Morandini *et al.* (2006).

### DNA extraction, PCR amplification and sequencing

Three tissue replicates used for genetic analysis were prepared from randomly selected specimens before specimens were fixed and preserved in 3% formalin. A small piece (0.5 cm x 0.5 cm) of mesoglea was excised and preserved in absolute alcohol (99% alcohol) at a ratio of 10 cl of alc to 1 cl of tissue. The tissues were rinsed before preservation to remove any adherent organisms. The fixed tissues were stored at 4 degrees Celsius for DNA analysis.

The genomic DNA was extracted using the commercial animal tissue extraction kit (OMEGA bio-tek, Inc., USA) or a CTAB/chloroform method described by Dawson *et al.* (1998). The nuclear 18S and mitochondrial 16S gene fragments were amplified using the primer pairs L18S: 5'-CGGAAGGGCACCACCAGGAG-3', 18Sb: 5'-GATCCTTCTGCAGGTTACACCTAC-3' and BRDGP-1: 5'-TCGACTGTTTACCAAAA-CATAGC-3', BRDGP-2: 5'-ACGGAATGAACTCAAATCATGTAAG-3', respectively (Bayha 2005; Bayha *et al.* 2010). PCR reactions were performed using a thermal cycler following the optimized protocol in Liu *et al.* (2016). The amplicons were directly sequenced bi-directionally on the ABI3130XL genetic analyser (Applied Biosystems, Inc., USA). In cases where direct sequencing was not applicable, amplicons were cloned using the TA cloning kits (Takara Biomedical Technology Co., Ltd., China) and then sequenced.

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**Figure 1.** Localities from where *Phyllorhiza* material from the Andaman Sea and the Gulf of Thailand were collected.

### Sequence analysis

The resulting sequences were cleaned for vector, primers and ambiguous nucleotides and subsequently aligned with the reference sequences downloaded from GenBank using the Clustal W algorithm (Thompson *et al.* 1994). The phylogenetic relationships between unknown specimens and

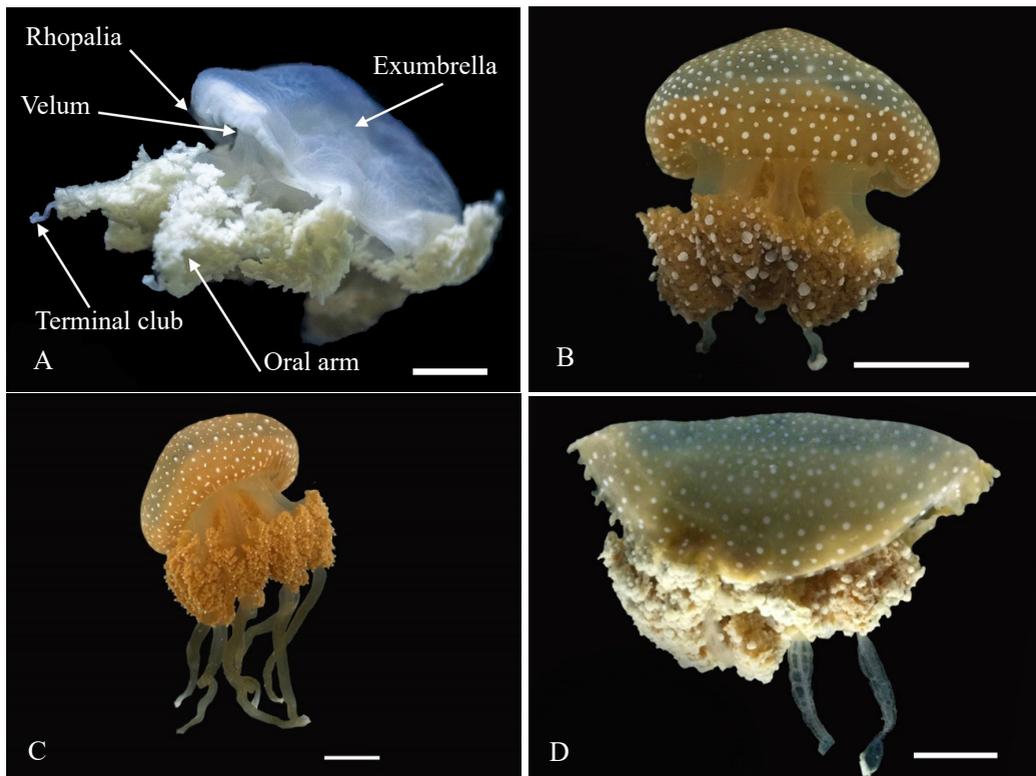
references were analyzed using maximum likelihood (ML) and neighbor joining (NJ) methods. Robustness of the resulting phylogenetic trees was assessed by bootstrapping for 1000 replicates. The best assignment of the unknown specimen was hypothesized, and the results from different genes compared to evaluate the consistency of the conclusions.

