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# The First Records of Peltogastrid Rhizocephalans (Crustacea: Cirripedia: Rhizocephala) on Hermit Crabs (Paguroidea) in Taiwan and Differences in Prevalences among Collection Sites

Ryuta Yoshida[1,*], Mamiko Hirose[1], Hin-Kiu Mok[2], and Euichi Hirose[1]

[1]*Faculty of Science, University of the Ryukyus, Nishihara, Okinawa 903-0213, Japan*
[2]*Institute of Marine Biology, National Sun Yat-Sen University, Kaohsiung 804, Taiwan*

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**Ryuta Yoshida, Mamiko Hirose, Hin-Kiu Mok, and Euichi Hirose (2012)** The first records of peltogastrid rhizocephalans (Crustacea: Cirripedia: Rhizocephala) on hermit crabs (Paguroidea) in Taiwan and differences in prevalences among collection sites. *Zoological Studies* **51**(7): 1027-1039. From collections of 3073 individual hermit crabs in Taiwan, representing 56 species, 53 individuals of 3 different species were found to be infested by 3 species of rhizocephalans: *Peltogaster postica* on *Pagurus angustus*, *Septosaccus* cf. *snelliusi* on *Diogenes tumidus*, and *Dipterosaccus indicus* on *Calcinus morgani*. Rhizocephalans were identified based on histological sections, and species identifications were consistent with partial sequences of the cytochrome *c* oxidase subunit I (COI) gene. This is the 1st record of peltogastrid rhizocephalans (Crustacea, Cirripedia) from Taiwan. The prevalence of peltogastrid species greatly differed among the collection sites, and hosts for *Pel. postica* and *Dip. indicus* differed from previously known hosts in the Ryukyus and other sites. The microhabitat of the host species may be crucial to rhizocephalan parasitism success. http://zoolstud.sinica.edu.tw/Journals/51.7/1027.pdf

**Key words:** Parasitic crustacean, Peltogastridae, Hermit crab, Prevalence, Taiwan.

The Rhizocephala (Crustacea, Cirripedia) comprises approximately 260 species, which are always parasitic on decapods and other crustaceans such as isopods, cumaceans, and balanomorph barnacles (Høeg 1995). While rhizocephalans have planktonic larval stages (nauplii and cyprids), the adults have an internal nutritive root system (interna) and an external reproductive portion (externa). The occurrence of rhizocephalans is usually recognized by the presence of an externa on a host's abdomen or other part of the body. The order Rhizocephala has 2 suborders, the Akentrogonida and Kentrogonida, that are discriminated from the presence or absence of an infective Kentrogon larva. The Kentrogonida comprises 3 families, the Lernaeodiscidae, Peltogastridae, and Sacculinidae, and all kentologonids are only parasitic on decapods. A molecular phylogeny based on 18S ribosomal (r)DNA sequences using 11 species of the Sacculinidae and 11 other rhizocephalans supported the monophyly of the Rhizocephala, while species parasitizing anomurans (Peltogastridae and Lernaeodiscidae) branched off as sister groups to the other rhizocephalans in the phylogenetic trees (Glenner and Hebsgaard 2006). Therefore, those authors suggested that anomurans were the ancestral hosts of the Rhizocephala. In Taiwan, 11 species of rhizocephalans are known from crab and shrimp hosts (Huang and Lützen 1998).

The Peltogastridae comprises 15 genera and 40 species. Among them, 26 species are known to live on hermit crabs (Høeg 1995,

*To whom correspondence and reprint requests should be addressed. Tel: 81-98-895-8880. Fax: 81-98-895-8576. E-mail:4cd.riutae@gmail.com

McDermott et al. 2010, Yoshida et al. 2011), but there are currently no records from Taiwan. We recently described 2 new species of peltogastrids, *Peltogaster postica* and *Ommatogaster nana*, from the Ryukyu Archipelago, Japan (Yoshida et al. 2011). These are the only new peltogastrid species described in the last 25 yr, and the 1st recorded from the Ryukyus. Species on hermit crabs can only be found when the gastropod shell in which the host hides is broken apart. These species are, therefore, inconspicuous in the field, even if they are commonly distributed on shallow-water hosts. The 1st author surveyed 56 species of hermit crabs at 25 sites on northern, western, and southern shores of Taiwan and in the Penghu Is. and found 3 peltogastrid species on 3 hermit crab species. Species identification was based on morphology (histological sections) and DNA barcodes (partial sequences of the cytochrome *c* oxidase subunit I (COI) gene). These 3 species were also recorded from the Ryukyus. This is the 1st record of peltogastrids from Taiwan. Herein, we also discuss the host specificity of each species and differences in prevalences among collection sites.

## MATERIALS AND METHODS

### Animals

Hermit crabs were collected at 25 sites on the northern, western, and southern shores of Taiwan and in the Penghu Is. between 30 June and 5 Aug. 2011 (Fig. 1). Hermit crabs were discovered visually and collected while walking or snorkeling in shallow water, with some hermit crabs caught in trawl nets generously provided by local fishermen at fishing ports in Dasi, Donggang, and Kezailiao. In the laboratory, the gastropod shells of the hermit crabs were broken with a hammer or a vise. After species were identified according to McLaughlin et al. (2007), we recorded the presence or absence of rhizocephalan externae and other parasites such as epicaridean isopods. Most hermit crabs bearing rhizocephalan externae were fixed in 10% formalin-seawater or Bouin's solution along with their parasites *in situ*. Some externae were fixed in 95% ethanol for DNA analysis. Some specimens were deposited in the National Museum of Natural Science (NMNS), Taichung, Taiwan. SL indicates the shield length of hermit crab hosts.

### Histology

Specimens fixed in Bouin's solution were dehydrated through an ethanol-xylene series and embedded in paraffin. Serial 10-μm-thick sections were stained with Delafield's hematoxylin and eosin for light microscopic observations. Some specimens fixed in 10% formalin-seawater were dehydrated through a graded series of ethanol. Specimens were then immersed in *t*-butanol and freeze-dried. Dried specimens were sputter-coated with gold-palladium and examined with a scanning electron microscope (SEM: JEOL JSM-6060LV, Tokyo, Japan) at 15 kV. The terminology used in this study followed that of Høeg and Lützen (1985) and Høeg (1992).

### DNA extraction, polymerase chain reaction (PCR) amplification, and sequencing

Tissue samples were preserved in ethanol at -30°C. Genomic DNA was extracted from the externae using a DNeasy Tissue Kit (Qiagen, Tokyo, Japan) following the manufacturer's protocol. PCR amplification of the partial COI gene was performed using Ex *Taq* DNA Polymerase (Takara, Shiga, Japan) and the primers crust-cox1 (Podsiadlowski and Bartolomaeus 2005) and HCO2198 (Folmer et al. 1994) under the following conditions: 94°C for 5 min followed by 35 cycles at 94°C for 30 s, 45°C for 30 s, and 72°C for 2 min, with a final extension at 72°C for 7 min. PCR products were treated with ExoSAP-IT (GE Healthcare, Piscataway, NJ, USA) prior to sequencing reactions using DTCS Quick Start Master Mix (Beckman Coulter, Brea, CA, USA). The products were analyzed using a CEQ8800 (Beckman Coulter) automated DNA sequencing system. Sequences were deposited in GenBank, the European Molecular Biology Laboratory (EMBL), and the DNA Data Bank of Japan (DDBJ).

