

Hawaiian Phoronida (Lophophorata) and Their Distribution in the Pacific Region¹

JULIE H. BAILEY-BROCK² AND CHRISTIAN C. EMIG³

ABSTRACT: Five *Phoronis* species are found in Hawaiian waters. Three were recorded previously, and two others, *P. muelleri* and *P. pallida*, are added here. *Phoronis ovalis* (the smallest) and *P. hippocreperia* are perforant species forming burrows in coral rock, shells, and barnacle encrustations, and *P. psammophila*, *P. muelleri*, and *P. pallida* are sand-dwellers. Species diagnosis in phoronids requires sectioning to estimate muscle formulas and arrangement of other internal organs. Included are a key to Hawaiian species based on visible external features (so not entirely accurate), description of each, and distribution in Hawaiian waters and the Pacific Ocean.

THE PHYLUM PHORONIDA as currently recognized comprises 10 known species in two genera, all from the Pacific Ocean. Five species are found in Hawaiian waters (Figure 1). Three were recorded from O'ahu, Hawai'i (Emig 1977, Sorden 1983), and described briefly in the revision of C. H. Edmondson's *Reef and Shore Fauna of Hawaii* (Emig and Bailey-Brock 1987): *Phoronis ovalis*, *P. hippocreperia*, and *P. psammophila*. During recent benthic surveys off the south and west shores of O'ahu, two other phoronid species were found: *Phoronis muelleri* and *P. pallida*. Phoronids have a simple morphology comprising a lophophore surrounding the mouth and epistome, and posterior trunk. Species are distinguished on 11 characters (Emig 1985*b*), such as habitat, structure of the nephridia, number of giant nerve fibers, number and type (feathery or bushy) of longitudinal muscles, and brooding patterns. Species identification requires microscopical examination of internal organs and systems as histological sections.

The Pacific distribution of the five species is discussed and a brief diagnosis is given of

each. A working key, based primarily on visible external structures, is included.

MATERIALS AND METHODS

Phoronids were collected from O'ahu reefs by snorkeling or wading in shallow water (0–5 m) and from depths of 33–70 m by scuba diving or with a van Veen grab operated from a boat. Sand, fouling materials on pier pilings, and coral rubble all yielded phoronids. Sand samples were preserved in formalin and the phoronids later transferred to 75% ethanol. Carbonate rubble was acid dissolved (Brock and Brock 1977) and phoronids sieved from the residue. Entire specimens were embedded in wax and thin sections (7 μ m) made for microscopic examination by C.C.E. Muscle formulas were determined for each species based on counts of longitudinal body-wall muscles in trunk quadrants limited by the four longitudinal mesenteries (Figure 2*a,b*).

RESULTS

Collecting locations, characteristics of the habitat, and brief diagnoses for the five *Phoronis* species known from Hawaiian waters are as follows. All locations are within 2 statute miles (3.2 km) of shore on west, south, and east coasts of O'ahu (Table 1).

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² Department of Zoology, University of Hawai'i at Mānoa, 2538 The Mall, Honolulu, Hawai'i 96822.

³ CNRS-UMR 6540, Centre d'Océanologie, Station Marine d'Endoume, Rue de la Batterie-des-Lions, 13007 Marseille, France.