## RESULTS

Specimens from both the Andaman Sea and the Gulf of Thailand were brown with white spots on the surface of the exumbrella (Fig. 2). Bell widths were measured and the average bell width exceeded 61 mm in all cases (Table 1 and Appendix 1). Morphological and molecular analysis revealed

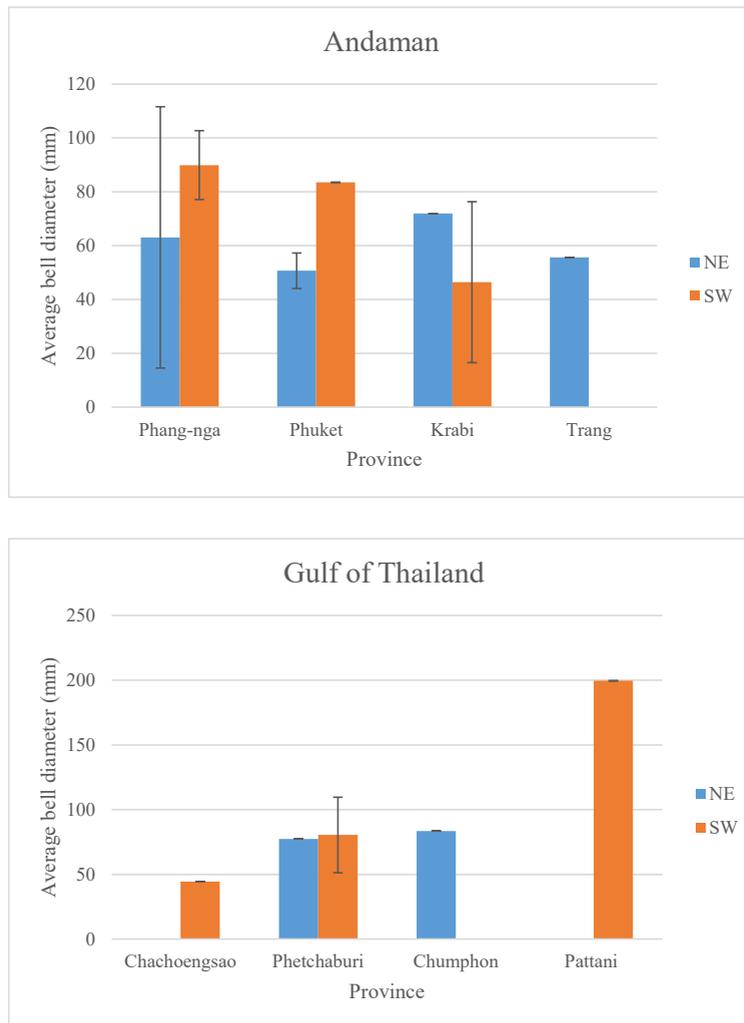
that specimens belonged to only one species, *Phyllorhiza punctata*.

The specimens from the Andaman Sea exhibited a trend for larger umbrella size during the southwest monsoon (Fig. 3). But it is difficult to conclude from the average bell width of the specimens from the Gulf of Thailand due to few collected specimens from the Gulf of Thailand.



**Figure 2.** *Phyllorhiza punctata*: A. Morphology of specimens in 3% formalin, B–D. Brown, D. White dots interspersed around the bell. A–C: PMBC 30210; D: PMBC 30338. (scale bar A= 1 cm, B–D = 2 cm).

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**Figure 3.** Average bell diameter of *Phyllorhiza punctata* from the Andaman Sea during 2009–2018 and from the Gulf of Thailand in 2015 and 2019.

**Table 1.** Bell width of *Phyllorhiza punctata* from the Andaman Sea during 2009–2018 and the Gulf of Thailand in 2015 and 2019.

| Provinces    | No. of specimens | Bell diameter (mm) |      |                 |
|--------------|------------------|--------------------|------|-----------------|
|              |                  | Mean               | S.D. | Range (min-max) |
| Phang-nga    | 6                | 76                 | 54.9 | 76–155          |
| Phuket       | 10               | 54                 | 15.2 | 45–84           |
| Krabi        | 3                | 55                 | 33.3 | 17–76           |
| Trang        | 2                | 56                 | 17.4 | 43–68           |
| Satun        | 20               | 56                 | 43.4 | 17–182          |
| Chachoengsao | 1                | 44                 | -    | -               |
| Phetchaburi  | 7                | 80                 | 25.3 | 52–126          |
| Chumphon     | 4                | 83                 | 32.5 | 55–130          |

### TAXANOMY

Family Mastigiidae Stiasny, 1921

Genus *Phyllorhiza* Agassiz, 1862

**Type species.** *Phyllorhiza punctata* von Lendenfeld, 1884.

**Diagnosis.** Broad, leaf-shaped oral arms with window-like openings in lateral membrane and numerous bulb-ended filaments, intracircular network of canal not connected to the perradial rhopalar canals, white warts present on the exumbrella.