### Molecular analysis

Initial alignment was performed using MUSCLE (Edgar 2004), and poorly aligned positions and divergent regions were eliminated using Gblocks (Castresana 2000) prior to the phylogenetic analyses. The alignment dataset of partial mitochondrial (mt) COI (16 taxa/522 sites) is available on request from the corresponding author. Base frequencies, pairwise base differences, and genetic distances were calculated using PAUP* 4.0 beta 10 (Swofford 2003). The

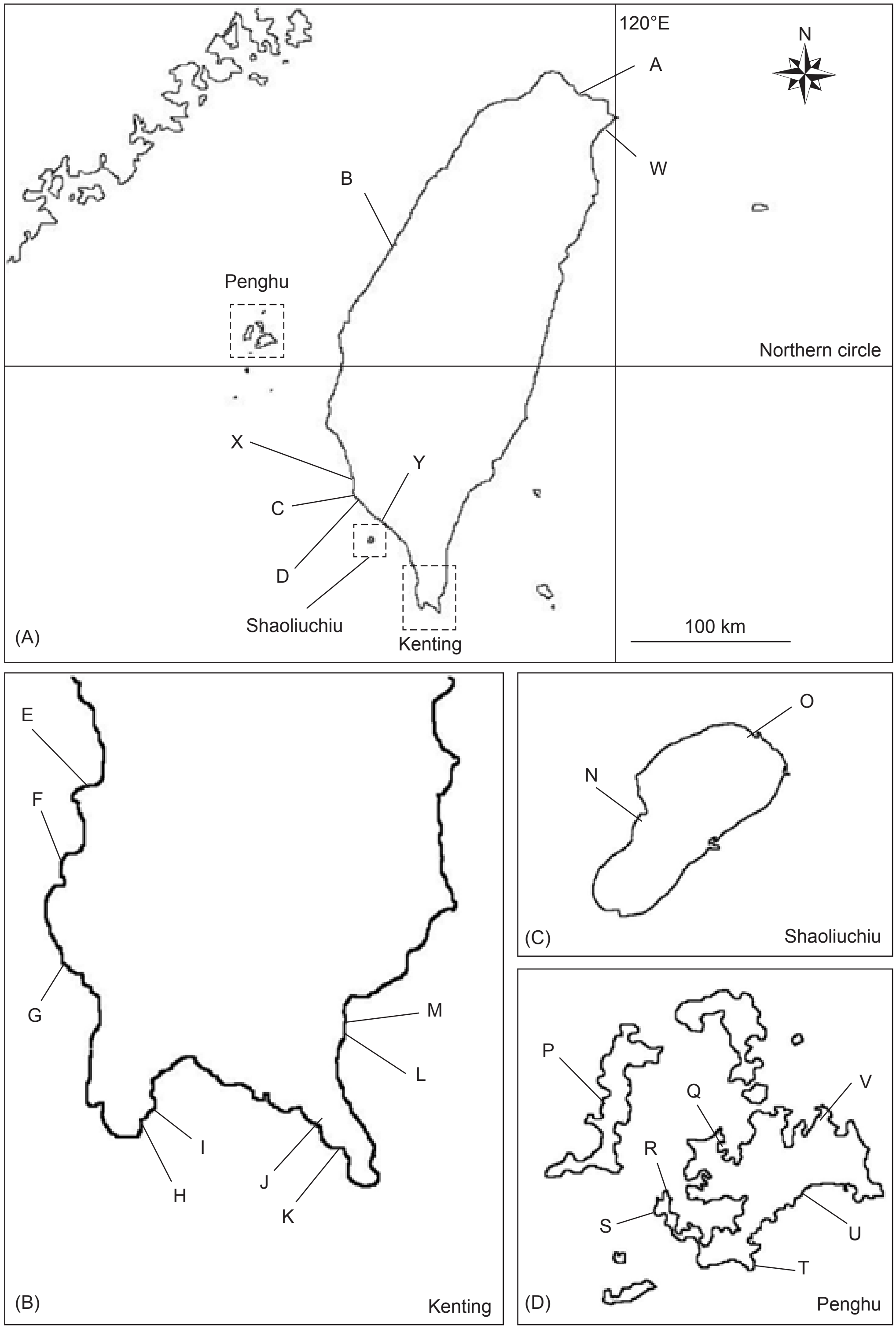


**Fig. 1.** Collection sites of the host hermit crabs in Taiwan and adjacent islands. (A) Enlargement of southern Taiwan (B), Shaoliuchiu (C), and Penghu Is. (D). Sites and collection dates in 2011 are as follows: A, Badouzih (15 July); B, Siansi (19 July); C, Sizihwan (6 July); D, Kaohsiung Harbor (5 July); E, Haikou (30 June); F, Houwan (27 July); G, Wanlitong (29 June); H, Leipashih (25 July); I, Dingtanzai (26 July); J, Chuanfanshih (27 July); K, Siadao (26 July); L, Akaohai Fishing Port (26 July); M, Gankou (26 July); N, Shanfu Fishing Port (29 July); O, Huapinyan (29 July); P, Chihsi (5 Aug.); Q, Siwei (2 Aug.); R, Shetoshan (2 Aug.); S, Fongguei (4 Aug.); T, Shanshuei (3 Aug.); U, Aimen Beach (4 Aug.); V, Cingluo (5 Aug.); W, Dasi Fishing Port (14 July); X, Kezailiao Fishing Port (23 June, 4, 17 and, 22 July, 9 Aug.); Y, Donggang Fishing Port (9 and 23 July).

following analyses were performed on the aligned DNA sequences of the partial COI gene: maximum likelihood (ML) using TREEFINDER Jan. 2008 vers. (Jobb 2008), and maximum parsimony (MP) and neighbor-joining (NJ) using PAUP* 4.0 beta10 (Swofford 2003). jModelTest 0.1.1 (Posada 2008) was used to select an appropriate nucleotide substitution model. The MP trees were sought using a heuristic approach with 100 random initial trees. Statistical support for the ML, MP, and NJ trees was evaluated using a non-parametric bootstrap test with 1000 resampling events.

## RESULTS

### Hermit crabs and their parasites

We collected 56 species of hermit crabs at 25 sites on the northern, western, and southern shores of Taiwan and in Penghu (Table 1), including 1 undescribed species and 6 species new to Taiwan. Details of the new records of hermit crabs will be presented elsewhere (Osawa et al. in preparation). Of 3073 individual hermit crabs, 53 hermit crabs of 3 species bore externae of rhizocephalans. Each host species was associated with only 1 rhizocephalan species, except for 2 individuals of *Pagurus angustus* which bore 2 externae. Other than rhizocephalans, some hermit crabs were associated with epicaridean isopods, burrowing barnacles (acrothoracicans), flatworms, and bivalves.

### Records of peltogastrid rhizocephalans

**Family Peltogastridae Lilljeborg, 1859**
**Genus *Peltogaster* Rathke, 1842**
***Peltogaster postica* Yoshida and Osawa, in Yoshida, Osawa, Hirose, and Hirose, 2011**

*Host*: *Pagurus angustus*.
*Collection sites*: Shetoushan, Magong, Penghu, intertidal, 2 Aug. 2011; Chihsi, Siyu, Penghu, intertidal, 5 Aug. 2011 (Fig. 1).

*Material examined*: Specimens were collected by the 1st author. The specimen in the live photograph (NMNS-6795-001) was collected at Shetoushan on 2 Aug. 2011 (host SL, 3.9 mm). Two specimens for histology were collected at Shetoushan on 2 Aug. 2011 (host SL, 3.5 and 4.8 mm). Specimens collected at Shetoushan on 2 Aug. 2011 (NMNS-6795-002: host SL, 3.8 mm) and at Chisi on 5 Aug. 2011 (NMNS-6795-003: host SL, 3.3 mm) were used for DNA extraction.

*Description*: *External morphology*: The mantle aperture is elevated as a tube-like projection and is situated terminally or subterminally on the side facing the host due to the sac curvature. The mantle opening is U-shaped in contracted specimens. The shield is elongated in shape, with growth rings that extend anteriorly and posteriorly from the stalk.