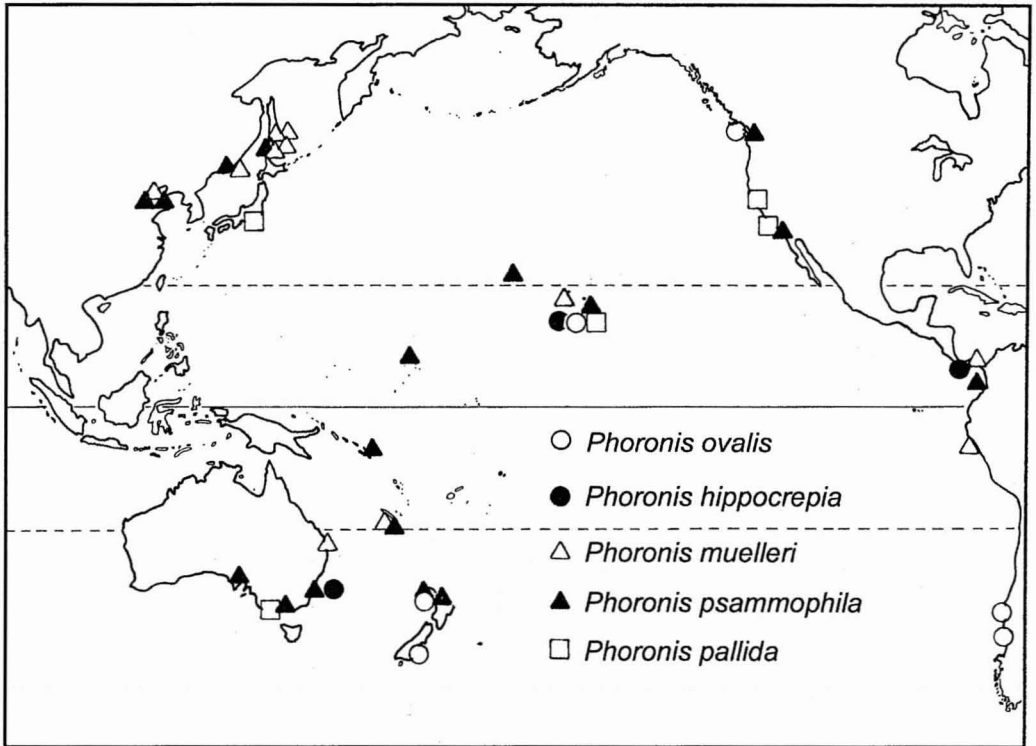


FIGURE 1. Distribution of the five *Phoronis* species in the Pacific region.

Genus *Phoronis* Wright, 1856

Absence of epidermal collar-fold below the lophophore.

Phoronis ovalis Wright, 1856

In Kāneʻohe Bay and off Mōkapu (33 m depth, March 1998), Waiʻanae (33 m depth).

Muscle formulas established on six specimens; mean and composite formulas for these specimens are as follows:

$$8/8 = 16, 7-8/7-9 [14-16]$$

DIAGNOSIS: *Phoronis ovalis* burrows into empty and decayed mollusk and barnacle shells and carbonate rocks. Collected from intertidal reef flats to about 55 m deep (typically 20–50 m).

Phoronis ovalis is the smallest phoronid species. Entire individuals measure up to 15 mm in length; most are 4–6 mm long and 0.15–0.35 mm in diameter. The anterior

body region retracts into a well-developed ampulla. These phoronids are transparent, some with brown pigment where the lophophore joins the trunk, on the distal portion of the tentacles, or over the whole body. The lophophore is oval, with 11 to 28 tentacles that are 0.3–1.2 mm long. Nephridia are straight ascending ducts with a single small, internal funnel that enlarges on maturation of the gonads. The nephridiopore opens distally, on the anal papilla at the base of the lophophore. Giant fibers are absent, although sometimes a left and a right one, about 2.5 μ m in diameter, may be present. Because the two lateral trunk mesenteries are lacking, the conventional formula of longitudinal muscle bundles in four quadrants cannot be established; consequently, the composite formula for the species is [14–39]: left coelom 7–21, right coelom 7–19; and the mean formula is $29 = 15/14$. Other taxonomic characters include absence of lateral

