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Diversity of Parasitic Peltogastrid Barnacles (Crustacea: Cirripedia: Rhizocephala) on Hermit Crabs in Korea

Jibom Jung[1,§], Ryuta Yoshida[2,§], and Won Kim[1,*]

[1]*School of Biological Sciences, Seoul National University, 1, Gwanak-ro, Gwanak-gu, Seoul 08826, Republic of Korea. *Correspondence: Tel: +82028806695. E-mail: wonkim@plaza.snu.ac.kr. E-mail: apociv@naver.com (Jung)*

[2]*Tateyama Marine Laboratory, Marine and Coastal Research Center, Ochanomizu University, Kou-yatsu, Tateyama, Chiba 294-0301, Japan. E-mail: 4cd.riutae@gmail.com*

[§]JJ and RY contributed equally to this work.

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We performed a diversity study on parasitic barnacles (Crustacea: Cirripedia: Rhizocephala: Peltogastridae) that parasitize hermit crabs in Korea. Their morphological, ecological, molecular (cytochrome c oxidase subunit I, 16S rRNA), and biogeographical characteristics were examined. Three species were identified based on GenBank sequences and the external morphology of the externa. In addition, this study proposes four new candidate species. This is the first report on the family Peltogastridae from Korea. Six hermit crab species were found to be new hosts to peltogastrids. Korean peltogastrids are less prevalent on their host hermit crabs than those from Japan are, especially in the west coast of Korea. *Peltogasterella gracilis* is widely distributed throughout Korea, *Peltogaster lineata* is located on the east coast, and *Peltogaster postica* is only located on Jeju Island.

Key words: Parasitic barnacle, Paguroidea, Morphology, DNA barcode, Ecology, Biogeography.

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BACKGROUND

Cirripedia barnacles are categorized into three superorders: Acrothoracica (Nielsen et al. 2016), Thoracica with various life styles (Yusa et al. 2013 2018; Buckeridge et al. 2018), and parasitic Rhizocephala (Yoshida et al. 2012). Rhizocephalan barnacles in the family Peltogastridae are highly adapted to decapod parasites, mostly infecting hermit crabs. Of the 46 species and 17 genera in this family (Boyko and Boxshall 2019), 28 species from 8 genera are parasitic on the abdomen of hermit crabs (see McDermott et al. 2010; Yoshida et al. 2011 2013 2015; Yoshida and Naruse 2016). The peltogastrid taxa exhibit extremely degenerated internal and external organ systems without sensory, respiratory, digestive, or excretory systems in the adult stage (Høeg 1992). In addition, the adults lack the segmentation and appendages observed in other crustaceans (Høeg and Lützen 1995). Owing to the externa giving the appearance of a membranous sac without any distinct morphological characteristics, the morphological identification of Rhizocephala are mainly based on the internal morphological characteristics based on paraffin sectioning of the externa and larval morphology (Yoshida et al. 2011). Recently, DNA sequencing has also provided additional support for taxonomic study of this group of animals (Yoshida et al. 2012 2014). Several new peltogastrid species have recently been reported based on morphological and molecular differences (Yoshida et al. 2011 2013 2015; Noever et al. 2016; Yoshida and Naruse 2016).

Peltogastrids have been reported from Europe (Rathke 1842; Reinhard 1942; Høeg and Lützen 1985) and East Asia, including southeast Russia (Kashenko and Korn 2003), Taiwan (Yoshida et al. 2012), and Japan (Shiino 1943; Utinomi and Kikuchi 1966; Nagasawa et al.1996; Yoshida et al. 2014). However, despite previous studies conducted in and near Korea, including plenty of systematics studies on hermit crabs (the peltogastrid's host) (Kim 1973; Oh 2000; Kim and Son 2006; Jung and Kim 2014 2015 2016), no peltogastrids have been reported in this region.

We conducted a taxonomic study of Korean hermit crab fauna and found some peltogastrid individuals attached to the abdomen of hermit crabs. To identify these samples, we assessed the external morphology of the externa and performed DNA barcoding. The results identified some peltogastrids that were not previously reported as parasitizing specific hermit crab species (see McDermott et al. 2010; Yoshida et al. 2014). We follow the methods in Yoshida et al. (2014), who described the ecological and biogeographical characteristics of Japanese peltogastrids with morphological and molecular identification. Herein we present results on morphological, ecological, biogeographical, and molecular characteristics of Korean peltogastrids.

MATERIALS AND METHODS

We examined the abdomens of 4,716 individual Korean paguroid specimens belonging to 48 species (Table 1) collected from 40 sites (administrative district, Si(city) or Gun(country)) deposited into the Laboratory of Systematic and Molecular Evolution (EVOSYS) and Marine Arthropods Depository Bank of Korea (MADBK) of Seoul National University, and the Ewha Womans University Natural History Museum. All specimens examined in the present study were preserved in 70%–99% ethyl alcohol.

The morphological examination methods for Korean peltogastrids generally followed those described by Yoshida et al. (2014) and Jung and Kim (2017). The shape of the externa, position and prominent rate of the mantle, shape of mantle opening, and presence of a chitinous shield in Korean peltogastrid specimens were examined using a macroscope and MZ8 dissection microscope (Leica, Wetzlar, Germany). Photographs were taken with a D200 digital camera (Nikon, Tokyo, Japan) and processed using a Helicon Focus software (Helicon Soft Ltd., Kharkov, Ukraine). Shield length (sl) was recorded to indicate the size of the host hermit crab specimen, measured from the tip of the rostrum to the midpoint of the posterior margin of the shield using a CD6CSX digital caliper (Mitutoyo, Kawasaki, Japan) to the nearest 0.1 mm.

Between one quarter and one-third of the externa tissue was excised from the posterior end of each peltogastrid specimen to extract the total DNA using a QIAamp DNA Micro Kit (QIAGEN, Hilden, Germany). Universal primers LCO1490 and HCO2198 were used to amplify the mitochondrial *COI* gene (cytochrome *c* oxidase subunit I, Folmer et al. 1994). 16SH2 and 16SL2 primers were used (Schubart et al. 2000) to amplify a 545 bp fragment of the mitochondrial 16S rRNA gene. The polymerase chain reaction (PCR) solution included 1 µL DNA template, 1 µL of each primer (10 µM), 0.3 µL Go Taq DNA polymerase (Promega, Madison City, WI, USA), 5 µL 5x color Go Taq reaction buffer, 1 µL dNTP mixture (10 mM) and 15.7 µL distilled H2O (total 25 µL). The amplification protocol followed that previously described by Yoshida et al. (2014). The size of PCR products was observed in 1% agarose gels. PCR products were analyzed in an ABI 3730 automated sequencer (Applied Biosystems, Foster City, CA, USA).

Table 1. Individual number and infestation rate (%) of peltogastrids on the Korean hermit crab hosts examined in this study

Host hermit crab Species	Total individuals	Infested individuals	Infestation rate
Areopaguristes japonicas	35	0	0.0%
Areopaguristes nigroapiculus	42	1	2.3%
Ciliopagurus krempfi	2	0	0.0%
Clibanarius virescens	5	0	0.0%
Dardanus arrosor	66	0	0.0%
Dardanus crassimanus	4	0	0.0%
Dardanus impressus	16	0	0.0%
Dardanus lagopodes	2	0	0.0%
Dardanus pedunculatus	8	0	0.0%
Diogenes deflectomanus	4	0	0.0%
Diogenes edwardsii	49	0	0.0%
Diogenes nitidimanus	15	0	0.0%
Diogenes penicillatus	4	0	0.0%
Elassochirus cavimanus	75	0	0.0%
Lophopagurus (*Australeremus*) *triserratus*	1	0	0.0%
Paguristes acanthomerus	3	0	0.0%
Paguristes digitalis	30	0	0.0%
Paguristes ortmanni	382	1	0.2%
Paguristes seminudus	1	0	0.0%
Paguristes versus	2	0	0.0%
Pagurus brachiomastus	100	1	1.0%
Pagurus constans	34	0	0.0%
Pagurus filholi	670	9 (*Peltogaster lineata*: 1, *P. postica:* 7, *Peltogasterella gracilis*: 2)	1.3%
Pagurus gracilipes	36	0	0.0%
Pagurus japonicus	93	3	3.2%
Pagurus lanuginosus	239	5	2.1%
Pagurus maculosus	133	4	1.5%
Pagurus middendorffii	47	1	2.1%
Pagurus minutus	1244	2	0.2%
Pagurus nigrivittatus	10	0	0.0%
Pagurus nigrofascia	46	0	0.0%
Pagurus ochotensis	68	1	1.5%
Pagurus parvispina	8	1	12.5%
Pagurus pectinatus	313	3	1.0%
Pagurus proximus	175	1	0.4%
Pagurus quinquelineatus	3	0	0.0%
Pagurus rathbuni	13	1	7.7%
Pagurus rectidactylus	2	0	0.0%
Pagurus rubrior	260	5	1.9%
Pagurus similis	18	0	0.0%
Pagurus simulans	274	0	0.0%
Pagurus spina	28	1	3.6%
Pagurus trigonocheirus	109	0	0.0%
Pagurus undosus	12	0	0.0%
Pomatocheles jeffreysi	4	0	0.0%
Porcellanopagurus nihonkaiensis	13	2	15.4%
Discorsopagurus maclaughlinae	13	0	0.0%
Discorsopagurus tubicola	5	0	0.0%
Total	4,716	41	0.9%