*Coloration in life*: Mature externae are usually brown but occasionally olive (Fig. 2A). The tube-like mantle apertures are light green. The root system (interna) is green.

*Anatomy of the externa*: The visceral mass is attached to the mantle aperture (Fig. 2B). The tube-like mantle aperture is approximately 300 μm long. The visceral mass is semicircular in transverse section (Fig. 2C), and the mesentery is nearly as broad. Two receptacles are present on the mesentery, each with comparatively thin walls of up to 10 μm thick and shaped like straight tubes that gradually pass into receptacle ducts. Two colleteric glands are present posterior to the anterior end of the receptacles and slightly anterior to the stalk level (Fig. 2C). At insertion into the host body wall, the stalk branches, the chitinous projections act as holdfasts, and no chitinous structures are present inside the stalk (Fig. 2C). The receptacle ducts are coiled, opening backwards on the lateral surface of the visceral mass.

*Distribution and host*: Penghu on *Pag. angustus*. Okinawa I. (type locality) on *Pag. minutus*. Japanese mainland on *Pag. nigrivittatus* (Table 2).

**Genus *Septosaccus* Duboscq, 1912**
***Septosaccus* cf. *snelliusi* Van Baal, 1937**

*Host*: *Diogenes tumidus*.
*Collection sites*: Shetoushan, Magong, Penghu, intertidal, 2 Aug. 2011; Siwei, Magong, Penghu, intertidal, 2 Aug. 2011 (Fig. 1).

*Material examined*: Specimens were collected by the 1st author. The specimen in the live photograph (NMNS-6795-004) was collected at Shetoushan on 2 Aug. 2011 (host SL, 2.2 mm). The specimen for histology and electron microscopy was collected at Shetoushan on 2 Aug. 2011 (host SL, 2.3 mm). For DNA extraction, we used NMNS-6795-004 and specimens collected at Shetoushan on 2 Aug. 2011 (host SL, 2.0 mm).

**Table 1.** Number of the hermit crabs examined at each site and occurrence of parasites

| | Taiwan | | | | | | | | | | | | | Shao-liuchiu | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Collection Sites[2] | A | B | C | D | E | F | G | H | I | J | K | L | M | N | O |
| Habitat[3] | r | s | r | r | c | c | c | c | c | c | c | c | g | c | c |
| Host Species[1] | | | | | | | | | | | | | | | |
| Diogenidae | | | | | | | | | | | | | | | |
| *Aniculus ursus* (Olivier, 1811) | - | - | - | - | - | - | - | - | - | - | - | 3 | - | - | - |
| *Calcinus elegans* (H. Milne Edwards, 1836) | - | - | 3 | - | - | - | - | 3 | - | - | 1 | - | - | - | - |
| *Calcinus gaimardii* (H. Milne Edwards, 1848) | - | - | 5 | 2 | 36 | 5 | - | - | 1 | 1 | 9 | 1 | - | 21 | 4 |
| *Calcinus guamensis* Wooster, 1984 | - | - | - | - | 6 | 16 | - | 3 | - | 14 | 11 | 1 | - | - | - |
| *Calcinus laevimanus* (Randall, 1840) | 7 | - | - | - | - | - | - | 2 | - | - | - | 8 | - | - | - |
| *Calcinus latens* (Randall, 1840) | 27 | - | 27 | - | 36 | - | - | 6 | - | 6 | 6 | - | - | 5 | 3 |
| *Calcinus lineopropodus* Morgan and Forest, 1991 | - | - | - | - | 1 | - | - | - | - | - | - | - | - | 9 | 8 |
| *Calcinus minutus* Buitendijk, 1937 | - | - | - | - | 1 | 1 | - | 1 | 1 | - | 4 | - | - | 13 | 4 |
| *Calcinus morgani* Rahayu and Forest, 1999 | 2 | - | 165 | 1 | 23 | 41 | - | 67 | 2 | 19 | 69 | 20 | - | 4 | 18 |
| *Calcinus pulcher* Forest, 1958 | - | - | - | - | - | - | - | - | - | - | - | - | - | 11 | - |
| *Calcinus vachoni* Forest, 1958 | - | - | 16 | 6 | 35 | 33 | - | - | - | 7 | 9 | 15 | - | 4 | 7 |
| *Ciliopagurus strigatus* (Herbst, 1804) | - | - | - | - | - | - | - | - | - | 6 | 1 | - | - | 7 | 24 |
| *Clibanarius corallinus* (H. Milne Edwards, 1848) | 1 | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - |
| *Clibanarius englaucus* Ball and Haig, 1972 | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - |
| *Clibanarius eurysternus* (Hilgendof, 1879) | - | - | - | - | - | - | 1 | 1 | - | - | - | - | - | - | - |
| *Clibanarius humilis* (Dana, 1851) | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Clibanarius longitarsus* (De Haan, 1849) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Clibanarius virescens* (Krauss, 1843) | 8 | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - |
| *Dardanus arrosor* (Herbst, 1796) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Dardanus aspersus* (Berthold, 1846) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Dardanus crassimanus* (H. Milne Edwards, 1836) | - | - | - | - | - | - | - | - | - | - | - | - | 2 | - | - |
| *Dardanus gemmatus* (H. Milne Edwards, 1848) | - | - | - | - | - | - | - | - | 3 | 1 | 2 | - | - | - | - |
| *Dardanus guttatus* (Olivier, 1811) | - | - | - | - | - | 1 | - | 2 | - | 1 | 1 | - | - | - | - |
| *Dardanus holthuisi* Rahayu, 2010* | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Dardanus impressus* (De Haan, 1849) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Dardanus lagopodes* (Forskål, 1775) | - | - | - | - | 11 | 5 | - | 3 | 2 | 1 | 2 | - | - | 19 | 10 |
| *Dardanus megistos* (Herbst, 1804) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Dardanus pedunculatus* (Herbst, 1804) | - | - | 4 | - | - | - | - | 1 | - | - | - | - | 2 | - | - |
| *Diogenes avarus* Heller, 1865 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Diogenes nitidimanus* Terao, 1913 | - | 84 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Diogenes pallescens* Whitelegge, 1897* | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Diogenes penicillatus* Stimpson, 1858 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Diogenes tumidus* Rahayu and Forest, 1995 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Paguristes gonagrus* (H. Milne Edwards, 1836) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Paguristes palythophilus* Ortmann, 1892 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Paguristes seminudus* Stimpson, 1858 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Paguristes* sp.* | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Pseudopaguristes* hians (Henderson, 1888)* | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Paguridae | | | | | | | | | | | | | | | |
| *Micropagurus polynesiensis* (Nobili, 1906)* | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - |
| *Nematopagurus australis* (Henderson, 1888) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Pagurodofleinia doederleini* (Doflein, 1902) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Pagurus angustus* (Stimpson, 1858) | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Pagurus conformis* De Haan, 1849 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Pagurus confusus* Komai and Yu, 1998 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Pagurus hirtimanus* (Miers, 1880)* | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - |
| *Pagurus minutus* (Hess, 1865) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Pagurus nigrivittatus* Komai, 2003 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Pagurus pitagsaleei* McLaughlin, 2002 | - | - | - | 5 | 1 | - | - | - | - | - | - | - | - | - | - |
| *Pagurus similis* (Ortmann, 1892) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Propagurus miyakei* (Baba, 1986) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Propagurus obtusifrons* (Ortmann, 1892) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Pylopaguropsis fimbriatus* McLaughlin and Haig, 1989* | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - |
| *Spiropagurus spiringer* (De Haan, 1849) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Parapaguridae | | | | | | | | | | | | | | | |
| *Paragiopagurus diogenes* (Whitelegge, 1900) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| *Sympagurus brevipes* (de Saint Laurent, 1972) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Pylochelidae | | | | | | | | | | | | | | | |
| *Pylocheles* (*Xylocheles*) *macrops* Forest, 1987 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Total | 47 | 85 | 222 | 14 | 150 | 102 | 2 | 89 | 10 | 56 | 115 | 48 | 4 | 95 | 78 |