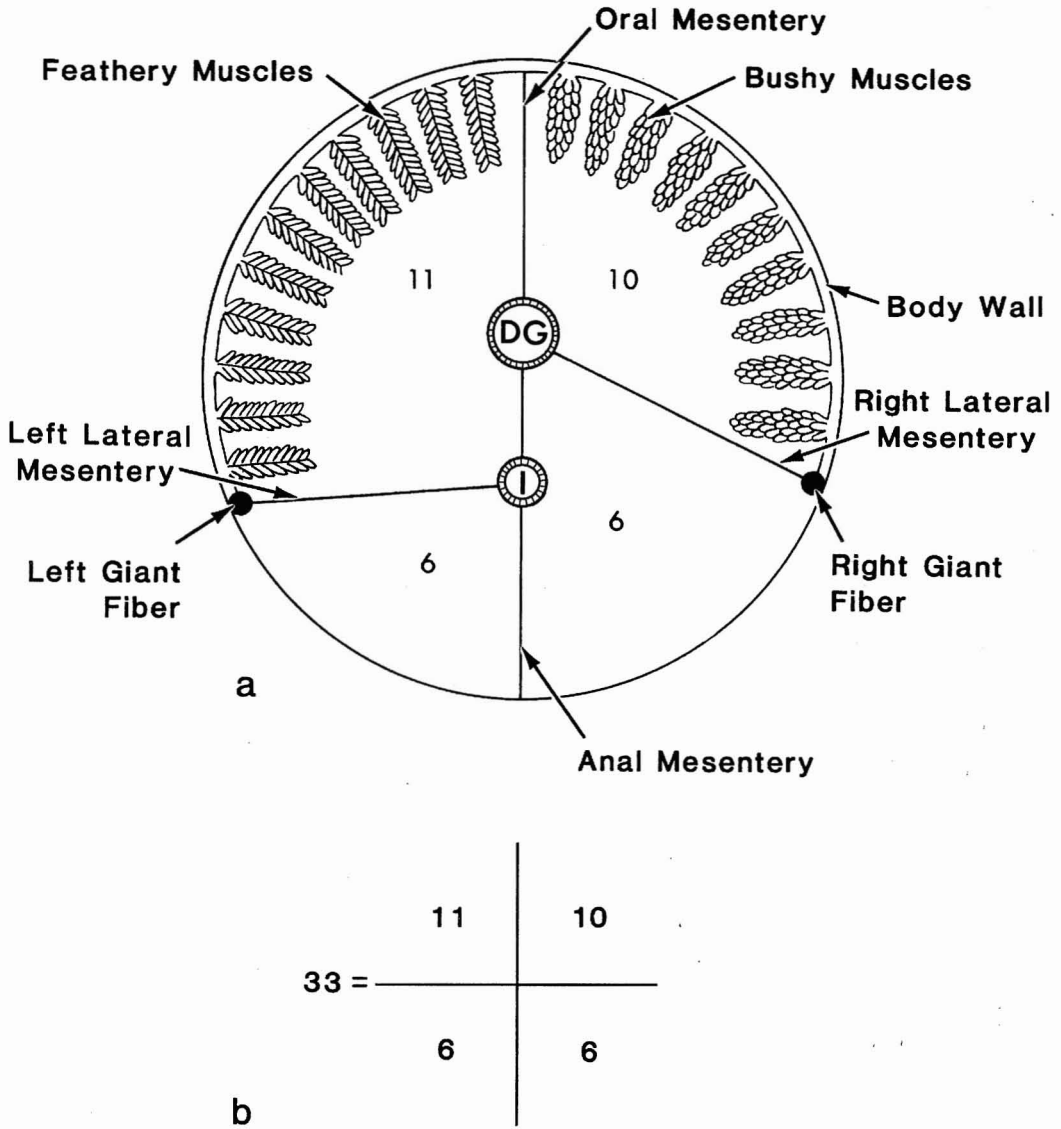


FIGURE 2. *a*, Cross section through the trunk of a diagrammatic phoronid showing the arrangement of internal organs, longitudinal mesenteries dividing the trunk coelom into four unequal quadrants, and the two types of longitudinal body-wall muscles (feathery and bushy). DG, descending gut region; I, intestine. Muscles omitted from lower left and right quadrants. *b*, Muscle formula based on number of muscles in each quadrant shown in *a*.

mesenteries, presence of an “accessory” blood vessel and a second lateral longitudinal blood vessel. Information on gonads is contradictory: hermaphroditic or dioecious. Nidamental glands are absent; but brooding occurs in the parental tube. *Phoronis ovalis* has great potential for asexual reproduction

by transverse fission, budding, or regeneration from autotomized lophophores. The embryo leaves the parental tube as a sluglike larva (this is not an actinotroch) for a short pelagic life before settling and boring into a carbonate substrate.

Larva: *Phoronis ovalis* Silén, 1954.

TABLE 1
DISTRIBUTION^a OF *Phoronis* SPECIES ON O'AHU, HAWAII

LOCALITY	<i>ovalis</i>	<i>hippocrepia</i>	<i>muelleri</i>	<i>pallida</i>	<i>psammophila</i>
Kāne'ōhe Bay: Lilipuna Pier	—	+	—	—	—
Kāne'ōhe Bay: reefs	+	—	—	—	+
Wai'anae*, 33 m	+	—	—	+	—
Mōkapu*, 33 m	+	—	—	—	—
Kewalo, 33 m	—	—	+	—	—
Sand Island*, 59–70 m	—	—	+	—	—
Barbers Point*, 61–70 m	—	—	+	—	—

^a+, Known at the location; —, not found at the location.