The molecular analysis methods followed those described by Jung et al. (2018a). The mitochondrial sequences of the collected specimens obtained by DNA extraction were checked and edited using SeqMan 5.0 (DNASTAR, Madison City, WI, USA) and DNA Sequence Polymorphism (DnaSP) version 6 software (Rozas et al. 2017); they were aligned using an ClustalW interface ClustalW in MEGA7 (MEGA, PA, USA) (Kumar et al. 2016). The mitochondrial sequences of the Korean peltogastrids plus 11 peltogastrid species from GenBank (Table 2) were used in a molecular evolutionary genetics analysis using MEGA7. Maximum likelihood analyses of *COI* and 16S rRNA sequences of the selected peltogastrids were performed based on the Tamura-Nei (TN93) (Tamura and Nei 1993) and Hasegawa-Kishino-Yano (Hasegawa et al. 1985) models, respectively, with 5 rate categories of gamma distribution (+G) and invariable sites (+I), which had the lowest Bayesian Information Criterion (BIC) scores in the Model Selection option of MEGA7. The consistency of topologies was assessed using bootstrap values with 1,000 replications. Interspecific and intraspecific sequence variations were obtained based on the K2P distance in MEGA7.

Table 2. Geographical locations of and sample information on the Korean peltogastrids and others in this study in the order of species name, host species, location, and specimen number.

Species	Host Species	Location	Specimen Number
*Briarosaccus auratum**	*Lithodes aequispinus*	Alaska, US	YPM 74383
*Briarosaccus regalis**	*Paralithodes camtschaticus*	Alaska, US	YPM 74281
*Dipterosaccus indicus**	*Calcinus morgani*	Okinawa, Japan	NSMT-Cr 22224
*Dipterosaccus shiinoi**	*Calcinus vachoni*	Okinawa, Japan	NSMT-Cr 22236
*Ommatogaster nana**	*Diogenes leptocerus*	Okinawa, Japan	
Peltogaster lineata	*Pagurus brachiomastus*	Yangyang, Korea	MADBK 430101_001
	Pagurus filholi	Busan, Korea	MADBK 160707_043
	*Pagurus nigrivittatus**	Shirahama, Japan	NSMT-Cr 22303
*Peltogaster paguri**	*Pagurus bernhardus*	Gullmar Fjord, Sweden	ZMUC CRU-9909
Peltogaster postica	*Pagurus filholi*	Jeju, Korea	MADBK 160707_009
			MADBK 160707_052
			MADBK 430102_001
	*Pagurus minutus**	Okinawa, Japan	
Peltogaster aff. *ovalis*	*Pagurus japonicus**	Wakayama, Japan	NSMT-Cr 22308
	Pagurus ochotensis	Busan, Korea	MADBK 160714_013
	Pagurus parvispina	Goseong, Korea	EWUNHM DP 20151217063
	Pagurus rathbuni	Yangyang, Korea	EVOSYS 260720#013
	Pagurus rubrior	Busan, Korea	EVOSYS 260717#012
			EWUNHM DP 20151125023
		Seogwipo, Korea	EVOSYS 260717#038
			MADBK 160717_007
		Yeosu, Korea	EVOSYS 260717#033
Peltogaster aff. *reticulatus*	*Pagurus proximus*	Shinan, Korea	MADBK 160718_040
Peltogaster sp. 1	*Pagurus japonicus*	Jeju, Korea	MADBK 160710_012
		Seogwipo, Korea	EVOSYS 260710#021
			MADBK 160710_002
Peltogaster sp. 2	*Areopaguristes nigroapiculus*	Pohang, Korea	EVOSYS 260510#008
Peltogaster sp. 3	*Paguristes ortmanni*	Pohang, Korea	MADBK 160513_050
Peltogaster sp. 4	*Pagurus minutus*	Namhae, Korea	MADBK 160706_065
			MADBK 160706_125
Peltogaster sp. *Areopaguristes japonicus**	*Areopaguristes japonicus*	Chiba, Japan	
Peltogaster sp. *Paguristes ortmanni**	*Paguristes ortmanni*	Chiba, Japan	
Peltogasterella gracilis	*Pagurus filholi*	Gyeongju, Korea	MADBK 160707_039
		Yeosu, Korea	MADBK 430103_001
	Pagurus lanuginosus	Busan, Korea	MADBK 160712_040
		Taean, Korea	EVOSYS 260712#023
		Uljin, Korea	MADBK 160712_020
		Ulsan, Korea	MADBK 160712_006
	Pagurus maculosus	Gangneung, Korea	MADBK 160722_004
		Pohang, Korea	MADBK 160722_013
		Ulleoung, Korea	MADBK 160722_023

			MADBK 160722_024
	Pagurus middendorffii	Goseong, Korea	MADBK 160713_007
	*Pagurus nigrivittatus**	Shizuoka, Japan	NSMT-Cr 22310
	Pagurus pectinatus	Busan, Korea	MADBK 160715_016
		Uljin, Korea	MADBK 160715_005
		Yeongdeok, Korea	EWUNHM DP 20151202019
	Pagurus spina	Ulleoung, Korea	MADBK 160726_003
Peltogasterella aff. *gracilis*	*Porcellanopagurus nihonkaiensis*	Jeju, Korea	MADBK 160730_002
*Peltogasterella sensuru**	*Pagurixus pseliophorus*	Okinawa, Japan	RUMF-ZC 03035
*Peltogasterella sulcata**	*Pagurus cuanensis*	Gullmar Fjord, Sweden	ZMUC CRU-9910
Septosaccus sp.*	*Diogenes tumidus*	Penghu, Taiwan	NMNS-6795-004

Species	Individual Number	*COI* Accession Number	16S rRNA Accession Number
*Briarosaccus auratum**	1	KR812208	KR812156
*Briarosaccus regalis**	1	KR812198	KR812177
*Dipterosaccus indicus**	1	AB618607	AB778078
*Dipterosaccus shiinoi**	1	AB742438	AB778083
*Ommatogaster nana**	1	AB602398	
Peltogaster lineata	1	MK604142	MK604159
	1	MK604143	MK604160
	1	AB778060	AB778092
*Peltogaster paguri**	1		FJ481958
Peltogaster postica	4	MK604144-MK604146	MK604161, MK604162
	1	MK604147, MK604148 (two externae)	MK604163, MK604164 (two externae)
	1	MK604149	MK604165
	1	AB602392	AB778105
Peltogaster aff. *ovalis*	1	AB778063	AB778095
	1		
	1		
	1		
	1		
	1		
	1		
	1		
	1		
Peltogaster aff. *reticulatus*	1		
Peltogaster sp. 1	1		
	1		

	1		
Peltogaster sp. 2	1		
Peltogaster sp. 3	1	MK604150	MK604166
Peltogaster sp. 4	1	MK604151	MK604167
	1		
Peltogaster sp. *Areopaguristes japonicus**	1	AB778074	AB778111
Peltogaster sp. *Paguristes ortmanni**	1	AB778075	AB778112
Peltogasterella gracilis	1		
	1	MK604152	MK604168
	1	MK604153	MK604169
	2		
	1	MK604154	MK604170
	1	MK604155	
	1	MK604156	MK604171
	1		
	1		
	1		
	1		
	1	AB778077	AB778114
	1	MK604157	MK604172
	1		
	1		
	1	MK604158	MK604173
Peltogasterella aff. *gracilis*	2		
*Peltogasterella sensuru**	1	LC013692	LC013700
*Peltogasterella sulcata**	1		FJ481955
Septosaccus sp.*	1	AB688772	

*: NCBI sequence

RESULTS

Based on the shape of the externa and mitochondrial sequences of the peltogastrids, we found 41 peltogastrid individuals belonging to 10 species from 15 collection sites (Fig. 1) on 17 host Korean hermit crab species (Table 2). Among the Korean peltogastrids, only seven and five species could be distinctly identified by morphological characteristics and molecular sequences, respectively; their morphological characteristics and status using for this identification are shown in Fig. 2 and Table 3. All the peltogastrid sequence data in this study are available in GenBank (Table 2); their phylogeny is shown in figures 3 and 4. We report the discovery of three peltogastrid species and four candidates for new species from Korea.