**Table 1.** (continued)

| | Penghu | | | | | | | Trawling | | | Total | Associating animals[4] | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Collection Sites[2] | P | Q | R | S | T | U | V | W | X | Y | | Pelto-gastrids | Others |
| Habitat[3] | r | s | r,s | c | r | r | r,s | | | | | | |
| Host Species[1] | | | | | | | | | | | | | |
| Diogenidae | | | | | | | | | | | | | |
| *Aniculus ursus* (Olivier, 1811) | - | - | - | - | - | - | - | - | - | - | 3 | None | None |
| *Calcinus elegans* (H. Milne Edwards, 1836) | - | - | - | - | 1 | 1 | - | - | - | - | 9 | None | None |
| *Calcinus gaimardii* (H. Milne Edwards, 1848) | - | - | - | 2 | - | - | - | - | - | - | 87 | None | Ac, Ep, Fw |
| *Calcinus guamensis* Wooster, 1984 | - | - | - | - | 1 | - | - | - | - | - | 52 | None | Ep |
| *Calcinus laevimanus* (Randall, 1840) | - | - | - | - | 69 | 51 | - | - | - | - | 137 | None | None |
| *Calcinus latens* (Randall, 1840) | 18 | - | 5 | - | 2 | 36 | - | - | - | - | 177 | None | None |
| *Calcinus lineopropodus* Morgan and Forest, 1991 | - | - | - | - | - | - | - | - | - | - | 18 | None | None |
| *Calcinus minutus* Buitendijk, 1937 | - | - | - | - | - | - | - | - | - | - | 25 | None | None |
| *Calcinus morgani* Rahayu and Forest, 1999 | - | - | - | 2 | 24 | 5 | - | - | - | - | 462 | D | Ac, Ep, Fw |
| *Calcinus pulcher* Forest, 1958 | - | - | - | - | - | - | - | - | - | - | 11 | None | None |
| *Calcinus vachoni* Forest, 1958 | - | - | - | 3 | 1 | 3 | - | - | - | - | 139 | None | Ep |
| *Ciliopagurus strigatus* (Herbst, 1804) | - | - | - | - | 1 | - | - | - | - | - | 39 | None | None |
| *Clibanarius corallinus* (H. Milne Edwards, 1848) | - | - | - | - | - | - | - | - | - | - | 2 | None | None |
| *Clibanarius englaucus* Ball and Haig, 1972 | - | - | - | - | 40 | - | - | - | - | - | 41 | None | None |
| *Clibanarius eurysternus* (Hilgendof, 1879) | - | - | - | - | 1 | - | - | - | - | - | 3 | None | None |
| *Clibanarius humilis* (Dana, 1851) | - | - | - | - | - | 3 | - | - | - | - | 4 | None | None |
| *Clibanarius longitarsus* (De Haan, 1849) | - | 2 | - | - | - | - | - | - | - | - | 2 | None | None |
| *Clibanarius virescens* (Krauss, 1843) | 7 | - | 4 | - | 60 | 506 | - | - | - | - | 586 | None | Ep |
| *Dardanus arrosor* (Herbst, 1796) | - | - | - | - | - | - | - | - | 1 | - | 1 | None | None |
| *Dardanus aspersus* (Berthold, 1846) | - | - | - | - | - | - | - | - | 1 | - | 1 | None | None |
| *Dardanus crassimanus* (H. Milne Edwards, 1836) | - | - | - | - | - | - | - | - | 1 | - | 3 | None | None |
| *Dardanus gemmatus* (H. Milne Edwards, 1848) | - | - | - | - | 2 | - | - | - | - | - | 8 | None | None |
| *Dardanus guttatus* (Olivier, 1811) | - | - | - | - | - | - | - | - | - | - | 5 | None | None |
| *Dardanus holthuisi* Rahayu, 2010* | - | - | - | - | - | - | - | - | 1 | - | 1 | None | None |
| *Dardanus impressus* (De Haan, 1849) | - | - | - | - | - | - | - | 6 | 44 | - | 50 | None | None |
| *Dardanus lagopodes* (Forskål, 1775) | 3 | - | - | 8 | - | 1 | - | - | - | - | 65 | None | Ep |
| *Dardanus megistos* (Herbst, 1804) | 1 | - | - | - | - | - | - | - | - | - | 1 | None | None |
| *Dardanus pedunculatus* (Herbst, 1804) | - | - | - | - | - | - | - | - | 1 | - | 8 | None | None |
| *Diogenes avarus* Heller, 1865 | - | 15 | - | - | - | - | - | - | - | - | 15 | None | None |
| *Diogenes nitidimanus* Terao, 1913 | - | - | - | - | - | - | - | - | - | - | 84 | None | Bc |
| *Diogenes pallescens* Whitelegge, 1897* | - | - | - | 11 | - | - | - | - | - | - | 11 | None | None |
| *Diogenes penicillatus* Stimpson, 1858 | - | - | - | - | - | - | - | - | 6 | - | 6 | None | None |
| *Diogenes tumidus* Rahayu and Forest, 1995 | 12 | 27 | 260 | - | - | - | 24 | - | - | - | 323 | S | Ep |
| *Paguristes gonagrus* (H. Milne Edwards, 1836) | - | - | - | - | - | - | - | - | 5 | - | 5 | None | None |
| *Paguristes palythophilus* Ortmann, 1892 | - | - | - | - | - | - | - | 1 | - | - | 1 | None | None |
| *Paguristes seminudus* Stimpson, 1858 | - | - | - | - | - | - | - | - | 207 | - | 207 | None | Ep |
| *Paguristes* sp.* | - | - | - | - | - | - | - | - | 39 | - | 39 | None | None |
| *Pseudopaguristes* hians (Henderson, 1888)* | - | - | - | 3 | - | - | - | - | - | - | 3 | None | None |
| Paguridae | | | | | | | | | | | | | |
| *Micropagurus polynesiensis* (Nobili, 1906)* | - | - | - | - | - | - | - | - | - | - | 1 | None | None |
| *Nematopagurus australis* (Henderson, 1888) | - | - | - | - | - | - | - | - | 1 | - | 1 | None | None |
| *Pagurodofleinia doederleini* (Doflein, 1902) | - | - | - | - | - | - | - | - | - | 1 | 1 | None | None |
| *Pagurus angustus* (Stimpson, 1858) | 6 | 3 | 101 | - | 7 | 1 | 202 | - | - | - | 322 | P | Ep |
| *Pagurus conformis* De Haan, 1849 | - | - | - | - | - | - | - | - | 1 | - | 1 | None | None |
| *Pagurus confusus* Komai and Yu, 1998 | - | - | - | - | - | - | - | 1 | - | - | 1 | None | None |
| *Pagurus hirtimanus* (Miers, 1880)* | - | - | - | - | - | - | - | - | - | - | 1 | None | None |
| *Pagurus minutus* (Hess, 1865) | - | 77 | - | - | - | - | - | - | - | - | 77 | None | None |
| *Pagurus nigrivittatus* Komai, 2003 | - | - | - | - | 4 | 11 | - | - | - | - | 15 | None | None |
| *Pagurus pitagsaleei* McLaughlin, 2002 | - | - | - | - | - | - | - | - | - | - | 6 | None | None |
| *Pagurus similis* (Ortmann, 1892) | - | - | - | - | - | - | - | 2 | - | - | 2 | None | None |
| *Propagurus miyakei* (Baba, 1986) | - | - | - | - | - | - | - | 1 | - | - | 1 | None | None |
| *Propagurus obtusifrons* (Ortmann, 1892) | - | - | - | - | - | - | - | 4 | - | - | 4 | None | None |
| *Pylopaguropsis fimbriatus* McLaughlin and Haig, 1989* | - | - | - | - | - | - | - | - | - | - | 1 | None | None |
| *Spiropagurus spiringer* (De Haan, 1849) | - | - | - | - | - | - | - | - | 2 | - | 2 | None | Ep |
| Parapaguridae | | | | | | | | | | | | | |
| *Paragiopagurus diogenes* (Whitelegge, 1900) | - | - | - | - | - | - | - | - | 1 | - | 1 | None | None |
| *Sympagurus brevipes* (de Saint Laurent, 1972) | - | - | - | - | - | - | - | - | - | 2 | 2 | None | None |
| Pylochelidae | | | | | | | | | | | | | |
| *Pylocheles* (*Xylocheles*) *macrops* Forest, 1987 | - | - | - | - | - | - | - | - | - | 1 | 1 | None | None |
| Total | 47 | 124 | 370 | 29 | 213 | 618 | 226 | 15 | 311 | 3 | 3,073 | | |