*Phyllorhiza punctata* (von Lendenfeld, 1884)  
Figs. 2A–D, 3A–D, 4A–D, 5A–D, Appendix 2

*Phyllorhiza punctata* von Lendenfeld, 1884: 296–297.  
*Phyllorhiza punctata* - Mayer 1910: 684–685; Kramp 1961: 361–362; Morandini *et al.* 2006: 5.

#### Material examined.

A total of 53 specimens were collected and examined (Appendix 1).

**Description.** Hemispherical bell with shield-shaped apex (Fig. 2); smooth exumbrella surface with round white spots evenly distributed (Figs. 2, 4A). No tentacle at bell margin. Six to eight rounded velar lappets in each octant with short furrow between each lappet and longer furrow between each pairs of velar lappets (Fig. 4B and 4D). Occasionally, small lappet formed between two lappets, in the furrow, in larger specimens (Fig. 4D). Eight clefts with rhopalia.

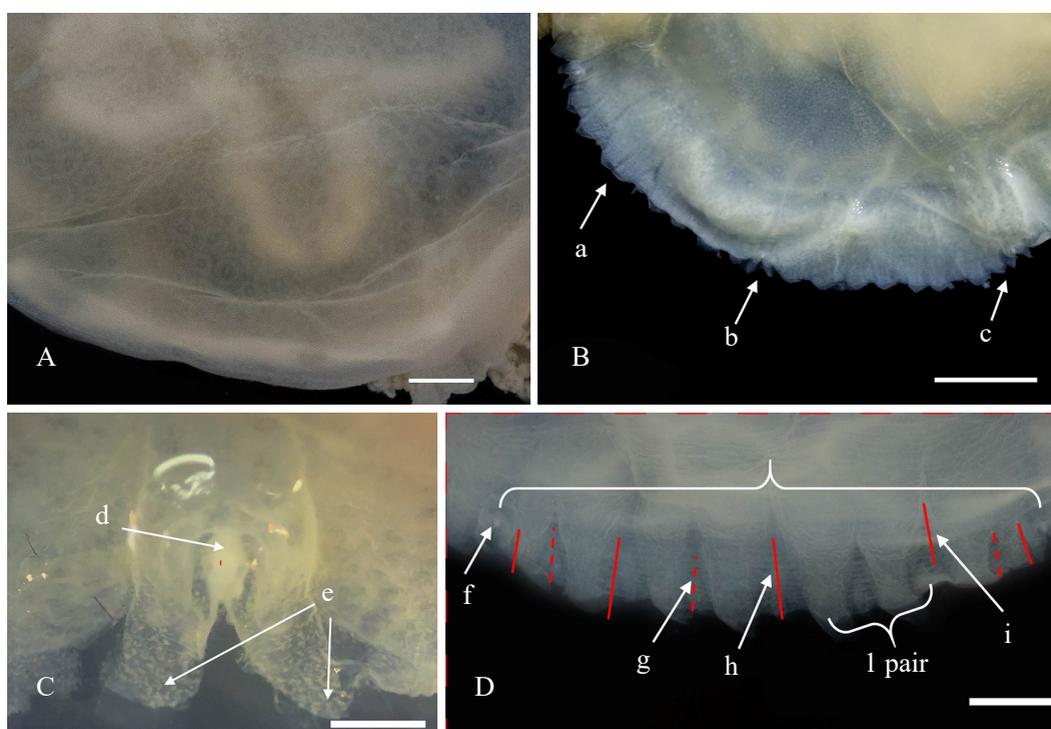
Eight rhopalia present in each cleft at umbrella margin, where perradial canal and interradian canal end (Fig. 4B), with two small and pointed rhopalar lappets. Rhopalia is oval-shaped (Fig. 4C).

Eight oral arms, 1/3 to 2/3 as long as bell diameter (Fig. 5A). Distal part develops to three wings with window-like opening and frills (Fig. 5B), number of bulb-ended appendages sometimes present. Each oral arm has one terminal club, sometimes ribbon-like; about 1/3 to 3 times of arm length, with bulb-like ending (sometimes not obvious) (Fig. 5D). Numerous filaments on oral disk (Fig. 5C).

