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The Fauna of Parasitic Barnacles (Cirripedia: Rhizocephala) in Korea

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Rhizocephala is a group of endoparasitic barnacles whose morphological characteristics were degenerated, and molecular identification has been actively conducted recently. Despite several recent studies of Korean rhizocephalans, a comprehensive analysis of Rhzicephalan fauna has not yet been investigated. In this study, we conducted morphological and molecular analyses of 64 rhizocephalan samples from 15 decapod hosts sampled across the Korean coast. We found 16 Rhizocephala species of six genera from four Rhizocephala families, *i.e.*, Peltogasterellidae, Peltogastridae, Polyascidae, and Sacculinidae. Combining morphological examination and molecular analysis of mitochondrial cytochrome c oxidase I revealed three new species candidates, i.e., *Peltogasterella* sp., *Peltogaster* sp., and *Parasacculina* sp. 1, and three rhizocephalans, i.e., *Parasacculina oblonga*, *Sacculina angulate*, and *Sacculina gracillis*, whose expanded their distribution range to Korean coast. A synthetic update of Korean Rhizocephala fauna including species checklist, distribution, and taxonomic remarks is also presented.

Key words: Rhizocephala, Cirripedia, Parasitic barnacles, Decapod hosts, Distribution pattern, Korean coast

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BACKGROUND

Rhizocephala is a group of parasitic barnacles that infect both the internal (endoparasitic) and external body (ectoparasitic) of crustacean hosts, mainly decapods. The organism has complicated life cycles, beginning with a planktonic larval stage, followed by an internal parasitic stage, and concluding with an external reproductive stage (Høeg 1992). In contrast to other crustacean species, they possess invisible and branch-shaped internal parasitic organ (interna) and visible and simplified external reproductive organ (externa) during the parasitic stage, lacking both segmentation and appendages (Høeg and Lützen 1995). Other organ systems such as respiratory, digestive, sensory, and excretory systems are degenerate in adult rhizocephalans (Høeg 1992; Øksnebjerg 2000). As a result of this simplified external morphology of the adult, the previous taxonomy system of rhizocephalans relied on the examination of morphological characteristics of larva and histological characteristics of adult externa (Yoshida et al. 2011; Kobayashi et al. 2018), and this system was further verified and partially modified through DNA barcode and molecular phylogenetic analysis (Yoshida et al. 2012 2014; Høeg et al. 2019; Chan et al. 2021).

Since the first report of parasitic barnacles *Parasacculina pinnotherae* in Korea (Shiino 1943), several systematic previous studies have been conducted on Korean parasitic barnacles (Lützen et al. 2016; Jung et al. 2019 2021). However, the rhizocephalan fauna in Korea has not yet been fully identified as only a limited number of hosts have been investigated (Jung et al. 2019 2021). For example, *Parasacculina oblonga* (Lützen and Yamaguchi 1999) was first reported from the host crab *Cyclograpsus intermedius* in Japan, but parasitism of *P. oblonga* was not reported in Korean *C. intermedius.* Therefore, we additionally collected Korean rhizocephalans and identified them based on morphological examination and molecular analyses of mitochondrial cytochrome c oxidase subunit I (*cox*I). In addition, we made a checklist and noted remarks of each rhizocephalan on Korean parasitic barnacles to help future research on Rhizocephala.

MATERIALS AND METHODS

We examined 64 Korean Rhizocephalans from 15 host decapods collected from 21 sampling sites in Korea (Table 1). Voucher specimens in this study were deposited in the National Institute of Biological Resources (NIBR) and the Honam National Institute of Biological Resources (HNIBR). All rhizocephalan specimens were fixed in 70–95% ethanol and subjected to morphological examination

and molecular analysis. For morphological analysis, the externa and mantle aperture were examined using an MZ8 dissection microscope (Leica, Wetzlar, Germany). Photographs were taken with a D200 digital camera (Nikon, Tokyo, Japan). The shield length (hermit crab) and carapace length (crab) of the host decapod were measured as the length from the tip of the rostrum to the midpoint of the posterior margin of the carapace using a CD6CSX digital caliper (Mitutoyo, Kawasaki, Japan) to the nearest 1 mm.