[1]Species recorded for the first time from Taiwan are marked with *. [2]A-Z are correspondent to those in figure 1. [3]c, coral reef; g, collected with gill net; r, rocky shore; s, sandy bottom. [4]D, *Dipterosaccus indicus*; P, *Peltogaster postica*; S, *Septosaccus* sp.; Ac, burrowing barnacle (acrothoracican); Ep, epicaridean isopod; Fw, flatworm; Bc, bivalves (*Curvemysella* spp.).

*Description*: *External morphology*: The externa is slightly curved, and its stalk side is concave. The mantle aperture is elevated as a tube-like projection and curved toward the right near the anterior end of the externa. The mantle aperture is a simple slit in the contracted specimen. The oval-shaped shield is very small around the stalk, almost imperceptible, and lacks growth rings. The stalk emerges from the posterior 1/2 of the externa.

*Coloration in life*: The mature externae are red (Fig. 2D). The root system is indistinguishable from the host's yellowish digestive gland.

*Anatomy of the externa*: The visceral mass

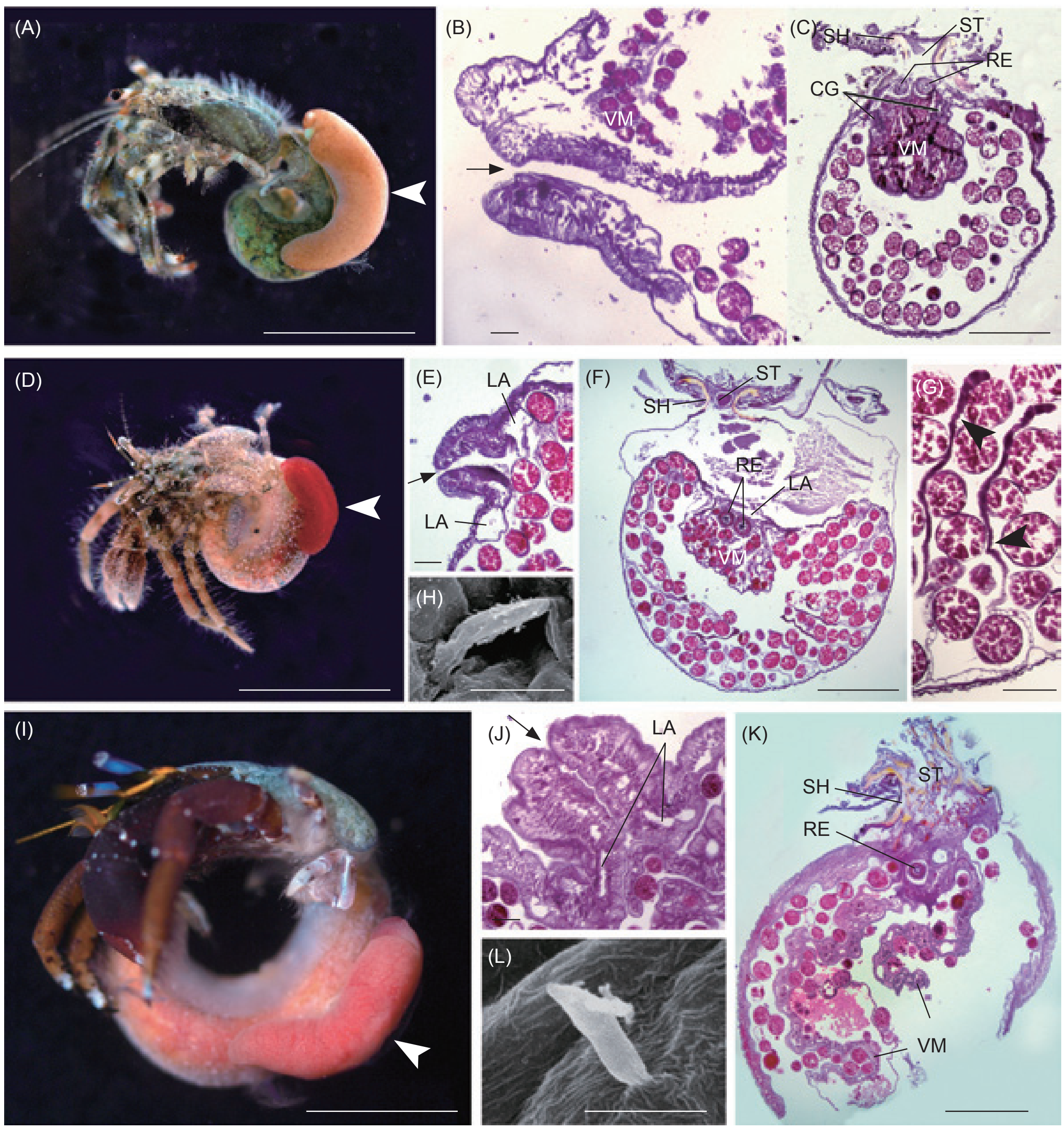


**Fig. 2.** *Peltogaster postica* (A-C), *Septosaccus* sp. (D-H), and *Dipterosaccus indicus* (I-L). Host hermit crabs bearing externae (white arrowheads): *Pagurus angustus* (NMNS-6795-001) (A), *Diogenes tumidus* (NMNS-6795-004) (D), and *Calcinus morgani* (NMNS-6795-005) (I). Sagittal sections of the mantle aperture. Black arrows indicate the mantle aperture (B, E, J). Cross-sections of externa and stalk (C, F, K). Many embryos were found in the mantle cavities. The externa of *Septosaccus* sp. was accidentally detached from the stalk in the section (F). Enlargement of the septa (G, black arrowheads). Retinacula (H, L: SEM). CG, colleteric gland; LA, lacuna; RE, receptacle; SH, shield; ST, stalk; VM, visceral mass. Scale bars: A, D, I = 5 mm; C, F, K = 500 µm; B, E, G, J = 100 µm; H, L = 5 µm.

is not attached to the mantle aperture. The tube-like mantle aperture is approximately 200 μm long. The tubular aperture wall tapers off towards the tip. The blood lacuna is behind the mantle aperture (Fig. 2E). The mantle cuticle is up to 15 μm thick. The outer surface of the mantle is smooth with grooves. The inner surface of the mantle has 17-25 septae (Figs. 2F, G). The receptacles are straight. Although running close to each other, the 2 receptacles do not fuse. Two tubular colleteric glands are attached to the anterior portion of the receptacles. The receptacles and ducts are approximately 0.5 mm long. A blood lacuna is present dorsally to the visceral mass, the lateral expansion of which is not obvious (Fig. 2F). At insertion into the host body wall, the stalk branches, the chitinous projections act as holdfasts, and no chitinous structures are present inside the stalk (Fig. 2F). The receptacle ducts uncoil backwards on the lateral surface of the visceral mass. The retinacula on the septa are setose spindles approximately 6 μm long (Fig. 2H).