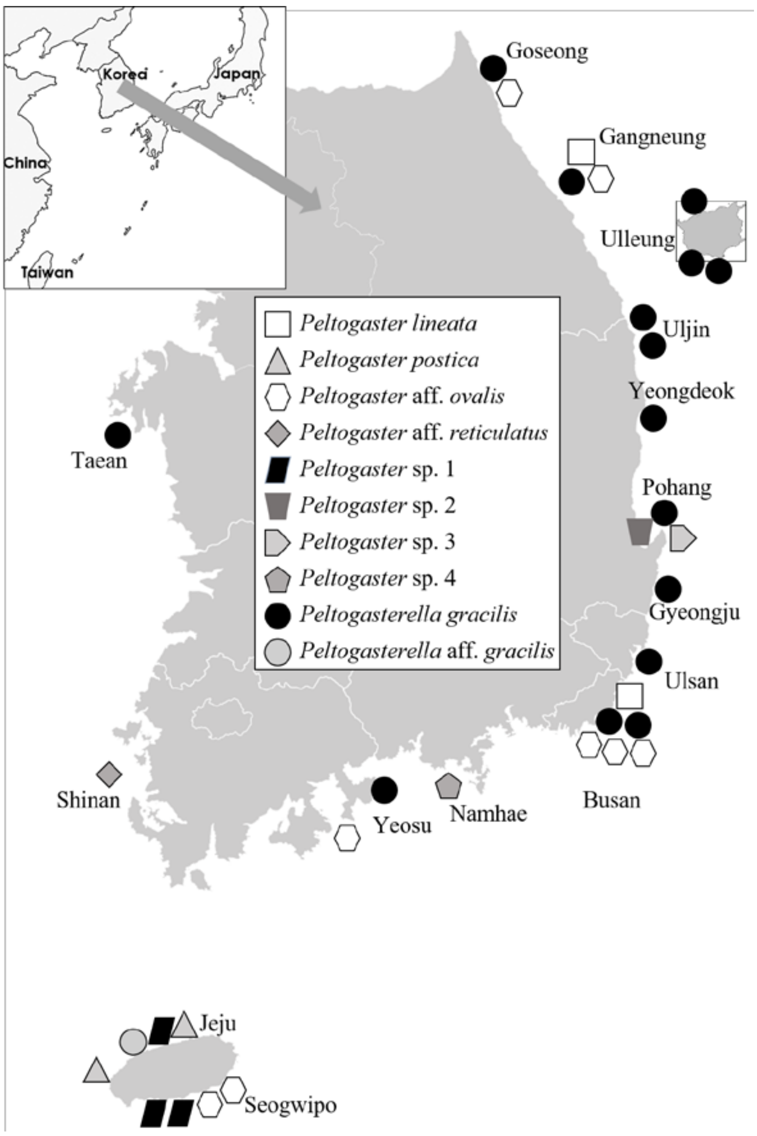

Fig. 1. Distribution map of Korean peltogastrids.

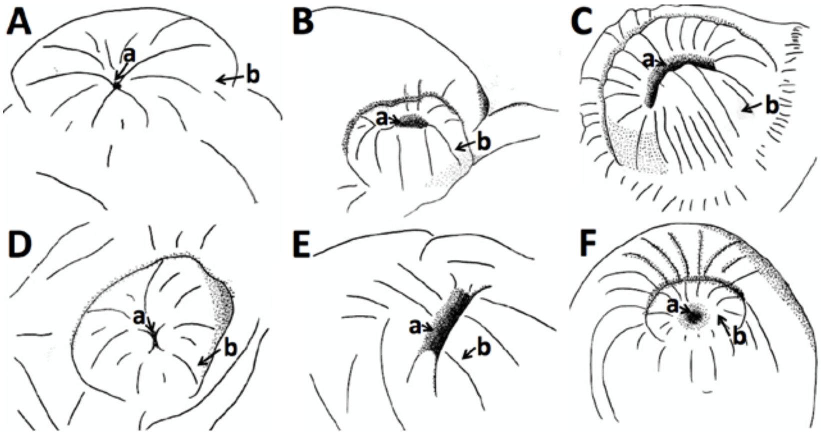

Fig. 2. Semi-diagrammatic figures of mantle aperture of Korean peltogastrids. A, *Peltogaster lineata*; B, *Peltogaster postica*; C, *Peltogaster* aff. *ovalis*; D, *Peltogaster* aff. *reticulatus*; E, *Peltogaster* sp. 2; F, *Peltogasterella gracilis*; a, mantle opening; b, mantle. Focus on the comparative rate of mantle projection and shape of mantle opening which are the most important characters on morphological identification of this study.

Table 3. Morphological characters of the externa of the Korean peltogastrids (modified from Yoshida et al. 2014).

Species	Whole externa	Mantle			Chitinous shield
		Projection	Opening	Position	
Peltogaster lineata	Oval	Slightly elevated	Circular or u-shaped	Termina	Yes
Peltogaster postica	Irregularly elongate	Elevated tube	U-shaped	Terminal or subterminal	Yes
Peltogaster aff. *ovalis*	Oval	Elevated	U-shaped	Terminal	Yes
Peltogaster aff. *reticulatus*	Oval	Elevated tube	X-shaped	Terminal	Yes
Peltogaster sp. 2	Oval	Slightly elevated	Slit-shaped	Terminal	Yes
Peltogasterella gracilis	Elongate, gregarious	Elevated	Circular	Termina	No

TAXONOMY

Peltogaster lineata Shiino, 1943

(Fig. 5A)

Peltogastridae Lilljeborg, 1859

Peltogaster Rathke, 1842

Material examined: On *Pagurus brachiomastus*: 1 Ind., Yangyang, 37°55'49.00"N 128°47'25.00"E, Scuba, 10 Apr. 2014, Coll. Park JH, MADBK 430101_001, host: male, sl 4.7 mm.

On *P. filholi*: 1 Ind., Busan, 35° 8'16.83"N 129° 9'37.01"E, 8 Oct. 2015, Coll. Jung J, MADBK 160707_043, host: male, sl 3.4 mm.

Hosts: *P. brachiomastus*, *P. filholi*, *P. nigrivittatus*, *P. maculosus* (Paguridae).

Distribution: Japan, Korea.

Remarks: Morphologically, the externa on the examined materials showed a single oval shape of whole externa, terminal located and slightly projected mantle, circular mantle opening, and presence of a chitinous shield, in close agreement with the original description (Shiino 1943) and re-description of *Peltogaster lineata* by Yoshida et al. (2014). In Korean *P. lineata*, the projection of the mantle aperture is slightly elevated. In addition, the mitochondrial sequence of the examined material (MK604142, MK604143, MK604159, MK604160) is similar to the DNA sequences (AB778060, AB778092) of the species reported by Yoshida et al. (2014). The present study reports *Pagurus brachiomastus* as the fifth host of *Peltogaster lineata* after *Pagurus japonicus*, *P. filholi*, *P. nigrivittatus,* and *P. maculosus* (Shiino 1943; Yoshida et al. 2014). In addition, the specimen of *Peltogaster lineata* (MADBK 430101_001) was found in Yangyang, Korea, much farther north (37°55'N) than the previous record in southern Japan (35°09'N) (Shiino 1943; Yoshida et al. 2014). Furthermore, this is the first report of this species collected from outside of Japanese waters.

The mantle of the *Pagurus filholi* specimen (MADBK 160707_043) has a U-shaped opening, similar to that of *Peltogaster postica*. However, the former's mitochondrial sequence (MK604143, MK604160) differed from that of *P. postica*, but it constituted a single clade of sequences with those of *P. lineata* in this study (MK604142, MK604159) and previous studies (AB778060, AB778092) (Figs. 3, 4). In addition, Yoshida et al. (2014) reported that *P. lineata* can parasitize *Pagurus filholi*. Therefore, the present study identified this specimen as *Peltogaster lineata* based on molecular and ecological characteristics.