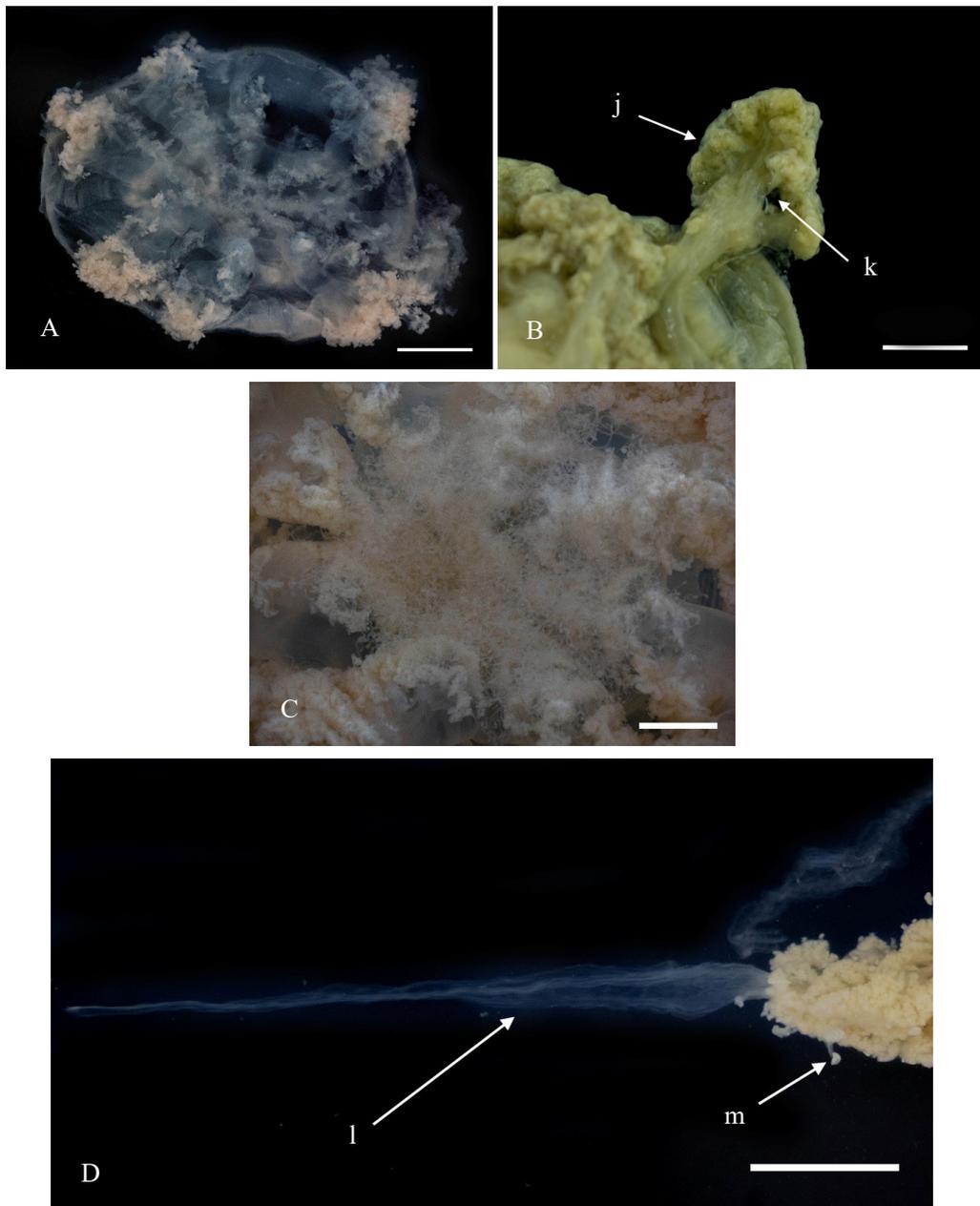
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Ring canal present with eight rhopalar radial canals, arising from central stomach to 8 rhopalia at the bell margin comprising 4 perradial canals and 4 interradian canals. Intracircular network of anastomosing canals connecting with ring canal and perradial-rhopalar canals. Beyond ring canal, each radius is connected to a mesh of canals, which becomes denser towards the bell margin (Fig. 6A). Corona muscle, folded, present in each octant covering 2/3 of bell radius towards the margin (Fig. 6B). Radius muscle absent. Gastrovascular cavity shape floret, divided in to 4 pouches (Fig. 6C). Gonads are yellowish-white and floret shape (Fig. 6D).

**Remarks.** The characters of umbrella, oral arm, velar lappets, rhopalial lappets and anastomosing canals, agree with those described by Morandini *et al.* (2006) (Appendix 2). The shape of terminal appendages in some of our specimens, however, diverged from their report: instead of filaments with terminal clubs, some ribbon-like projections were observed (Fig. 4D). This character was also mentioned by Larsen and Perry ([https://gcr1.usm.edu/fisheries\\_center/docs/brochure.sea.jellies.MS.sound.pdf](https://gcr1.usm.edu/fisheries_center/docs/brochure.sea.jellies.MS.sound.pdf)) in their publication ‘Guide to the Sea Jellies of the Northern Gulf of Mexico’. In some specimens, the filaments / terminal club were missing.