*Remarks*: The present specimens share some morphological features with *Septosaccus snelliusi* Van Baal, 1937: the red externa is concave on the stalk side, the mantle opening is a simple slit, the outer surface of the mantle has small grooves, and a blood lacuna is present dorsally to the visceral mass. Morphological details of the mantle aperture, retinacula, and shield are not

**Table 2.** List of sequences of part of the mitochondrial COI gene from the Peltogastridae species included in phylogenetic analysis for this study

| Species | Host | Collection site and date | | Accession No. |
|---|---|---|---|---|
| *Dipterosaccus indicus* | *Calcinus morgani* | Inannse, Okinawa, Japan | Jan. 29 2010 | AB618607 |
| *Dipterosaccus indicus* | *Calcinus morgani* | Benoki, Okinawa, Japan | Apr. 30 2010 | AB618608 |
| *Dipterosaccus indicus* | *Calcinus morgani* | Haikou, Kenting, Taiwan | June 30 2011 | AB688765 |
| *Dipterosaccus indicus* | *Calcinus morgani* | Shizuwan, Kaohsiung, Taiwan | July 6 2011 | AB688766 |
| *Dipterosaccus indicus* | *Calcinus morgani* | Houwan, Kenting, Taiwan | July 27 2011 | AB688767 |
| *Ommatogaster nana* | *Diogenes leptocerus* | Makiya, Okinawa, Japan | Mar. 16 2010 | AB602398 |
| *Ommatogaster nana* | *Diogenes leptocerus* | Makiya, Okinawa, Japan | May 28 2011 | AB688768 |
| *Peltogaster postica* | *Pagurus minutus* | Awase, Okinawa, Japan | Apr. 5 2008 | AB602392 |
| *Peltogaster postica* | *Pagurus minutus* | Awase, Okinawa, Japan | June 11 2009 | AB602393 |
| *Peltogaster postica* | *Pagurus nigrivittatus* | Wakagawa, Wakayama, Japan | Mar. 31 2010 | AB602397 |
| *Peltogaster postica* | *Pagurus filholi* | Shimoda, Shizuoka, Japan | July 21 2010 | AB688769 |
| *Peltogaster postica* | *Pagrus angustus* | Chisi, Penghu, Taiwan | Aug. 5 2011 | AB688770 |
| *Peltogaster postica* | *Pagrus angustus* | Shetoshan, Penghu, Taiwan | Aug. 22 2011 | AB688771 |
| *Septosaccus* sp. | *Diogenes tumidus* | Shetoshan, Penghu, Taiwan | Aug. 2 2011 | AB688772 |
| *Septosaccus* sp. | *Diogenes tumidus* | Shetoshan, Penghu, Taiwan | Aug. 2 2011 | AB688773 |

| Species | Host | Abbreviation | Voucher ID | Ref. |
|---|---|---|---|---|
| *Dipterosaccus indicus* | *Calcinus morgani* | *D. ind*_Inanse | | Yoshida et al. (2011) |
| *Dipterosaccus indicus* | *Calcinus morgani* | *D. ind*_Benoki | | Yoshida et al. (2011) |
| *Dipterosaccus indicus* | *Calcinus morgani* | *D. ind*_Haikou | NMNS-6795-005 | This study |
| *Dipterosaccus indicus* | *Calcinus morgani* | *D. ind*_Shizuwan | | This study |
| *Dipterosaccus indicus* | *Calcinus morgani* | *D. ind*_Houwan | | This study |
| *Ommatogaster nana* | *Diogenes leptocerus* | *O. nana*_01 | | Yoshida et al. (2011) |
| *Ommatogaster nana* | *Diogenes leptocerus* | *O. nana*_02 | NMNS-6795-007 | This study |
| *Peltogaster postica* | *Pagurus minutus* | *P. pos*_Awase01 | | Yoshida et al. (2011) |
| *Peltogaster postica* | *Pagurus minutus* | *P. pos*_Awase02 | | Yoshida et al. (2011) |
| *Peltogaster postica* | *Pagurus nigrivittatus* | *P. pos*_Wakayama | | Yoshida et al. (2011) |
| *Peltogaster postica* | *Pagurus filholi* | *P. pos*_Shimoda | | This study |
| *Peltogaster postica* | *Pagrus angustus* | *P. pos*_Chisi | NMNS-6795-003 | This study |
| *Peltogaster postica* | *Pagrus angustus* | *P. pos*_Shetoshan | NMNS-6795-002 | This study |
| *Septosaccus* sp. | *Diogenes tumidus* | *Septosaccus* sp._01 | NMNS-6795-004 | This study |
| *Septosaccus* sp. | *Diogenes tumidus* | *Septosaccus* sp._02 | | This study |

documented for *Sep. snelliusi* (Van Baal 1937, Boschma 1955, Ball and Haig 1972).

### Genus *Dipterosaccus* Van Kampen and Boschma, 1925
### *Dipterosaccus indicus* Van Kampen and Boschma, 1925

*Dipterosaccus indicus* Van Kampen and Boschma 1925, p. 3; Boschma 1931, p. 6; Van Baal 1937, p. 25; Shiino 1943, p. 9; Boschma 1955, p. 51.

*Host*: *Calcinus morgani*.

*Collection site*: Haikou, Pingtung, intertidal, 30 June 2011; Sizihwan, Kaohsiung, subtidal, 5 July 2011; Leipashih, Pingtung, subtidal, 25 July 2011; Houwan, Pingtung, subtidal, 27 July 2011 (Fig. 1).

*Material examined*: The specimen in the live photograph (NMNS-6795-005) was collected by the 1st author at Houwan on 27 July 2011 (host SL, 4.0 mm). We used the specimen collected by Shih-Wei Su in Haikou on 30 June 2011 (host SL, 3.4 mm) for histology, electron microscopy, and DNA extraction. NMNS-6795-005 and the specimen collected in Sizihwan on 6 July 2011 (host SL, 7.5 mm) were also used for DNA extraction.

*Description*: *External morphology*: The externa has an elongated-oval shape. The anterior end of the externa tapers off towards the posterior end. The mantle aperture is an elevated tube-like projection toward the stalk side. The mantle opening is slit-shaped in the contracted specimen. The thick aperture wall has many wrinkles. The exterior surface is smooth. The fusiform shield has growth rings.

*Coloration in life*: The mature externae are red (Fig. 2I). The root system is pale yellow.

*Anatomy of the externa*: The visceral mass is not attached to the mantle aperture. The tube-like mantle aperture is approximately 500 μm long. The tubular aperture wall is approximately 200 μm thick (Fig. 2J). Two blood lacunae are behind the mantle aperture (Fig. 2J). The mantle cuticle is up to 120 μm thick. The outer surface of the mantle is smooth with grooves. The inner surface of the mantle has no septae. Two tubular colleteric glands are attached to the anterior part of the receptacles. The receptacles are straight. The 2 receptacles run closely and parallel to each other, but do not fuse. The visceral mass extends through the entire mantle cavity (Fig. 2K). Upon insertion into the body wall of the host, the stalk has intricate, chitinous projections (Fig. 2K). The receptacle ducts are uncoiled and directed backwards on the lateral surface of the visceral mass. The retinacula is clavate and 5-8 μm long (Fig. 2L).

*Distribution and host*: Indonesia on *Calcinus latens* and *Clibanarius striolatus* (Van Baal 1937). Japanese mainland on *Cal. laevimanus* (Shiino 1943). New Guinea on *Cal. gaimardii* and *Cal. latens* (Boschma 1955). Taiwan and Okinawa I. on *Cal. morgani* (Yoshida et al. 2011).