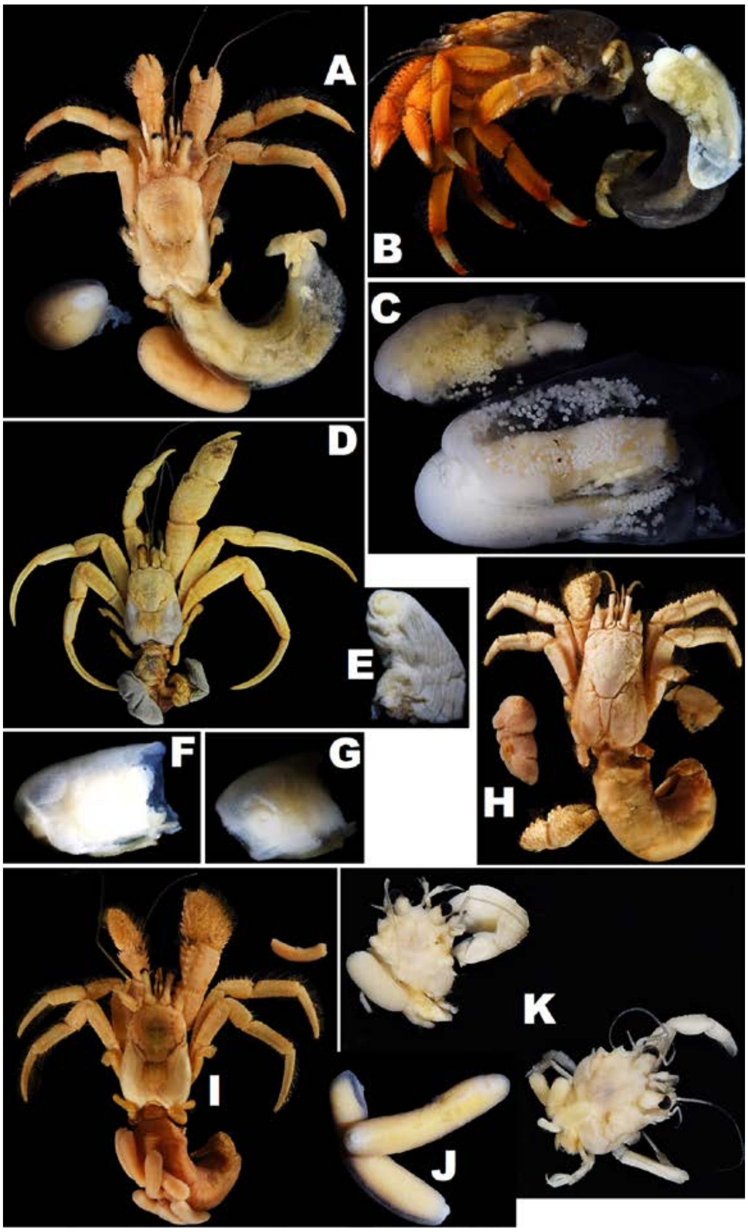

Fig. 5. Korean peltogastrids. A, *Peltogaster lineata* on *Pagurus brachiomastus* and its mantle, MADBK 430101_001; B, *Peltogaster postica* on *Pagurus filholi* , MADBK 160707_009; C, mantle of B; D, *Peltogaster* aff. *ovalis* on *Pagurus rathbuni*, EVOSYS 260720#013; E, mantle of D; F, G, *Peltogaster* aff. *reticulatus* on *Pagurus proximus* and its mantle, MADBK 160718_040; H, *Peltogaster* sp. 2 on *Areopaguristes nigroapiculus* and its mantle, EVOSYS 260510#008; I, *Peltogasterella gracilis* on *Pagurus pectinatus*, MADBK 160715_016; J, mantle of I; K, *Peltogasterella* aff. *gracilis* on *Porcellanopagurus nihonkaiensis*, MADBK 160730_002.

***Peltogaster postica* Yoshida and Osawa in Yoshida, Osawa, Hirose, and Hirose, 2011**

(Figs. 5B, 5C)

Material examined: On *Pagurus filholi*: 4 Inds., Jeju, 33°31'38.25"N 126°35'4.60"E, 31 Oct. 2010, Coll. Kang SH, MADBK 160707_009, host: 3 males, sl 3.1-4.0 mm, 1 female, sl 3.3 mm; 1 Ind. (2 externae), Jeju, 33°31'23.00"N 126°33'31.60"E, 4 May 2016, Coll. Jung J, MADBK 160707_052, host: male, sl 3.7 mm; 1 Ind., same as MADBK 160707_052, MADBK 430102_001, host: male, sl 3.2 mm.

Host: *P. filholi*, *P. minutus, P. nigrivittatus*, *P. angustus* (Paguridae).

Distribution: Southern Honshu and Okinawa (Japan), Taiwan, Korea.

Remarks: The externa of examined materials had morphological characteristics, such as irregularly elongated body, terminal-posited elevated mantle, *U*-shaped mantle opening, and chitinous shield similar to the original description (Yoshida et al. 2011) and re-description of *Peltogaster postica* by Yoshida et al. (2014). Furthermore, the *COI* (MK604144-MK604149) and 16S rRNA sequences (MK604161-MK604165) of the examined material belonged to a single clade of DNA sequences (AB602392, AB778105) as that of *P. postica* reported by Yoshida et al. (2011 2014). According to Yoshida et al. (2011 2014), *P. postica* is found on *Pagurus filholi* as well as on *P. minutus* and *P. nigrivittatus* in Japan. However, the Korean *Peltogaster postica* is found in the abdomen of *Pagurus filholi* only, even though *P. minutus* and *P. nigrivittatus* are also present in Korea. Therefore, the examination of additional specimens is necessary to determine whether *Peltogaster postica* is parasitic on Korean *Pagurus minutus* and *P. nigrivittatus*.

***Peltogaster* aff. *ovalis* Krüger, 1912**

(Figs. 5D, 5E)

Material examined: On *Pagurus ochotensis*: 1 Ind., Busan, 35° 8'16.83"N 129° 9'37.01"E, fishing trap, 31 Jan. 2016, Coll. Jung J, MADBK 160714_013, host: male, sl 10.2 mm.

On *P. parvispina*: 1 Ind., Goseong, 22 Nov. 1980, Coll. Rho BJ, EWUNHM DP 20151217063, host: female, sl 5.3 mm.

On *P. rathbuni*: 1 Ind. (2 externae), Yangyang, 21 May 2002, EVOSYS 260720#013, host: male, sl 12.5 mm.

On *P. rubrior*: 1 Ind., Busan, fishing trap, 15 Jul. 1972, EVOSYS 260717#012, host: male, sl 9.8 mm; 1 Ind., Busan, 9 Feb. 1971, EWUNHM DP 20151125023, host: female, sl 11.7 mm; 1 Ind. (3 externae), Seogwipo, 13 Jul. 1972, fishing net, Coll. Lee KS, EVOSYS 260717#038, host: female, sl 19.4 mm; 1 Ind. (2 externae), Seogwipo, 33°14'10.13"N 126°31'2.71"E, 14 Nov. 2008, Coll. Kim SH, MADBK 160717_007, host: male, sl 19.2 mm; 1 Ind., Yeosu, St. 1, 21 Jun. 2002, EVOSYS 260717#033, host: male, sl 19.1 mm.

Hosts: *P. ochotensis*, *P. parvispina*, *P. rathbuni*, *P. rubrior* (Paguridae).

Distribution: Korea.

Remarks: The externa of the examined materials had similar morphological characteristics to that of *Peltogaster ovalis* specimen described by Krüger (1912), including an oval body, terminally located elevated projection of the mantle aperture, U-shaped mantle opening, and a chitinous shield. However, no *P. ovalis* were reported on these four host species (*i.e.*, *Pagurus ochotensis*, *P. parvispina*, *P. rathbuni*, and *P. rubrior*) in the previous study. We could not obtain the sequencing data on the present materials. Therefore, we tentatively identified these species as *Peltogaster* aff. *ovalis*. Additional information and further studies, such as histological examination and larval morphology, are necessary to confirm the identity of these species.

The morphological characteristics of the specimen attached to *Pagurus rathbuni* (EVOSYS 260720#013) were slightly different to these of *Peltogaster* aff. *ovalis* in Yoshida et al. (2014). However, the main characteristics, such as oval shape of the whole externa, elevated mantle located on the terminal margin of the externa, and U-shaped mantle opening are similar to those of *P*. aff. *ovalis* from Yoshida et al. (2014). Therefore, we identified the specimen as *P*. aff. *ovalis*.

Some of the examined specimens (MADBK 160717_007, EVOSYS 260717#038 EVOSYS 260720#013) had two and three externae (28.57% and 14.29% of total individuals, respectively), whereas others had a single externa. In the original description of *Peltogaster ovalis* by Krüger, 1912, and in the re-description of *P.* aff. *ovalis* by Yoshida et al. (2014), there are no descriptions of multiple externae for this species. However, variation in the number of externae has been reported in previous studies. For example, Reinhard (1942) reported that some specimens of *P. paguri* on *Pagurus pubescens* produced multiple externae, whereas most possessed a single externa. In addition, Høeg and Lützen (1985) showed that some *Peltogaster curvatus* members have a single externa on their host *Pagurus cuanensis* in Scandinavian waters, whereas in the Mediterranean Sea, they had two to four externae on one-third of their two hosts (*P. cuanensis* and *P. prideaux*). Therefore, the multiple externae of these specimens were regarded as the result of an invasion of different larvae or from asexual budding.