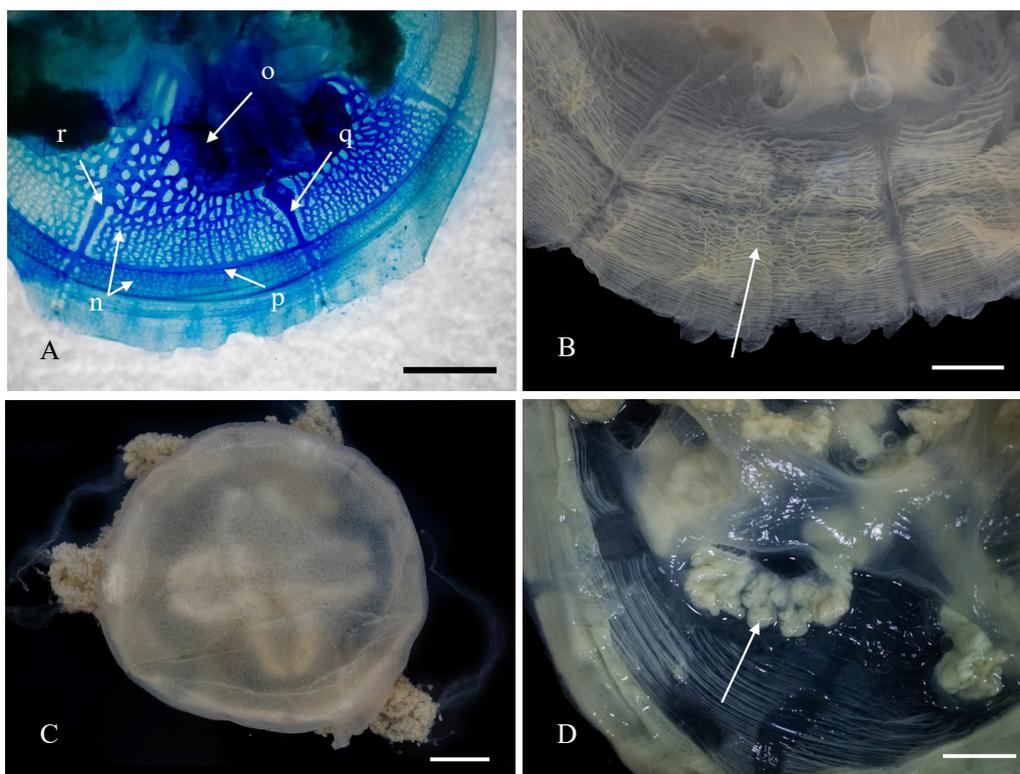


**Figure 4.** *Phyllorhiza punctata*: A. White warts, B. Velar lappet (a), rhopalium (b) and rhopalial lappet (c), C. Rhopalium (d) and rhopalial lappet (e), D. Rhopalia (f), short furrow (g), long furrow (h), small lappet in the furrow (i). A and D: PMBC 30213, B and C: PMBC 30211. (scale bar A–D = 1 cm).



**Figure 5.** *Phyllorhiza punctata*: A. Eight oral arms, B. Frills (j) and window-like opening (k), C. Filament on oral disk, D. Filament with bulb (l) and ribbon-like terminal club (m). A: PMBC 30215, B: PMBC 30211, C: PMBC 30214, D: PMBC 30213. (scale bar A, D = 2 cm, B–C = 1 cm)

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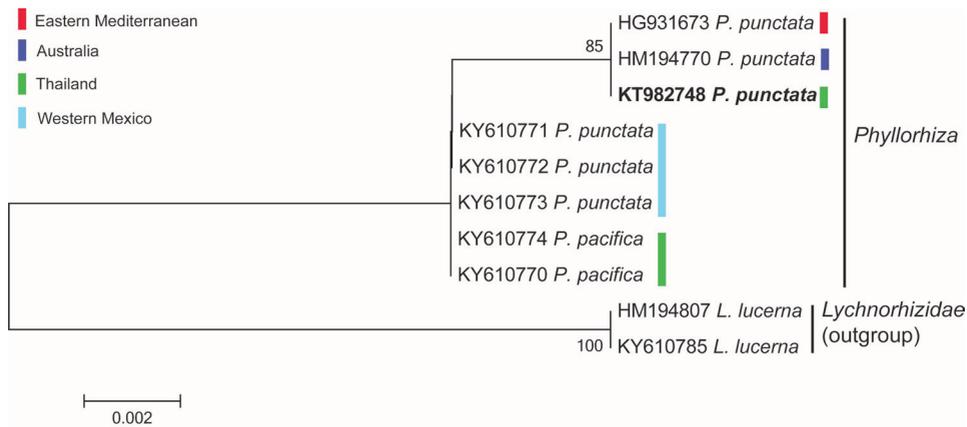
**Figure 6.** *Phyllorhiza punctata*: A. Network of canals (n) visible after injection of blue dye into the central stomach (o) connect ring canal (p), perradial-rhopalar canal (q) and interradial-rhopalar canal (r); B. Corona muscle fold (arrow); C. Apical view shows floret-shape gastrovascular cavity; D. Gonad (arrow). A: PMBC 30207, B and C: PMBC 30213, D: PMBC 30216. (scale bar A–B, D = 1 cm, C = 2 cm)