*, Municipal sewage outfalls.

Distribution in the Pacific Ocean (Figure 1): USA: Hawai'i: Kāne'ōhe Bay (Emig and Bailey-Brock 1987), Wai'anae (Russo et al. 1998); Washington State: Puget Sound (Marsden 1959), San Juan Archipelago (Emig 1977). Chile: Tumbes Peninsula (Emig 1969), Mehuin (Arenas 1972). New Zealand: Piha (Morton and Miller 1968), Otago (Silén 1956).

Phoronis hippocrepia Wright, 1856

Synonyms: *Phoronis (Crepina) gracilis* Van Beneden, 1858; *Phoronis caespitosa* Cori, 1889; *Phoronis kowalevskii* Benham, 1889; *Phoronis capensis* Gilchrist, 1907

In Kāne'ōhe Bay in coral rock from fringing reefs in south and north regions of the bay, and with fouling communities on Lilipuna Pier.

Muscle formulas established on 79 specimens; mean and composite formulas as follows:

$$\frac{10}{4} \left| \frac{14}{5} \right. = 33 \quad \frac{7-13}{3-6} \left| \frac{10-17}{3-7} \right. [27-41]$$

DIAGNOSIS: *Phoronis hippocrepia* is a burrowing and encrusting species inhabiting hard substrates (i.e., rocks, empty mollusk shells, *Caryophyllia* [cup-corals], *Lithothamnion* [crustose coralline algae], wood). Distribution ranges from the intertidal, near the low-tide mark, to 55 m (generally 0–10 m); densities can reach more than 57,000 individuals per square meter.

Phoronis hippocrepia is about 100 mm in length and 0.3–1.5 mm in diameter. It is greenish gray, yellowish, or fleshy in color. The lophophore is horseshoe-shaped with the ends turned medially; up to 190 tentacles, 2–3 mm in length. Nephridia have two internal funnels, the anal larger than the oral; the descending branch lacks and the ascending branch forms two horizontal chambers, the upper one the nephridial ridge, on which the nephridiopore opens above or at the level of the anus. Two giant fibers are present, one on the left (4–10 μm in diameter) and one on the right (1–7 μm in diameter), at the attachment of the lateral mesenteries and body wall. The longitudinal muscle bundles are the bushy type. The composite and mean formulas of longitudinal muscles are as follows:

$$\frac{7-20}{3-7} \left| \frac{7-17}{3-10} \right. [23-44] \quad 32 = \frac{11}{4} \left| \frac{12}{5} \right.$$

Phoronis hippocrepia is hermaphroditic. Embryos are brooded in paired lophophoral masses on the inner surface of the tentacles; the nidamental glands are type A (i.e., on the floor of the lophophoral concavity). Asexual reproduction is by transverse fission.

Larva: *Actinotrocha hippocrepia* Silén, 1954.

Distribution in the Pacific Ocean (Figure 1): Australia: Sydney, Port Jackson (Haswell 1893). USA: Hawai'i, Kāne'ōhe Bay (Emig 1977, White 1980, Emig and Bailey-Brock 1987). Panama: Miraflores Locks (Emig 1982).

Phoronis muelleri Selys-Longchamps, 1903

Barbers Point (61–70 m depth), Sand Island (59–70 m depth), off Kewalo (33 m depth).

Muscle formulas established on 10 specimens; mean and composite formulas are as follows:

$$\begin{array}{c} 8 \\ \dots \\ 4 \end{array} \left| \begin{array}{c} 8 \\ \dots \\ 4 \end{array} \right. = 24 \quad \begin{array}{c} 5-11 \\ \dots \\ 3-6 \end{array} \left| \begin{array}{c} 5-12 \\ \dots \\ 3-5 \end{array} \right. \quad [17-32]$$

DIAGNOSIS: *Phoronis muelleri* is embedded vertically in muddy sand or sand with a high organic content. Coarse particles of detritus and suspended material are often present in the habitat (Thomassin and Emig 1983). Distribution extends from the intertidal zone to about 400 m depth, mainly between 10 and 60 m depth. Densities may reach about 3000 individuals per square meter. *Phoronis muelleri* is frequently recorded in *Macoma* and *Amphiuira* communities.