Peltogaster aff. *reticulata* Shiino, 1943

(Figs. 5F, 5G)

Material examined: On *Pagurus proximus*: 1 Ind., Shinan, 34°35'49.24''N 125°45'58.02''E, 16 Oct. 2008, Coll. Hong J, MADBK 160718_040, host: female, sl 2.9 mm.

Host: *P. proximus* (Paguridae).

Distribution: Korea.

Remarks: *Pagurus proximus* is reported as one of the hosts of *Peltogaster reticulata* (Kashenko and Korn 2003). The specimens examined in this study had a single externa, an elevated mantle with X-shape opening, and a chitinous shield similar to that of *P. reticulata* in Russia. Because we could not obtain sequencing data using the present materials, our results tentatively suggest that the present specimen is *P. reticulata*, although further investigation is necessary to identify this specimen more definitively.

***Peltogaster* sp. 1**

Material examined: On *Pagurus japonicus*: 1 Ind., Jeju, Korea, 13 Apr. 2014, MADBK 160710_012, Coll. Park J, host: male, sl 9.1 mm; 1 Ind., Seogwipo, Korea, Scuba, 25 Aug. 2007, EVOSYS 260710#021, host: male, sl 8.3 mm; 1 Ind., Seogwipo, 33°33'45.99"N 126°28'19.14"E, Scuba, 12 Aug. 2009, MADBK 160710_002, host: female, sl 8.1 mm.

Host: *P. japonicus* (Paguridae).

Distribution: Korea.

Remarks: The externae of the present specimens were single with an oval shape and have a chitinous shield. However, mantle could not be examined because the specimens were damaged. Because mitochondrial sequences could not be obtained, we tentatively identified these specimens as *Peltogaster* sp. 1. Additional specimens and further research is needed to make a more precise identification. McDermott et al. (2010) reported that *Pagurus japonicus* has two parasitic barnacle species, *Peltogaster lineata* and *P. ovalis*, which have a single oval shape for the whole externa (Yoshida et al. 2014). Therefore, the present specimens might be regarded as one of these two species, based on their host and shape of the whole externa.

***Peltogaster* sp. 2**

(Fig. 5H)

Material examined: On *Areopaguristes nigroapiculus*: 1 Ind., Pohang, fishing net, 7 Sep. 2001, EVOSYS 260510#008, host: male, sl 7.0 mm.

Host: *A. japonicus* (Diogenidae).

Distribution: Korea.

Remarks: We reported *A. nigroapiculus* as a new host of peltogastrid species. In addition, the morphological characteristics of the externa of the specimens, such as a single oval shape of the whole externa, slightly elevated terminal-located mantle aperture with slit-shaped opening, and present of a chitinous shield agreed with the description of *Peltogaster* sp. parasite on *A. japonicus* reported by Yoshida et al. (2014). Because we could not obtain sequencing data on the specimens, additional data are necessary to identify this species.

***Peltogaster* sp. 3**

Material examined: on *Paguristes ortmanni*: 1 Ind., Pohang, 36° 0'40.98"N 129°37'29.55"E, hand, 17 Sep. 2011, Coll. Jung J, MADBK 160513_050, host: female, sl 6.8 mm.

Host: *P. ortmanni* (Diogenidae).

Distribution: Japan, Korea.

Remarks: The mitochondrial sequence of the specimen examined on *P. ortmanni* (MK604150, MK604166) was similar to the DNA sequence of *Peltogaster* sp. on *Paguristes ortmanni* (AB778075, AB778112) reported by Yoshida et al. (2014). However, we could not examine the morphological characteristics of the mantle aperture on this specimen except single externa with a chitinous shield because it was damaged. Additional data and further investigations are needed to describe this species.

***Peltogaster* sp. 4**

Material examined: On *Pagurus minutus*: 1 Ind., Namhae, 34°52'40.83"N 127°56'43.61"E, 14 Nov. 2012, Coll. Jung J, MADBK 160706_065, host: female, sl 3.7 mm; 1 Ind (2 externae), Namhae, 34°52'40.83"N 127°56'43.61"E, 12 May 2018, Coll. Jung J, MADBK 160706_125, host: female, sl 2.9 mm.

Host: *P. minutus* (Paguridae).

Distribution: Korea.

Remarks: Only one peltogastrid species, *Peltogaster postica*, is known to parasitize *P. minutus* (Yoshida et al. 2011). As in *P. postica*, the examined specimens had a single externa and without a chitinous shield, but the specimen’s mantle characteristics could not be examined due to damage. On the other hand, mitochondrial sequences from the specimen in this study (MK604151, MK604167) were clearly different from those of *P. postica* from the Okinawa islands in Japan (AB602392, AB778105) reported by Yoshida et al. (2011). These results suggest that the present specimen is not *P. postica*, but an unreported species, though further data are needed to confirm this.

Jung et al. (2018a) showed that the Korean and Taiwan–Okinawa populations of *Pagurus minutus* are different based on molecular, morphological, and color characteristics. Morphological examination of the host *P. minutus* individuals infested with *Peltogaster postica* shows that the host reported by Yoshida et al. (2011) belonged to the Taiwan–Okinawa Group (TOG), whereas the host in this study belongs to the Major Group (MAG). This result indicates that these two groups of *Pagurus minutus* might have different parasites, and population separation can be enhanced by observing the prevalence of specialized hosts of these peltogastrids.

***Peltogasterella gracilis* (Boschma, 1927)**

(Figs. 5I, 5J)

Peltogasterella Krüger, 1912

Material examined: On *Pagurus filholi*: 1 Ind., Gyeongju, 35°48'17.25"N, 129°30'13.41"E, 25 Jan. 2015, Coll. Jung J, MADBK 160707_039, host: male, sl 4.3 mm; 1 Ind. (3 externae), Yeosu, 34° 1'10.11"N 127°18'19.22"E, 25 Apr. 2013, Coll. Park JH, MADBK 430102_001, host: female, sl 3.7 mm.

On *P. lanuginosus*: 1 Ind., Busan, 35°04'07.28"N 129°03'52.95"E, 7 Oct. 2015, Coll. Jung J, MADBK 160712_040, host: female, sl 4.9 mm; 2 Inds. (5 externae and 7 externae), Taean, 18 May 2000, EVOSYS 260712#023, hosts: female, sl 5.5 mm; female, sl 5.4 mm; 1 Ind. (5 externae), Uljin, 37° 0'9.87"N 129°25'23.09"E, 16 Aug. 2011, Coll. Lee S, MADBK 160712_020, host: female, sl 6.3 mm; 1 Ind. (11 externae), Ulsan, 35°38'32.50"N 129°30'36.44"E, 30 Apr. 2009, Coll. Shin M, MADBK 160712_006, host: male, sl 8.0 mm.

On *P. maculosus*: 1 Ind. (6 externae), Gangneung, 37°54'37.03"N 128°51'11.41"E, 21 Oct. 2010, Coll. Lee SK, MADBK 160722_004, host: male, sl 7.0 mm; 1 Ind., Pohang, 36° 0'40.98"N 129°37'29.58"E, hand, 17 Sep. 2011, Coll. Jung J, MADBK 160722_013, host: male, sl 5.4 mm; 1 Ind., Ulleoung, 37°27'32.54"N 130°51'23.42"E, Scuba, 16 Nov. 2013, Coll. Park JH, MADBK 160722_024, host: female, sl 4.7 mm.

On *P. middendorffii*: 1 Ind. (5 externae), Goseong, 38°28'1.05"N 128°33'33.66"E, 25 Jul. 2011, Coll. Lee SK, MADBK 160713_007, Host: male, sl 7.0 mm.

On *P. pectinatus*: 1 Ind., Busan, 35° 8'16.83"N 129° 9'37.01"E, 12 Nov. 2010, Coll. Kim SH, MADBK 160715_016, host: male, sl 7.2 mm; 1 Ind., Uljin, 36°58'40.71"N 129°25'8.81"E, 2 Jul. 2009, Coll. Yeom D, MADBK 160715_005, host: male, sl 9.1 mm; 1 Ind., Yeongdeok, 10 Aug. 1971, Coll. Rho BJ, EWUNHM DP 20151202019, host: female, sl 8.3 mm.

On *P. spina*: 1 Ind., Ulleung, 37°27'32.54"N 130°51'23.42"E, Scuba, 16 Nov. 2013, Coll. Park JH, MADBK 160726_003, host: male, sl 4.1 mm.

Hosts: *Discorsopagurus schmitti*, *Labidochirus splendescens*, *Pagurus aleuticus*, *P. dalli*, *P. edwardsi*, *P. filholi*, *P. hemphilli*, *P. hirsutiusculus*, *P. lanuginosus*, *P. maculosus*, *P. middendorffii*, *P. nigrivittatus*, *P. ochotensis*, *P. pectinatus*, *P. spina* (Paguridae).