### DNA sequencing

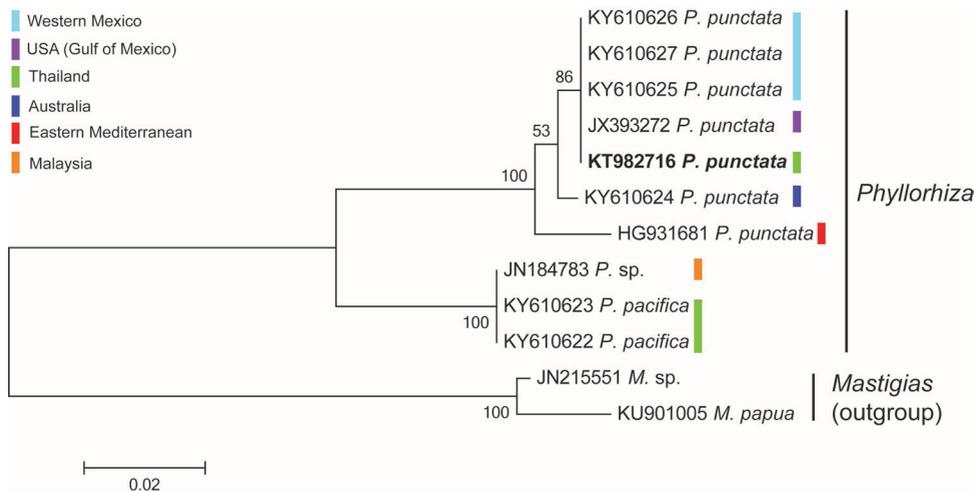
DNA sequences, partial 16S and 18S genes, were generated from three samples (PMBC 30227, 30228 and 30338). The three 18S sequences were 100% identical, and were deposited in NCBI GenBank as one representative sequence (KT982748). Similarly, the identical 16S sequences were deposited as KT982716. These sequences were then aligned with those *Phyllorhiza* spp. sequences available from NCBI database, including seven 18S genes and nine 16S genes.

The resulting trees based on both 18S and 16S genes reveal a similar phylogenetic status of our samples. As in Figure 7 and 8, KT982748 and KT982716 fell within the clades of *Phyllorhiza punctata* in 18S and 16S trees, respectively. The other 3 retrieved 16S sequences (JN184783,

KY610623 and KY610622) from Malaysia and Thailand, reported by Dalio and Dawson (2017), formed a monophyletic clade of *P. pacifica* which was sister to *P. punctata*. Whereas, the five 18S sequences (KY610770–4) from Western Mexico and Thailand, reported by Dalio and Dawson (2017), formed a polyphyletic clade next to *P. punctata*, which was probably due to few polymorphic nucleotides (only 2) between these two groups of sequences. Although, our specimens of *Phyllorhiza* and those used in Daglio and Dawson (2017) are from the same geographic regions, Phang-nga and Phuket Provinces, the clades are separate, supporting the morphological differences of *P. punctata* and *P. pacifica*, albeit limited by the absence of sequences for related species in the same genus, such as *P. peronlesueuri* and *P. luzoni*.



**Figure 7.** Maximum-Likelihood tree based on the partial 18s ribosomal DNA sequences. Numbers on each node are bootstrapping support after 1000 replicates. The sequences of *Lychnorhizidae lucerna* (HM194807 and KY610785) were treated as an outgroup. Bold font indicates sequence from this study. Locations of the sequences in *Phyllorhiza* were labelled with the colour bars and noted in the key on the at the upper left corner of the Figure.



**Figure 8.** Maximum-Likelihood tree based on the partial 16s ribosomal DNA sequences. Numbers on each node are bootstrapping support after 1000 replicates. The sequences of *Mastigias* spp. (JN215551 and KU901005) were treated as an outgroup. The sequence KT982716 (in bold) is derived from this study. Locations of the sequences in *Phyllorhiza* were labelled with the colour bars and noted in the key on the upper-left corner of the Figure.

## DISCUSSION AND CONCLUSION

This is the first detailed description of *Phyllorhiza punctata* from this area even if the species was previously recorded from the Andaman Sea and the Gulf of Thailand by Aungtonya and

Chanachon (2012) and Department of Marine and Coastal Resources (2017). All specimens from the Andaman Sea and an additional specimen from the Gulf of Thailand have the same morphotype, brown umbrella and white spots on the exumbrella. *Phyllorhiza* materials from the Andaman Sea were

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genetically identical to those from the Gulf of Thailand, therefore, *P. punctata* is the only species reported in this study. The species is characterized by a very thick exumbrella with white spots evenly distributed, 8 rounded velar lappets and 2 pointed rhopalar lappets in each octant, three-winged oral arms, the lower parts of which have a number of bluntly-ending filaments and terminal clubs. A network of canals connects the central stomach, ring canal, and rhopalar canal but not the perradial rhopalar canals. The canal mesh outwards of the ring canal fuses with the radial-canals.