### Molecular identification with DNA barcodes

In total, 12 haplotypes were obtained from the partial COI genes of 15 Peltogastridae specimens (Table 2). We confined our analysis to a specific subset of 530-536 bp of partial COI sequences. The aligned amino acid sequences of the 4 peltogastrid species contained 2 insertion/deletion sites (of 3 bp each). The average base frequencies of all 3 codon positions, including the 12 haplotypes, from the 4 peltogastrid species, were 23.6% A, 14.4% C, 18.9% G, and 43.1% T, and the A+T composition frequency was 66.7%. Average base frequencies of the 3rd codon positions alone were 30.2% A, 5.6% C, 13.1% G, and 50.0% T, and the A+T composition frequency was 79.8%.

*Sacculina carcini* (Sacculinidae, accession no. DQ059768) was used as the outgroup. The alignment dataset of the partial COI gene (with 536 positions) was reduced to 522 positions because poorly aligned and divergent regions were detected by Gblocks. The following analyses were performed using a no-gaps dataset. Sequences of the partial COI gene were identical between the *O. nana* specimens from different collection dates. In other Peltogastridae species, sequence differences within each species were low: 0%-0.8% (0-4/522 bp) in *Dip. indicus*; 0.2%-1.9% (1-10/522 bp) in *Pel. postica*; and 0.6% (3/522 bp) in *Septosaccus* sp. Within the 4 peltogastrid species, the lowest percentage of interspecific sequence divergence ("uncorrected p-distance"), 24.7% (129/522 bp), was between *Septosaccus* sp. and *Dip. indicus*. The highest divergence of 31.4% (164/522 bp) was between *Septosaccus* sp. collected from Shetoshan (Penghu) and *Pel. postica* collected from Shetoshan (Penghu). The mean sequence divergence among the peltogastrid species was 28.9%.

For data with all codon positions, the general time-reversible model with invariant rates among sites and a gamma distribution (GTR+I+G) was selected as the best model according to the Akaike information criterion (AIC). Therefore, we chose the GTR+I+G substitution model for the ML and NJ analyses. Figure 3 shows the unrooted ML tree using the GTR+I+G substitution model (log-likelihood = -2367.262). Because the topologies of the ML, MP, and NJ phylogenetic trees were nearly identical, the strict-consensus MP tree and NJ tree under the GTR+I+G substitution model are not shown. The monophyly of each species (*O. nana*, *Septosaccus* sp., *Dip. indicus*, and *Pel. postica*) was supported by high bootstrap values. Whereas *O. nana*, *Septosaccus* sp., and *Dip. indicus* formed a clade supported by moderate bootstrap values (ML = 74%, MP = 89%, and NJ = 89%), the monophyly of the clade comprising the 4 peltogastrid species was not supported in our tree.

### Prevalence among collection sites

Among the 8 sites where *Pag. angustus* was collected, *Pel. postica* was found only at 2 sites in Penghu: two of 6 hosts in Chihsi (33.3 %) and 32 of 101 hosts in Shetoushan (31.7 %) were infested with *Pel. postica* (Fig. 4A). Among the 4 sites where *Dio. tumidus* was collected, *Septosaccus* sp. was found at only 2 sites in Penghu: one of 27 hosts at Siwei (3.7%) and 13 of 260 hosts at Shetoushan (5.0%) were infested by *Septosaccus* sp. (Fig. 4B). Among the 15 sites where *Cal. morgani* was collected, *Dip. indicus* was found at 4 sites in Taiwan: one of 165 hosts at Sizihwan (0.6%), one of 23 hosts at Haikou (4.3%), two of 41 hosts at Houwan (4.9%), and one of 67 hosts at Leipashih (1.5%) were infested with *Dip. indicus* (Fig. 4C).

## DISCUSSION

The following species of the Peltogastridae are first recorded from Taiwan: *Pel. postica* on *Pag. angustus*, *Septosaccus* cf. *snelliusi* on *Dio. tumidus*, and *Dip. indicus* on *Cal. morgani*. Specimens were identified based on histological sections, and species identifications were consistent with partial sequences of the COI gene.

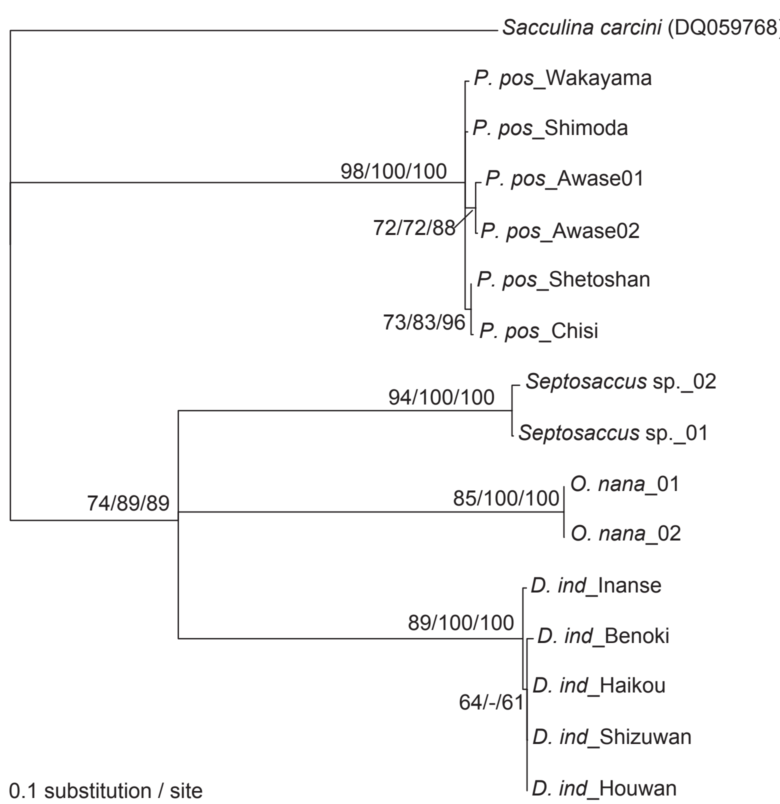


**Fig. 3.** Maximum likelihood (ML) tree of partial mitochondrial cytochrome *c* oxidase subunit I (COI) gene sequences. The GTR+I+G substitution model was used for the analysis. Bootstrap values of > 50% are shown near nodes for the ML, maximum parsimony, and neighbor-joining analyses, respectively.

DNA barcodes are helpful tools for the taxonomy of this group since the external structures of the adults are usually too reduced to provide many useful characteristics for identification, and a histological investigation is often necessary for species identification of rhizocephalans.

Rhizocephalans on hermit crabs are often overlooked in the field because they can be found only when the gastropod shells are removed from the hosts. Therefore, the distribution range of most species has been poorly documented, particularly in tropical and subtropical regions. *Peltogaster postica* was recently described as a new species from the Ryukyus, and this species was also found on the main island of Japan (Yoshida et al. 2011). *Dipterosaccus indicus* was recorded in the Moluccas, Kei Is., and Japan (Van Baal 1937, Shiino 1943, Boschma 1955). These