Distribution: Western United States, Chile, Peru, eastern Russia, Japan, Korea.

Remarks: Many aspects of the externa morphology of the examined materials agreed with that of the original description (Boschma 1927) and re-description of *Peltogasterella gracilis* by Yoshida et al. (2014), such as elongate and colonial externae, terminal-posited circular-opened mantle aperture, and no chitinous shield, the exception being the projection of mantle aperture, which was elevated. In addition, the mitochondrial sequences of the examined materials (MK604152-MK604158, MK604168-MK604173) were similar to those reported for this species (AB778077, AB778114) by Yoshida et al. (2014). A total of 14 host hermit crab species for *P. gracilis* have been reported (McDermott et al. 2010; Yoshida et al. 2014), and *Pagurus spina* is newly recorded as a peltogastrid host in the present study.

In the present, the DNA sequence of the specimen on *P. middendorffii* could not be obtained; however, the morphological characteristics of the specimens were similar to those of *Peltogasterella gracilis*. Thus, we identified the specimen as *P. gracilis*.

Peltogasterella* aff. *gracilis

(Fig. 5K)

Material examined: on *Porcellanopagurus nihonkaiensis*: 2 Inds., Jeju, 33°25'17.44"N 126° 9'38.96"E, Scuba, 24 Sep. 2011, Coll. Lee SK., MADBK 160730_002, host: males, sl 2.1, 2.3 mm.

Host: *P. nihonkaiensis* (Paguridae).

Distribution: Korea.

Remarks: This is the first report of peltogastrid species on *Porcellanopagurus* species host. The elongated and gregarious externae and absence of a chitinous shield on the present specimens reflect the characteristics of *Peltogasterella gracilis*. However, a mantle was not found and sequencing data could not be obtained from the present materials. Therefore, we tentatively identified these specimens as *P.* aff. *gracilis*. Additional data are necessary to confirm this identification.

One of the specimens attached on the *Porcellanopagurus nihonkaiensis* had only a single externa, which is not a characteristic of *Peltogasterella gracilis* morphology. However, Høeg and

Lützen (1985) has shown that the majority of *Peltogasterella sulcata* specimens have gregarious externae, whereas some specimens have a single externa. Accordingly, the single externa of this specimen may be regarded as an individual variation.

Molecular Analysis

A total of 17 *COI* sequences (658-660 bp) and 15 sequences of 16S rRNA (372-432 bp) were obtained from the examined samples (Table 2). The composition of these sequences was 22.21% of A, 42.59% of T, 20.96% of G, and 14.24% of C in *COI*; and 35.18% of A, 35.90% of T, 10.24% of G, and 18.69% of C in 16S rRNA. The *COI* and 16S rRNA alignment was 657 bp and 326 bp long, and had 303 and 142 variable sites (46.12%, 43.56%) and 266 and 120 parsimony informative sites (40.49% and 36.81%), respectively.

In the *COI* and 16S rRNA phylogenetic trees (Figs. 3, 4), the sequences of Korean peltogastrids are located near the sequences of the same species from NCBI, and they form a single clade. As mentioned above, the *Peltogaster* sp. 4 sequence formed a single clade, separate from those of other species.

The *COI* and 16S rRNA sequences of Korean peltogastrid species exhibited larger genetic gaps than the minimum interspecific variation of *COI* between *Dipterosaccus indicus* and *D. shiinoi* (7.80%, Fig. 3) or those of 16S rRNA between *Briarosaccus auratum* and *B. regalis* (2.71%, Fig. 4). Intraspecific variation in Korean peltogastrid species were very low (Tables 4, 5).

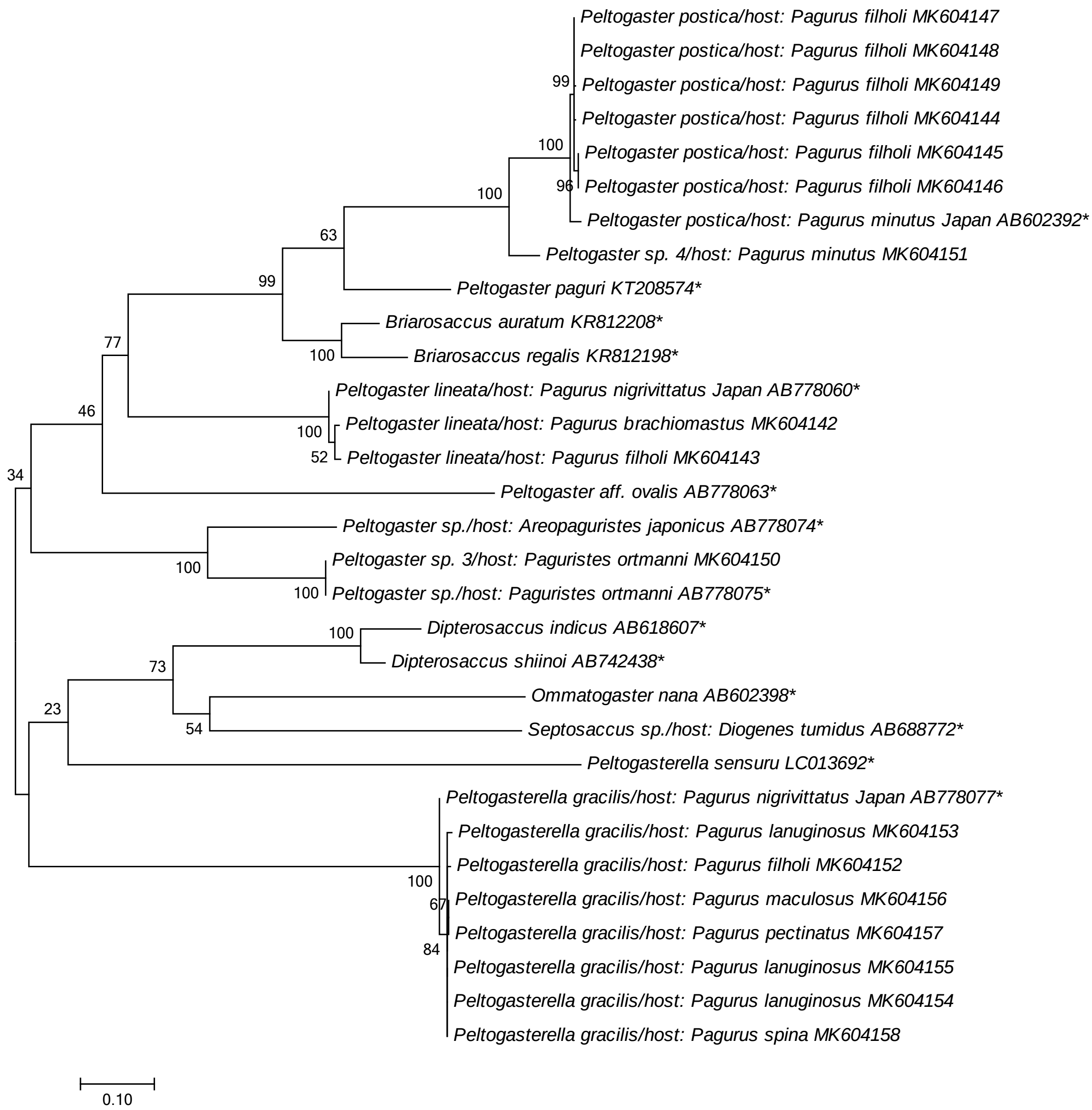

Fig. 3. Maximum likelihood rooted trees of *COI* sequences of Peltogastridae from Korea and NCBI. The number next to the branches is the percentage of replicate trees in which the associated taxa clustered together in the bootstrap test. *means NCBI sequence.