For molecular analysis, the lateral end of the externa tissue of each rhizocephalan specimen was excised for total genomic DNA extraction using the QIAamp DNA Micro Kit (QIAGEN, Hilden, Germany). Universal primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') were used to amplify a fragment of *cox1* (Folmer et al. 1994). Polymerase chain reaction (PCR) was performed in reaction volumes of 50 µL that included 2 µL DNA template, 5 µL 10 x Ex Taq Buffer, 2 µL of each primer (10 µM), 0.25 µL Go Taq DNA polymerase (Promega, Madison City, WI, USA), 2.5 µL dNTP mix (10 mM), and 35.75 µL distilled H_2O. PCR amplification was performed using the following steps: 5 min denaturation at 94ºC followed by 35 cycles of 30 sec at 94ºC, 1 min at 52ºC, 1 min at 72ºC, and a final extension of 7 min at 72ºC. PCR products were visualized on 1% agarose gels and sequenced with an ABI PRISM 3730xl DNA analyzer (Applied Biosystems, Foster City, CA, USA). Nucleotide sequences of mtDNA *cox1* fragments were analyzed and edited using Geneious v. 9.1.8 (Kearse et al. 2012). *cox1* sequences in this study were deposited in GenBank (Table 1). Molecular identification of each sample was conducted through BLAST results of the sequences.

To determine the fauna of Korean rhizocephalans, the results of morphological and molecular identification on the 64 individuals were combined with taxonomy information from previous studies of Korean Rhizocephala.

RESULTS

Based on the morphological examination of externae (shape and the number of externae and mantle aperture) and *cox1* sequence information, we identified 16 rhizocephalan species belonging to six genera, and four families *i.e.*, Peltogasterellidae, Peltogastridae, Polyascidae, and Sacculinidae, from 64 samples and 46 *cox1* sequences (Table 1). Three rhizocephalans identified by this study *i.e.*, *Parasacculina oblonga*, *Sacculina angulate*, and *Sacculina gracillis* were expanded their distribution

range and first reported from Korea by this study. In addition, we found three new species candidates, *i.e.*, *Peltogasterella* sp., *Peltogaster* sp., and *Parasacculina* sp. 1. As a result of including rhizocephalans reported in previous studies (Shiino 1943; Kim and Hong 2002; Lützen et al. 2016; Jung et al. 2019 2021), the presence of 22 rhizocephalans in Korea was identified. The distribution of Rhizocephala in South Korea is shown in figure 1, and a checklist was prepared for 16 species with confirmed species names and molecular data. Brief information on the externa morphology of 22 Korean rhizocephalans is presented in table 2. A brief remark is provided on the Korean Rhizocephala which noteworthy biological characteristics were discovered compared to previous studies. The information such as diagnosis and distribution similar to previous studies were omitted.

Table 1. Geographical locations and sample information of Korean rhizocephalans in this study in order of species name, host species, location and specimen number

Species	Host Species	Location (Korea)	Specimen Number	*coxI* Accession Number
Heterosaccus papillosus	*Charybdis* (*Charybdis*) *japonica*	Incheon	NIBRIV0000895329	OR481955
			NIBRIV0000895330	
Parasacculina imberbis	*Pachygrapsus crassipes*	Jeju	Koreakr10	OR481956
		Seogwipo	Koreax8	OR481963
		Tongyeong	Korearr54	OR481962
Parasacculina oblonga	*Cyclograpsus intermedius*	Ulleung	DSEVIV0000000050	OR481965
			DSEVIV0000000051	OR481966
			DSEVIV0000000054	OR481967
			DSEVIV0000000055	OR481968
			DSEVIV0000000056	OR481969
Parasacculina pinnotherae	*Arcotheres sinensis*	Jindo	KoreaJD1	
Parasacculina pilosella	*Pugettia intermedia*	Goseong	GS 2381	
		Sokcho	Korearr1	
Parasacculina yatsui	*Cyclograpsus intermedius*	Ulleung	Korearr40	
	Hemigrapsus penicillatus	Gangneung	Korearr10	
		Goseong	GS12	
	Hemigrapsus sanguineus	Goheung	KoreaN14	OR481973
		Goseong	Korea71	OR481975
		Tongyeong	Korea39	OR481974
	Pachygrapsus crassipes	Gangneung	Korearr9	OR481977
		Jeju	Koreakr9	OR481976
		Samcheok	Korearr25	OR481978
		Yeongdeok	Korea72	
Parasacculina shiinoi	*Upogebia major*	Namhae	Korea56	
Parasacculina sp. 1	*Hemigrapsus sanguineus*	Goheung	Korea6N	OR481970
			Korea13N	OR481971
			Korea16N	OR481972
Peltogasterella gracilis	*Pagurus maculosus*	Shinan	Korea61	OR481992
Peltogasterella sp.	*Porcellanopagurus nihonkaiensis*	Jeju	MADBK 160730_002	
		Seogwipo	KoreaPN1	OR481994
Peltogaster reticulata	*Pagurus minutus*	Namhae	MADBK 160706_065	MK604151*
			MADBK 160706_125	
	Pagurus proximus	Shinan	MADBK 160718_040	
Peltogaster sp. 1	*Pagurus lanuginosus*	Gangneung	DSEVIV0000000053	OR481985
	Pagurus maculosus	Seogwipo	DSEVIV0000000057	OR481986
		Shinan	DSEVIV0000000052	OR481987