Fully extended specimens are 120 mm in length, 0.2–1 mm in diameter. The trunk is pink (after preservation with rose bengal) and the lophophore transparent, occasionally bearing spots. The lophophore is horseshoe-shaped with ends sometimes turned medially. Up to 100 tentacles, length 1–2 mm, but they become shorter in the middle of the oral side. Nephridia open into both oral and anal compartments of the metacoelom by a single funnel, descending and ascending branches ending at the nephridiopore on the anal papilla opening at anus level. There is a single giant nerve fiber, on the left side, 7–40 μ m in diameter; a very thin nerve fiber rarely present on right side. Left lateral mesentery absent except at left nephridium level (indicated by a dotted line in the muscle formulas). Longitudinal muscle bundles are the feathery type. The composite and mean formulas are as follows:

$$[17-39] \quad \begin{array}{c} 5-13 \\ \dots \\ 2-8 \end{array} \left| \begin{array}{c} 5-12 \\ \dots \\ 2-8 \end{array} \right. \quad 26 = \dots \left| \begin{array}{c} 9 \\ \dots \\ 4 \end{array} \right.$$

Sexual reproduction is dioecious; females shed ova freely in the seawater; males have

large, glandular lophophoral organs. Asexual reproduction is by transverse fission.

Larva: *Actinotrocha branchiata* Müller, 1846. Probable synonyms are *Actinotrocha brownei* Selys-Longchamps, 1907; *Actinotrocha* B Ikeda, 1901; *Actinotrocha* D Ikeda, 1901.

Distribution in the Pacific Ocean (Figure 1): Russia: Sakhalin (Mamkaev 1962, Emig 1984, 1985a); Poss'yet Bay, Peter-the-Great Bay (Emig and Golikov 1990). China: Changshan Islands (Emig 1984, 1985a). Australia: Moreton Bay (Emig 1977). New Caledonia: Nouméa lagoon (Emig and Rolandán 1992). USA: Hawai'i: O'ahu. Panama: Naos Island, Culebra Island, Perico Island, Las Perlas Island (Emig 1982). Ecuador coast (Emig 1984, 1985a).

Phoronis psammophila Cori, 1889

Synonyms: *Phoronis sabatieri* Roule, 1889; *Phoronis architecta* Andrews, 1890

From the sand flats on a fringing reef in the southern region of Kāne'ohe Bay.

Muscle formulas established on two specimens:

$$\begin{array}{c} 10 \\ 7 \end{array} \left| \begin{array}{c} 10 \\ 7 \end{array} \right. = 34 \quad \begin{array}{c} 11 \\ 6 \end{array} \left| \begin{array}{c} 10 \\ 6 \end{array} \right. = 33$$

DIAGNOSIS: *Phoronis psammophila* is embedded vertically in sandy to muddy soft sediments and in seagrass beds. Distribution from the intertidal zone to 52 m depth. Densities to 18,000 individuals per square meter.

Fully extended specimens up to 190 mm in length, the diameter from 0.5 to 2 mm. Color in life pink, lophophore transparent with white (occasionally yellow, green, or red) pigment spots. Lophophore horseshoe-shaped, ends turned medially. Up to 190 tentacles, from 1.5 to 2.5 mm long. Nephridia with a single internal funnel, with descending and ascending branch; nephridiopore opens on anal papilla below anus. A single giant nerve fiber, on the left side, 7–27 μ m in diameter; a very thin nerve fiber rarely present on right side. Longitudinal muscle bundles feathery. Composite and mean formulas as follows:

$$[24-53] \quad \frac{7-19}{4-11} \mid \frac{7-18}{4-11} \quad 35 = \frac{12}{6} \mid \frac{11}{6}$$

Sexual reproduction is dioecious; females brood embryos in a single mass in the lophophoral cavity through type C nidamental glands (i.e., formed by the fusion of the inner row of lophophore tentacles); males have large, glandular lophophoral organs. Asexual reproduction is by transverse fission.

Larva: *Actinotrocha sabatieri* Roule, 1896.

Synonyms are *Actinotrocha metschnikoffi* Selys-Longchamps, 1907; *A. wilsoni* Selys-Longchamps, 1907; *A. hatscheki* Selys-Longchamps, 1907; *A. ashworthi* Selys-Longchamps, 1907.