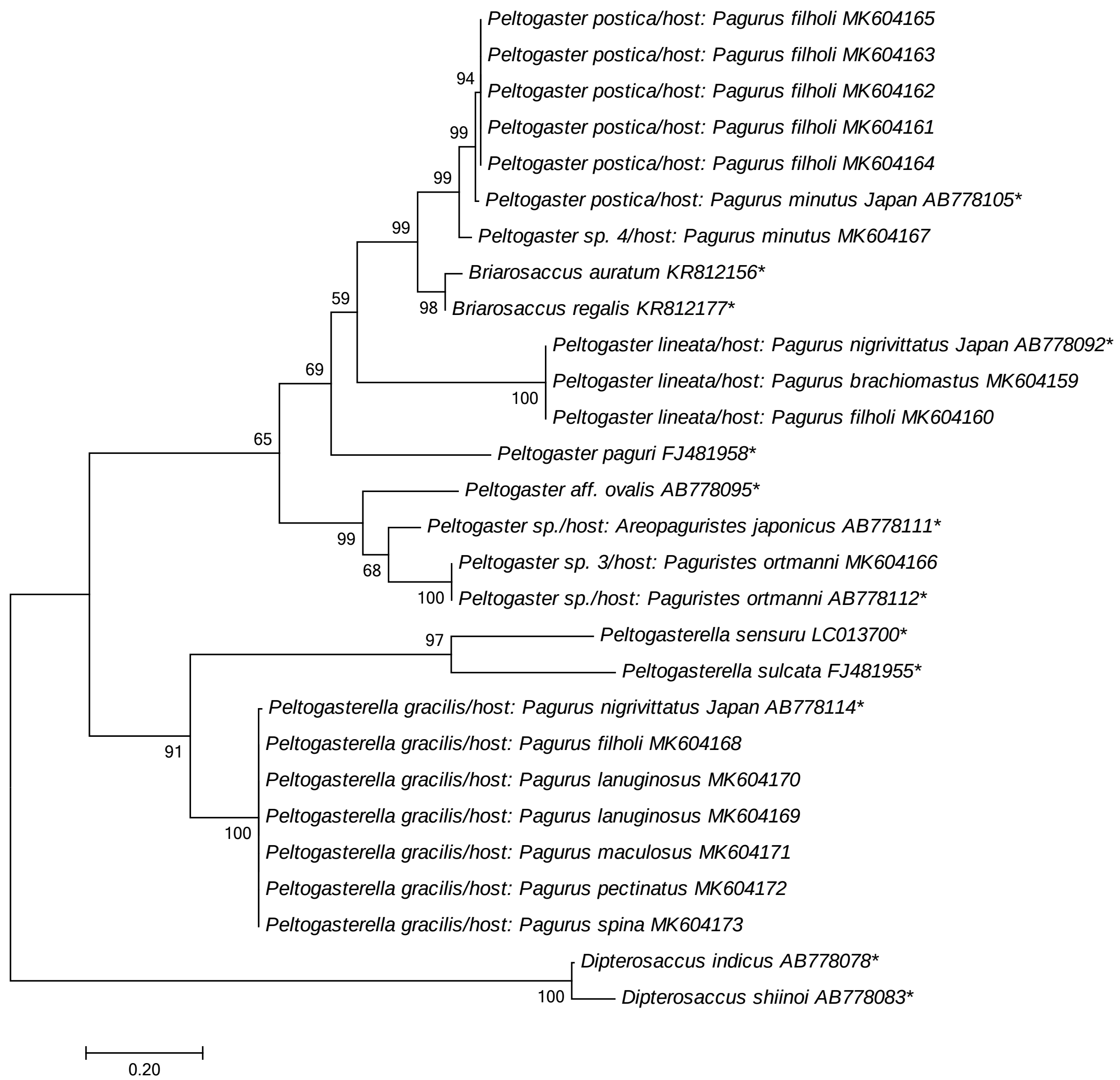

Fig. 4. Maximum likelihood rooted trees of 16S rRNA sequences of Peltogastridae from Korea and NCBI. The number next to the branches is the percentage of replicate trees in which the associated taxa clustered together in the bootstrap test. *means NCBI sequence.

Table 4. *COI* sequence pairwise distances for species of Korean peltogastrids using pairwise distance (%) (the bracket in the value cell represents the mean value of each distance)

Groups	Distances (%)				
	Within species	Between species			
		1	2	3	4
1. *Peltogaster lineata*	1.34-1.53 (1.40)				
2. *Peltogaster postica*	0-2.29 (0.91)	26.15-27.29 (26.62)			
3. *Peltogaster* sp. 3	0	27.29-27.67 (27.48)	29.20-29.39 (29.31)		
4. *Peltogaster* sp. 4	0	26.15-26.53 (26.27)	9.92-10.50 (10.17)	29.39	
5. *Peltogasterella gracilis*	0-1.53 (0.56)	29.01-29.96 (29.47)	32.25-33.21 (32.73)	27.29-28.05 (27.84)	30.92-31.49 (31.15)

Table 5. 16S rRNA sequences pairwise distances for species of Korean peltogastrids using pairwise distance (%) (the bracket in the value cell represents the mean value of each distance)

Groups	Within species	Distances (%)			
		Between species			
		1	2	3	4
1. *Peltogaster lineata*	0				
2. *Peltogaster postica*	0-1.36 (0.45)	22.62-23.08 (23.00)			
3. *Peltogaster* sp. 3	0	28.05	26.24-27.15 (27.00)		
4. *Peltogaster* sp. 4	0	22.17	4.52-4.98 (4.90)	27.15	
5. *Peltogasterella gracilis*	0-0.45 (0.13)	30.77-31.22 (30.83)	29.41-30.32 (29.85)	30.32-30.77 (30.38)	28.96-29.41 (29.02)

DISCUSSION

The results of this study show that Korean peltogastrids have slightly different host prevalence from peltogastrids in other regions. A total of 10 species of Korean peltogastrids were found on 17 paguroid species (Table 2). Among the Korean paguroid hosts, six species (*i.e.*, *Areopaguristes nigroapiculus*, *Pagurus rubrior*, *P. parvispina*, *P. rathbuni P. spina*, and *Porcellanopagurus nihonkaiensis*) are reported to be hosts of peltogastrids. Among the paguroids in Korea without peltogastrids, *Pagurus constans* and *P. trigonocheirus* have been reported to be hosts of peltogastrids in other regions (McDermott et al. 2010). In addition, the host prevalence of the three peltogastrid species in Korea that also living in other East Asian regions (Fig. 6), *Peltogaster lineata*, *P. postica*, and *Peltogasterella gracilis*, also differ from that of other Asian countries. For example, Korean *P. postica* parasite only on *Pagurus filholi* whereas Taiwanese one parasite only on *Pagurus angustus*, and Japanese one parasite mostly on *Pagurus minutus* but also parasite on *Pagurus filholi* and *P. nigrivittatus*. These difference of host prevalence by countries also found in other two peltogastrid species, *Peltogaster lineata* and *Peltogasterella gracilis* (Fig. 7). These differences in host prevalence between peltogastrids from Korea and other regions are considered to be due to geographical variation (Yoshida et al. 2014).

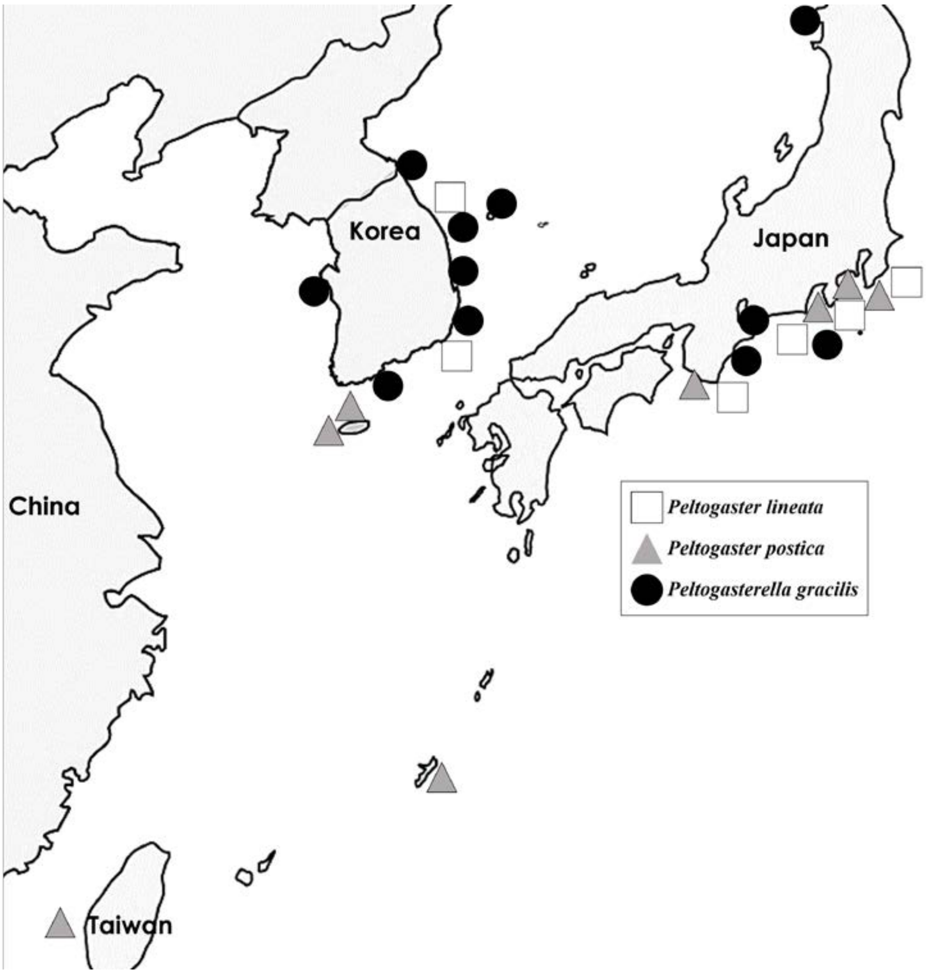

Fig. 6. Distribution map of three peltogastrids in East Asia. The distribution of other countries except Korea was derived from Nagasawa et al. (1996) and Yoshida et al. (2011 2012 2014).