			KoreaHS1	OR481988
			KoreaHS2	OR481989
			KoreaHS3	OR481990
			KoreaHS4	OR481991
Polyascus cf. *gregarius*	*Hemigrapsus sanguineus*	Busan	Korearr60	OR482023
		Goheung	Korea1N	OR481995
		Jindo	Koreakr1	OR482016
		Shinan	Korearr58	OR482022
		Tongyeong	Korearr56	OR482021
		Wando	Korea47	OR482011
		Yeosu	Korea45	OR482010
Sacculina angulata	*Thalamita sima*	Busan	NIBRIV0000895328	OR482032
		Sacheon	NIBRIV0000895331	
Sacculina confragosa	*Gaetice depressus*	Goheung	Korea52	OR482037
	Hemigrapsus sanguineus	Gangneung	Korearr22	OR482050
		Goheung	Korea7N	OR482033
		Jindo	Koreakr2	OR482038
		Pohang	Korearr59	OR482062
	Pachygrapsus crassipes	Gangneung	Korearr8	OR482049
		Jeju	Korea74	
		Samcheok	Korearr53	OR482061
		Seogwipo	Koreakr11	OR482041
		Sokcho	Korea73	
		Uljin	Korearr28	OR482053
Sacculina gracilis	*Thalamita sima*	Seogwipo	NIBRIV0000895332	OR482063
		Tongyeong	NIBRIV0000895334	OR482064
Sacculina upogebiae	*Upogebia major*	Boryeong	NIBRIV0000453552	
		Incheon	NIBRIV0000453567	

*: NCBI sequence.