The morphotype of our specimens agree with those reported by Bolton and Graham (2004), Haddad and Noqueira-Junior (2006), Morandini *et al.* (2006), Abed-Navandi and Kikinger (2007), Galil *et al.* (2009), Ocaña-Luna *et al.* (2010), Gülşahin and Tarkan (2012), Gueroun *et al.* (2015), Deidun *et al.* (2017), and Low (2017). They all report the surface of the exumbrella of *P. punctata* from Australia, Gulf of Mexico, Mexico, Brazil, western USA, Mediterranean Sea, Turkey, Puerto Rico, and Malaysia to have different degrees of brown colouration, and white spots. In contrast with a study from Malaysia (Maghsoudlou *et al.* 2016), where at least three different morphotypes of *Phyllorhiza* spp. have been recorded, *e.g.*, *Phyllorhiza punctata* (recorded as *Phyllorhiza* sp. 1), *Phyllorhiza* sp. 2 and *Phyllorhiza* sp. 3. The morphotypes of *Phyllorhiza* sp. 2 are blue, pink, and purple in colour, with no white dots interspersed around the bell, whereas *Phyllorhiza* sp. 3 are dark brown, with no dots neither. However, they concluded that the variation in colour was not enough to classify

*Phyllorhiza* sp.2 and sp.3 as new species of *Phyllorhiza*. This conclusion agrees with Bolton and Graham (2004), who suggested that variation in colour may be due to endosymbiotic zooxanthellae in the tissue. The identification of *Phyllorhiza* sp. 2 and *Phyllorhiza* sp. 3 requires further clarification. Nevertheless, the DNA sequence of *P. pacifica* from the Andaman Sea was clarified by Daglio and Dawson in 2017, while the present study clarified the morphology and DNA sequence of *P. punctata* from the Andaman Sea and the Gulf of Thailand. The morphology of *P. pacifica* in Thai waters is yet to be analysed and requires further studies.

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**Appendix 1.** *Phyllorhiza punctata*: selected materials for deposit in the PMBC Reference Collection (\* indicates samples used for DNA sequencing).

| PMBC no. | Locality             | Province  | Collecting Date | No. of specimens | Bell Diameter (mm) |
|----------|----------------------|-----------|-----------------|------------------|--------------------|
| 30208    | Song Phi Nong Island | Phang-nga | 19/7/2012       | 1                | 41.51              |
| 30214    | Song Phi Nong Island | Phang-nga | 5/9/2012        | 1                | 155.38             |
| 30207    | Mak Noi Island       | Phang-nga | 5/9/2012        | 1                | 72.87              |
| 30216    | Phang-nga Bay        | Phang-nga | 14/3/2013       | 1                | 130.35             |
| 30227*   | Kuey Bay             | Phang-nga | 24/12/2014      | 1                | 41.16              |
| 30228*   | Nam Kem Village      | Phang-nga | 5/2/2015        | 1                | 17.66              |
| 26276    | Nam Bor Bay          | Phuket    | 30/11/2009      | 4                | 56.02              |
|          |                      |           |                 |                  | 44.91              |
|          |                      |           |                 |                  | 35.02              |
|          |                      |           |                 |                  | 37.34              |
| 30417    | Mapraw Yai Island    | Phuket    | 27/7/2011       | 1                | 83.52              |
| 26869    | Sapam Bay            | Phuket    | 29/11/2011      | 5                | 58.47              |
|          |                      |           |                 |                  | 71.45              |
|          |                      |           |                 |                  | 46.48              |
|          |                      |           |                 |                  | 60.21              |
|          | 46.05                |           |                 |                  |                    |
| 30220    | Hong Island          | Krabi     | 13/3/2013       | 1                | 71.93              |
| 30219    | Lanta Island         | Krabi     | 19/8/2013       | 1                | 76.33              |
| 30206    | Kaw Kwang Beach      | Krabi     | 30/10/2013      | 1                | 16.55              |
| 30217    | Sukorn Island        | Trang     | 13/2/2013       | 2                | 43.35              |