Distribution in the Pacific Ocean (Figure 1): Russia: Sakhalin (Emig 1984, 1985a, Emig and Golikov 1990), Poss'yey Bay, Mordinov Gulf (Emig 1984, 1985a, Emig and Golikov 1990). China: Changshan Islands, Dalni, Potonoman (Emig 1984, 1985a). Solomon Islands: (Emig 1977). Australia: Cabbage Tree Basin (Rainer and Fitzhardinge 1981), Port Phillip Bay, Western Port (Emig et al. 1977), Spencer Gulf (Emig and Roldán 1992). New Caledonia: Nouméa lagoon (Emig and Roldán 1992). New Zealand: Ranganna Bay, Doubtless Bay (Emig and Roldán 1992), Howick, Whangateau Harbor, Waitemata, Jellicoe (Jillett 1971, Gordon and McKnight 1983, Emig and Roldán 1992). USA: Hawai'i: O'ahu (Emig 1977, Emig and Bailey-Brock 1987); Midway (Sorden 1983, Emig and Roldán 1992); Washington State: Point Defiance (Marsden 1959); California: Los Angeles, Long Beach, Newport Bay (Marsden 1959, Reish 1959). Panama: Naos Island, Perico Island, Venado Beach (Emig 1982).

Phoronis pallida Silén, 1952

Wai'anae (33 m depth).

Muscle formulas established on four specimens; the composite formula is as follows:

$$\frac{5}{4} \mid \frac{5}{3-4} = 17-18$$

DIAGNOSIS: *Phoronis pallida* is embedded vertically in soft sediments, generally sand to muddy sand. Bathymetric range from the upper subtidal to 25 m. Densities to 74,000 individuals per square meter.

Length in extension about 140 mm, diameter 0.3 to 1 mm. Color in life pink yellowish. Lophophore horseshoe-shaped, ends sometimes turned medially. Up to 140 tentacles, 2-2.5 mm in length. Nephridia with two pseudo-funnels, the anal slightly larger than oral, a descending and ascending branch; nephridiopore opens on anal papilla at anus level. A single giant nerve fiber, on the left side at the level of the attachment of the left lateral mesentery to the body wall, 10-20 μ m in diameter. Longitudinal muscle bundles feathery, developed into six longitudinal zones and circular musculature with three sphincters; the composite and mean formulas are as follows:

$$[17-19] \quad \frac{4-6}{4-5} \mid \frac{5}{3-4} \quad 18 = \frac{5}{4} \mid \frac{5}{4}$$

Sexual reproduction is hermaphroditic; ova freely discharged in the seawater; lophophoral organs of males large and glandular.

Larva: *Actinotrocha pallida* Schneider, 1862.

Distribution in the Pacific Ocean (Figure 1): Japan: Tokyo Bay (coll. T. Furota). Australia: Port Phillip Bay, Western Port (Emig et al. 1977). USA: Hawai'i: Wai'anae, O'ahu; California: Point Richmond (Marsden 1959, Jones 1961), Los Angeles (Marsden 1959, Reish 1959).

KEY TO ADULTS OF *Phoronis* SPECIES OCCURRING IN HAWAIIAN WATERS

Accurate identification of *Phoronis* requires examination of histological sections from different body levels (especially the trunk) to ascertain genus and species. A short key based primarily on visible features (therefore not accurate) is given below to allow tentative identification of a phoronid species.

1. Lophophore oval; burrowing generally in empty shells, up to 15 mm long *P. ovalis*
Lophophore horseshoe-shaped 2
2. Burrowing in or encrusting on hard substrates..... *P. hippocrepi*
Dwelling vertically in soft substrates 3
3. Prebuccal and postanal tentacles of the same length, lateral tentacles longer *P. muelleri*
Prebuccal and lateral tentacles of the same length 4
4. Three circular horizontal muscle sphincters present..... *P. pallida*
No horizontal muscle sphincters *P. psammophila*

CONCLUSIONS

Because the Hawaiian Islands are the most isolated island group in the world, it is not surprising that only the plesiomorphous phoronid species (Emig 1985b) are represented: respectively, the perforant species *Phoronis ovalis* and *P. hippocrepi* and sediment-dwellers *P. muelleri*, *P. psammophila*, and *P. pallida*. All five species are distributed along East and West Pacific coasts and seem to be cosmopolitan species. Only *P. hippocrepi* has few records compared with the wider distribution of the closely related species *P. ijimai* (= *P. vancouverensis*).

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