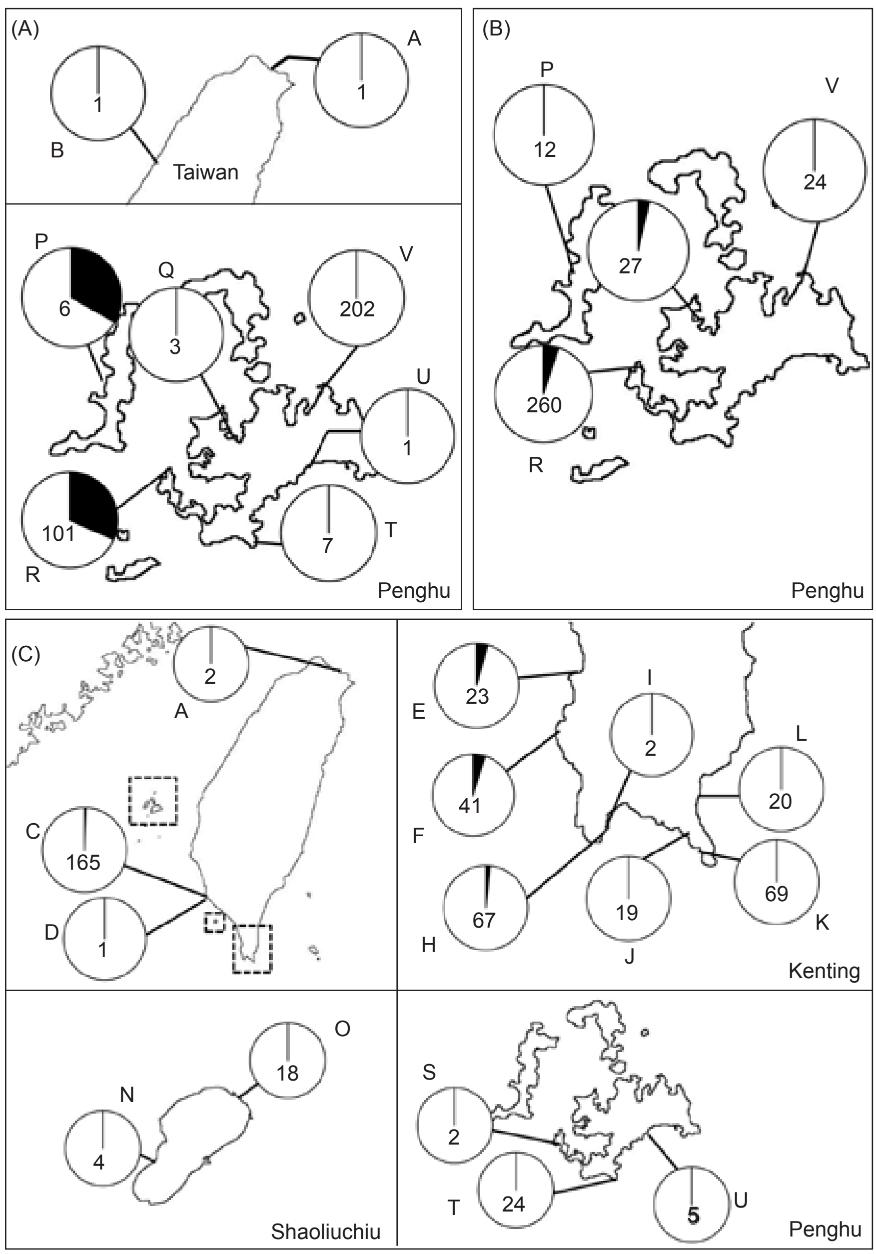


**Fig. 4.** Prevalences of *Peltogaster postica* on *Pagurus angustus* (A), *Septosaccus* sp. on *Diogenes tumidus* (B), and *Dipterosaccus indicus* on *Calcinus morgani* (C) at each collection site. Black sectors indicate prevalence, while the numbers indicate the numbers of host hermit crabs examined.

2 species may have a broad distribution range in warm waters of the West Pacific. In contrast, *Septosaccus* sp. appears to be distributed in tropical waters, because no *Septosaccus* species has ever been recorded from Japan, including the Ryukyus. Among the 3 *Septosaccus* species described to date, *S. snelliusi* from Indonesia (type locality) and New Guinea is the most similar in morphology to *Septosaccus* sp. recorded in this study, but the host species in the present study differed from that of *S. snelliusi*. Careful comparison with Indonesian specimens is necessary to confirm the species identity of the Taiwanese specimens.

No peltogastrids were found on the other 53 species of hermit crabs collected in the present survey (Table 1), although nine of these species (*Cal. gaimardii*, *Cal. laevimanus*, *Cal. latens*, *Clibanarius virescens*, *Dardanus arrosor*, *Dar. impressus*, *Pag. hirtimanus*, *Pag. minutus*, and *Pag. nigrivittatus*) were previously reported as peltogastrid hosts in Indonesia or Japan (see McDermott et al. 2010, Yoshida et al. 2011). We examined only 1 specimen of *Dar. arrosor*, 1 *Pag. hirtimanus*, and 15 *Pag. nigrivittatus*; therefore, a further survey may show the occurrence of peltogastrid parasites on some of these species in Taiwan. Undescribed and/or unrecorded peltogastrids potentially remain to be discovered in the Taiwan and Ryukyu regions.

Host specificity is not known to be very strict in many rhizocephalans, e.g., *Sacculina carcini* parasitizes *Carcinus maenas* in Sweden, England, and Denmark, *Liocarcinus marmoreus* in Ireland, and *L. holsatus* in Wales (Gurney et al. 2006). Many species of the Peltogastridae have different host species at different collection sites (Boschma 1953); thus, the distribution range of these peltogastrids might not be restricted by the distribution range of a single host species. In the present study, the hosts for *Pel. postica* and *Dip. indicus* also differed from their hosts in Japan (Table 3). Although *Pag. minutus* and *Pag. angustus* are distributed in both Taiwan and the Ryukyus, *Pel. postica* in Taiwan was exclusively found on *Pag. angustus*, and the same species in the Ryukyus was never found on *Pag. angustus*. It is unknown why host species replacement occurred between Taiwan and the Ryukyus. Microhabitats of the host species may be crucial for successful parasitism by rhizocephalans.

As shown in figure 4, the prevalence of peltogastrid species vastly differed among collection sites: no peltogastrids were found at 1 site, while nearly 1/3 of host individuals had externae of peltogastrids at another site. It is uncertain what caused these differences (Fig. 4). Similar observations were reported in some other rhizocephalans, e.g., *Sacculina* sp. that was identified as *Polyascus polygenea* by Glenner and Lützen (Glenner et al. 2003) and parasitized *Hemigrapsus sanguineus* (Yamaguchi et al. 1994) and *Lernaeodiscus porcellanae* that parasitized *Petrolisthes cabrilloi* (Sloan et al. 2010).

Epicarideans (Crustacea: Isopoda) infested some species of hermit crabs in this study: *Pag. angustus*, *Dio. tumidus*, and *Cal. morgani*. Interestingly, peltogastrids and epicarideans were never found on the same host individuals in this study, whereas McDermott et al. (2010) reported the co-occurrence of bopyrids and rhizocephalans on hermit crabs. Epicarideans have never been found on these host species in the Ryukyus. Moreover, some *Cal. morgani* were also associated with flatworms, and the flatworms were exclusively found on hermit crabs harboring neither

**Table 3.** Host hermit crabs for *Pel. postica* and *Dip. indicus* in Taiwan, Okinawa (Ryukyus), and Wakayama (main island of Japan)

| Site | Peltogastrid | | | | |
|---|---|---|---|---|---|
| | *Peltogaster postica* | | | *Dipterosacus indicus*[1] | |
| | Host species | | | | |
| | *Pagurus angustus* | *Pag. minutus* | *Pag. nigrivittatus* | *Calcinus morgani* | *Cal. laevimanus* |
| Taiwan (21°-25°N) | + | - | - | + | - |
| Okinawa (26°N) | - | + | - | + | - |
| Wakayama (33°N) | (-) | - | + | - | +[2] |

+, Peltogastrid was found; -, Peltogastrid was not found; (-), Host species are not distributed. [1], *D. indicus* were also found on *C. latens*, *C. striolatus*, and *C. gaimardii* from Indonesia (Van Baal, 1937). [2], Reported by Shiino (1943).

peltogastrids nor epicarideans. These flatworms were possibly non-parasitic symbionts with the hermit crabs (Lytwyn and McDermott 1976).

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