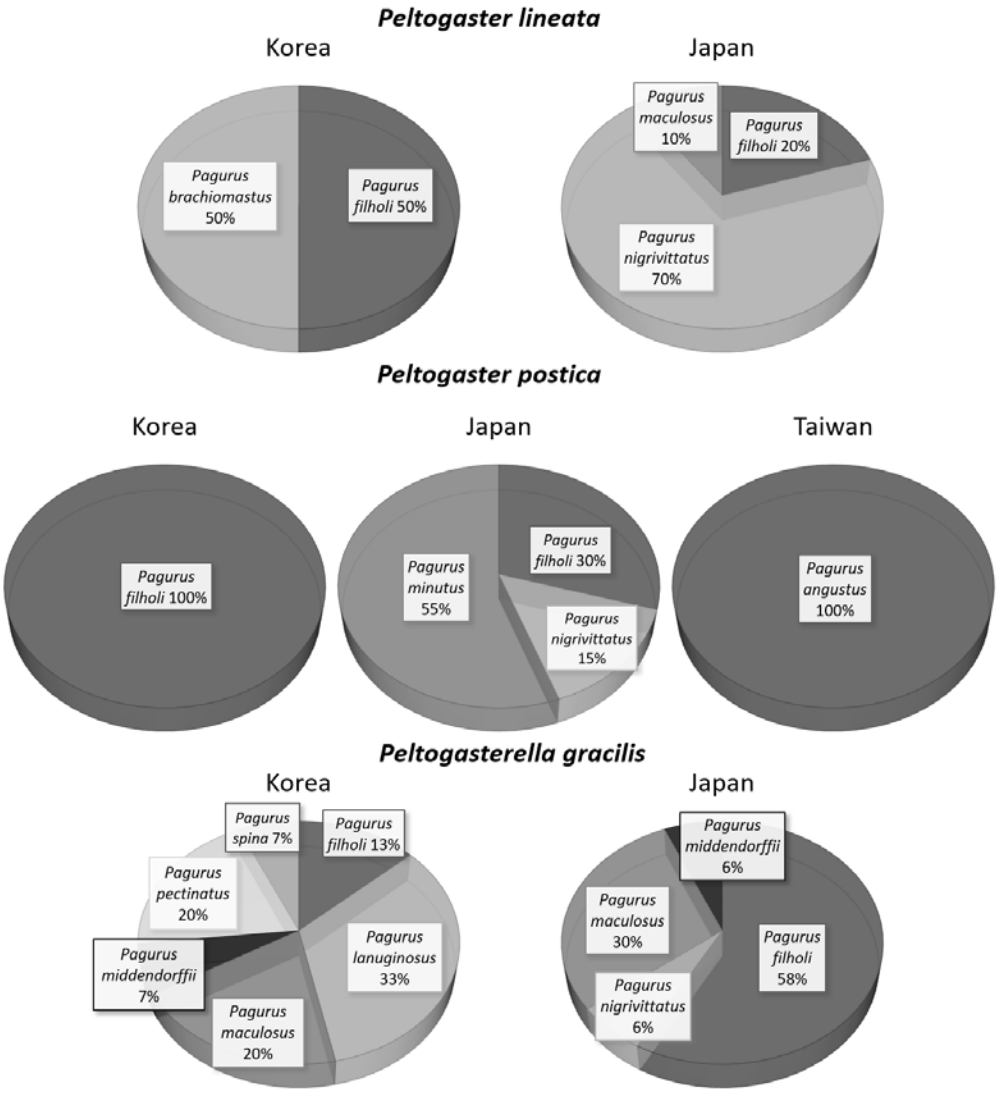

Fig. 7. Pie chart of the prevalence of hermit crab species for each peltogastrids in Korea, Japan, and Taiwan. The pie chart of Japan was derived from Nagasawa et al. (1996) and Yoshida et al. (2011 2014). The pie chart of Taiwan was derived from Yoshida et al. (2012).

That Korean peltogastrid hosts change depending on geographical location in Korea is another example of how geographical variation contributes to the prevalence of peltogastrid hosts. *Peltogasterella gracilis* parasitizes multiple hosts (McDermott et al. 2010; Yoshida et al. 2014); however, its main host slightly varies at different locations, although other host candidates are still present (Table 2). In addition, *Pagurus filholi* is parasitized by different peltogastrids depending on location (Table 2), a difference reflected in the study by Yoshida et al. (2014).

The intraspecific variation in the East Asian peltogastrids in this study is weakly supported by the biogeographical variation in the sequence data. The intraspecific variations in Korean and Japanese peltogastrids are very low, even when the host hermit crab is different (Figs. 3, 4) (Yoshida et al. 2014). However, after combining the Korean and Japanese sequences of *Peltogaster* *postica*, the variation between the groups showed a slightly higher genetic gap compared with those of each population. This phenomenon was also found in *Peltogasterella gracilis* (Figs. 3, 4). This result suggests that habitat location might somewhat affect divergence in these peltogastrid sequences.

The sites at which Korean peltogastrids were collected show that the peltogastrids exhibit some habitat preferences. A total of 15 and 21 Korean peltogastrid specimens were collected from the eastern and southern coasts of Korea, respectively (Fig. 1). However, only two individuals were collected from the western coast of Korea, in spite of the high abundance of hosts (Jung et al. 2018b). The lack of peltogastrids on the western coast of Korea might be related to the development rate of larvae in the environment. Kashenko and Korn (2003) demonstrated that low temperature and low salinity negatively affect the development of larvae of the peltogastrid *Peltogaster reticulata*. The water on the western coast of Korea is cold in the winter due to its shallow depth and has low salinity due to a great inflow of fresh water (Park et al. 2017). These factors could decrease the development rate of larvae and the abundance of peltogastrids on the western coast of Korea.

Korean peltogastrids infest their host hermit crabs at a lower rate than those from Japan. In Japan, Yoshida et al. (2014) found 87 individual peltogastrids (6 species) on 2,282 individual hermit crabs (23 species), an infestation rate of 3.8%. However, the infestation rate by Korean peltogastrids is lower, at 0.9% (Table 1). According to Kashenko and Korn (2003), Korean peltogastrids may have a lower infestation rate because the water temperature in Korea is lower than in Japan. The high infestation rates (> 7%) for *Pagurus parvispina*, *P. rathbuni*, and *Porcellanopagurus nihonkaiensis* might be biased by the small sample size.

CONCLUSIONS

In this study, we demonstrated the presence of peltogastrid parasitic barnacles in Korea using morphological and molecular analysis and found six new species of hermit crabs that are peltogastrid hosts. In addition, we noted that the host prevalence of Korean peltogastrids differs slightly from what has been previously reported. Furthermore, this study slightly expanded the distribution range of some peltogastrids species.

This is the first systematic study on peltogastrid species in Korea, and it emphasizes the need for further studies on Korean peltogastrids to identify their morphological, molecular, ecological, and biogeographical characteristics.

List of abbreviations

Sl, shield length.
COI, cytochrome *c* oxidase subunit I.
EVOSYS, Laboratory of Systematics and Molecular Evolution.
MADBK, Marine Arthropod Depository Bank of Korea.

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Authors' contributions: Jibom Jung and Ryuta Yoshida contributed equally to this work. Ryuta Yoshida conceived of the study. Jibom Jung and Ryuta Yoshida designed the study. Jibom Jung and Won Kim performed the field work and analyzed the specimens. Jibom Jung, Ryuta Yoshida, and Won Kim contributed to the acquisition of the sequence data. Jibom Jung and Ryuta Yoshida contributed to the analysis and interpretation of the sequence data. Jibom Jung and Won Kim drafted the manuscript. Ryuta Yoshida participated in critical revisions to the manuscript.

Competing interests: The authors declare that they have no conflict of interest.

Availability of data and materials: All sequence data in this study are available in GenBank. All examined and sampled specimens are available from the Laboratory of Systematic and Molecular Evolution (EVOSYS), Marine Arthropods Deposited Bank of Korea (MADBK) of Seoul National University, and Ewha Womans University Natural History Museum, Seoul, Republic of Korea.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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