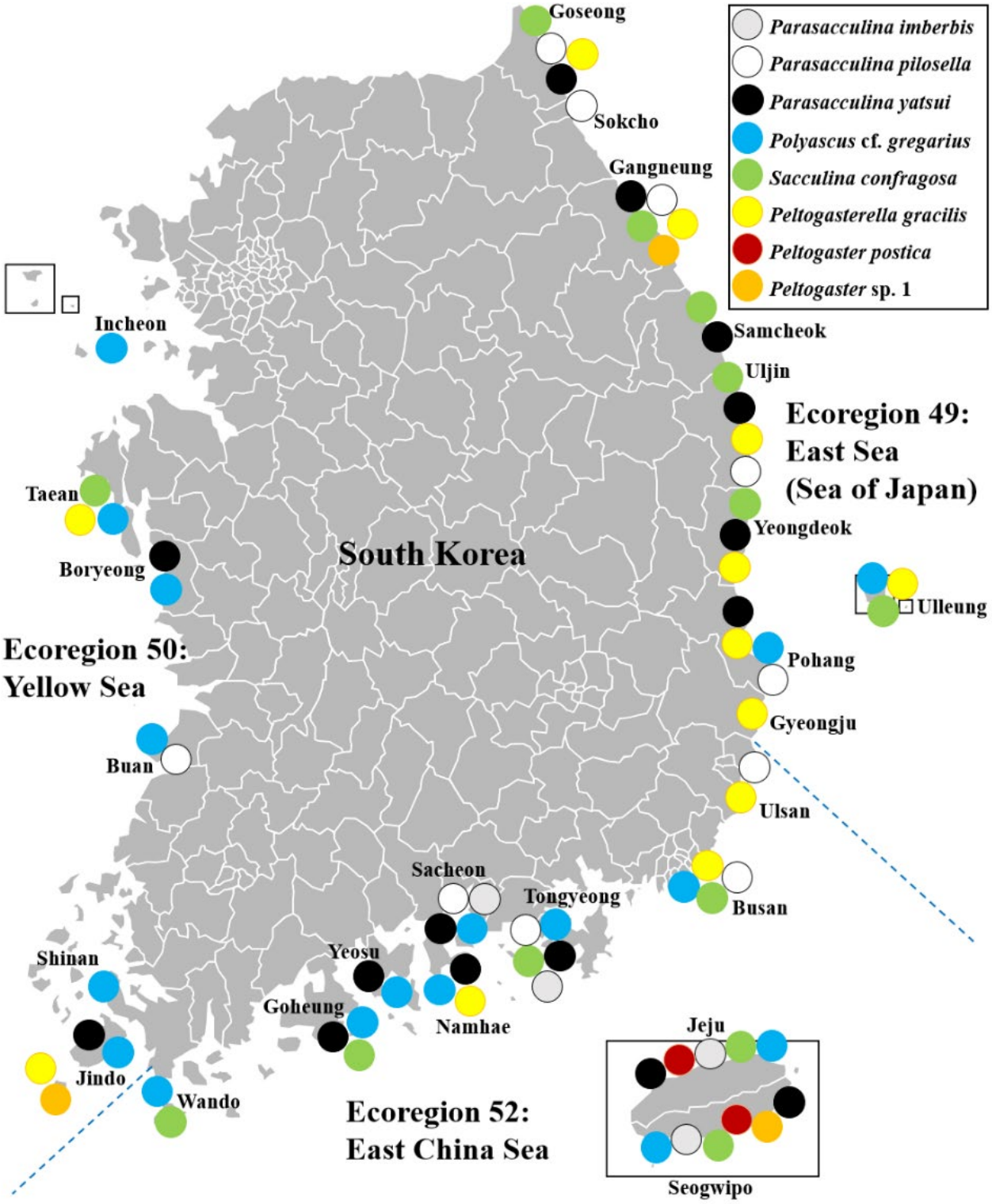

Fig. 1. Distributions map of the eight most common Korean rhizocephalans. Blue dotted line: dividing line between Ecoregions mentioned in Muhammad et al. (2022) and Kim et al. (2020 2022).