| PMBC no. | Locality                | Province     | Collecting Date | No. of specimens | Bell Diameter (mm) |
|----------|-------------------------|--------------|-----------------|------------------|--------------------|
|          |                         |              |                 |                  | 67.93              |
| 30215    | Tanyong Po Cape         | Satun        | 17/11/2012      | 1                | 102.13             |
| 30213    | Ban Bo Chet Luk         | Satun        | 28/1/2014       | 3                | 98.61              |
|          |                         |              |                 |                  | 100.93             |
|          |                         |              |                 |                  | 116.53             |
| 30211    | Rawai Beach             | Satun        | 28/11/2017      | 1                | 61.59              |
| 30212    | Rawai Beach             | Satun        | 28/11/2017      | 1                | 61.28              |
| 30210    | Rawai Beach             | Satun        | 27/3/2018       | 10               | 33.04              |
|          |                         |              |                 |                  | 29.97              |
|          |                         |              |                 |                  | 28.93              |
|          |                         |              |                 |                  | 31.14              |
|          |                         |              |                 |                  | 31.83              |
|          |                         |              |                 |                  | 59.65              |
|          |                         |              |                 |                  | 19.93              |
|          |                         |              |                 |                  | 17.86              |
|          |                         |              |                 |                  | 16.97              |
|          |                         |              |                 |                  | 16.66              |
| 30209    | Rawai Beach             | Satun        | 24/4/2018       | 3                | 26.21              |
|          |                         |              |                 |                  | 39.22              |
|          |                         |              |                 |                  | 51.52              |
| 30218    | Rawai Beach             | Satun        | 9/6/2018        | 1                | 182                |
| 11503    | Bang Pakong River Mouth | Chachoengsao | 8/7/2019        | 1                | 44.45              |
| 30338    | Chaam Beach             | Phetchaburi  | 26/2/2015       | 1                | 77.31              |
| 11594    | Naresuan Camp Beach     | Phetchaburi  | 11/7/2019       | 1                | 125.57             |
| 11803    | Chao Samran Beach       | Phetchaburi  | 9/7/2019        | 1                | 56.49              |
| 11804    | Cha-am Beach            | Phetchaburi  | 10/7/2019       | 4                | 51.61              |
|          |                         |              |                 |                  | 75.58              |
|          |                         |              |                 |                  | 74.51              |
|          |                         |              |                 |                  | 98.52              |
| 11805    | Thung Kha-Sawi Bay      | Chumphon     | 19/2/2019       | 4                | 54.87              |
|          |                         |              |                 |                  | 70.6               |
|          |                         |              |                 |                  | 78.3               |
|          |                         |              |                 |                  | 129.97             |

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**Appendix 2.** Diagnosis characteristic and distribution of *Phyllorhiza* spp. (Modified after von Lendenfeld 1884; Mayer 1910, 1915; Light 1921; Kramp 1961; Elliot *et al.* 1996; Haddad and Noqueira-Junior 2006; Morandini *et al.* 2006; Abed-Navandi and Kikinger 2007; Ocaña-Luna *et al.* 2010; Yap and Ong 2012; Gueroun *et al.* 2015; Deidun *et al.* 2017; Collins *et al.* 2019; Larsen and Perry ([https://gcr1.usm.edu/fisheries\\_center/docs/brochure.sea.jellies.MS.sound.pdf](https://gcr1.usm.edu/fisheries_center/docs/brochure.sea.jellies.MS.sound.pdf)) and present study).

|   | <i>P. punctata</i><br>von Lendenfeld, 1884  | <i>P. luzoni</i> Mayer, 1915  | <i>P. pacifica</i> (Light, 1921)  |
|---|---|---|---|
| <b>Distribution</b>                                   | Western Pacific, Mediterranean Sea, Mexico, Gulf of Mexico, Caribbean Sea, Hawaii, Southern Brazil and North East Brazil, Malaysia, Thailand (Andaman Sea and Gulf of Thailand)   | Philippines   | Philippines, Strait of Malacca, Thailand (Andaman Sea)  |
| <b>Bell diameter</b>                                  | up to 62 cm   | 6 cm wide   | up to 40 cm   |
| <b>Exumbrella</b>                                     | very thick with white spots   | finely granular   |   |
| <b>Lappets</b>  | 8 rounded velar lappet and 2 pointy rhopalar lappets in each octant   | 9 rounded velar lappets in each octant  | 8 velar lappet in each octant, two double lappets in the middle with two single lappet and one ocular pointed lappet on each side |
| <b>Mouth-arms</b>                                     | three-winged oral arms (2/3 as long as umbrella diameter), lower part with number of bluntly-ending filaments (2/3 as long as oral arms themselves) and terminal club   | slender, strongly compressed naked upper part (first 13 mm.), three-winged lower part without appendage         | mouth-arms with terminal appendages as long as oral arm and predominantly purple  |
| <b>Anastomosis between canals and stomach</b>         | Network of canals connect central stomach, ring canal, and rhopalar canal but intracircular canal not connect with the perradial rhopalar canals, outer side of ring canal with network of vessel which fuse with radial-canals | 6–9 inter-rhopalar canal join with rhopalar canals in each octant   |   |
| <b>Radial-canals (rhopalar canals) and ring canal</b> | 8 radial-canals (4 perradial-canals and 4 interradia l-canals) arise from central stomach to the 8 marginal sense-clubs; rhopalia, and connect with ring-canal  | 8 radial-canals arise from central stomach to the 8 marginal sense-clubs; rhopalia, and connect with ring-canal |   |

|         | <i>P. punctata</i><br>von Lendenfeld, 1884 | <i>P. luzoni</i> Mayer, 1915                                     | <i>P. pacifica</i> (Light, 1921) |
|---------|--|--|----------------------------------|
| Remarks |  | This species is <i>nomen dubium</i> (Collins <i>et al.</i> 2019) |                                  |

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