Table 1. Morphological characteristics of externae of 22 Korean Rhizocephala

Species	Externa number	Externa shape	Mantle aperture			Chitinous shield	host family
			Projection	Opening	Position		
Peltogasterella gracilis	Gregarious	Elongate banana-shaped	Elevated	Circular	Terminal	No	Paguridae
Peltogasterella sp.	1-3	Elongate	Vestigial	Circular	Terminal	No	Paguridae
Peltogaster lineata	1	Elongate oval	Slightly elevated or elevated tube	Circular	Terminal or subterminal	Yes	Paguridae
Peltogaster postica	1-2	Irregularly elongate	Elevated tube	U-shaped	Terminal	Yes	Paguridae
Peltogaster reticulata	1	Banana-shaped	Elevated tube	X-shaped	Terminal	Yes	Paguridae
Peltogaster sp. 1	1	Irregularly elongate	Slightly elevated	Circular	Terminal or subterminal	Yes	Paguridae
Peltogaster sp. 2	1	Irregularly elongate			Terminal or subterminal	Yes	Diogenidae
Parasacculina imberbis	1	Smooth round-rectangular or bilobed	Slightly elevated	X-shaped	Terminal	No	Grapsidae
Parasacculina pilosella	1	Smooth and slightly flat oval	Vestigial	Circular	Terminal	No	Epialtidae
Parasacculina pinnotherae	1-2	Smooth or slightly wrinkled flat oval or cordiform	Elevated	Dot shaped	Terminal	No	Pinnotheridae
Parasacculina shiinoi	1	Smooth oval	Vestigial	Circular	Terminal	No	Upogebiidae
Parasacculina yatsui	1	Slightly wrinkled flat oval or flat cordiform	Elevated	Slit shaped	Terminal	No	Grapsidae, Varunidae
Parasacculina oblonga	1	Smooth or slightly wrinkled oval	Elevated	Y-shaped	Terminal	No	Varunidae
Parasacculina sp. 1	1	Smooth or slightly wrinkled flat cordiform	Slightly elevated	Circular	Terminal	No	Varunidae
Parasacculina sp. 2	1	Smooth or slightly wrinkled oval	Elevated	Circular	Terminal	No	Xanthidae
Parasacculina sp. 3	1	Smooth oval	Slightly elevated	Circular	Terminal	No	Xanthidae
Polyascus cf. *gregarius*	1-3	Smooth or slightly wrinkled flat cordiform	Elevated	Slit shaped	Terminal	No	Varunidae
Heterosaccus papillosus	1	Smooth or slightly wrinkled reversed cordiform	Slightly elevated or elevated	Large circular	Terminal	No	Portunidae
Sacculina upogebiae	1	Oval with a very shallow groove along the dorsal margin	Vestigial	Circular	Terminal	No	Upogebiidae
Sacculina confragosa	1-2	Wrinkled flat cordiform	Elevated tube	Circular	Terminal	No	Grapsidae, Varunidae
Sacculina angulata	1-3	Slightly wrinkled irregular pentagon	Elevated tube	Large circular	Terminal	No	Portunidae

Sacculina gracilis	1	Smooth round fusiform	Slightly elevated	Y-shaped	Terminal	No	Portunidae

Checklist of Korean Rhizocephala

Phylum Arthropoda von Siebold, 1848

Class Thecostraca Gruvel, 1905

Subclass Cirripedia Burmeister, 1834

Infraclass Rhizocephala Müller, 1862

Family Peltogasterellidae Høeg & Glenner in Høeg, Noever, Rees, Crandall & Glenner, 2019

Genus *Peltogasterella* Krüger, 1912

1. *Peltogasterella gracilis* (Boschma, 1927)

Family Peltogastridae Lilljeborg, 1861

Genus *Peltogaster* Rathke, 1842

2. *Peltogaster lineata* Shiino, 1943
3. *Peltogaster postica* Yoshida & Osawa in Yoshida, Osawa, Hirose & Hirose, 2011
4. *Peltogaster reticulata* Shiino, 1943

Family Polyascidae Høeg & Glenner in Høeg, Noever, Rees, Crandall & Glenner, 2019

Genus *Parasacculina* Høeg & Glenner in Høeg, Noever, Rees, Crandall & Glenner, 2019

5. *Parasacculina imberbis* (Shiino, 1943)
6. *Parasacculina pilosella* (Van Kampen & Boschma, 1925)
7. *Parasacculina pinnotherae* (Shiino, 1943)
8. *Parasacculina shiinoi* (Lützen, Itani, Jespersen, Hong, Rees & Glenner, 2016)
9. *Parasacculina yatsui* (Boschma, 1936)
10. *Parasacculina oblonga* (Lützen & Yamaguchi, 1999)

Genus *Polyascus* Glenner, Lützen & Takahashi, 2003

11. *Polyascus* cf. *gregarius* (Okada & Miyashita, 1935)

Family Sacculinidae Lilljeborg, 1861

Genus *Heterosaccus* Smith, 1906

12. *Heterosaccus papillosus* (Boschma, 1933)

Genus *Sacculina* Thompson, 1836

13. *Sacculina upogebiae* Shiino, 1943
14. *Sacculina confragosa* Boschma, 1933

15. *Sacculina angulata* Van Kampen & Boschma, 1925
16. *Sacculina gracilis* Boschma, 1931

Peltogasterellidae Høeg & Glenner in Høeg, Noever, Rees, Crandall & Glenner, 2019

***Peltogasterella* Krüger, 1912**

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

(Fig. 2A, see Jung et al. 2019)

Additional material examined: On *Pagurus maculosus*: 1 individual, Sinan, 34°40'55.1"N, 125°26'38.1"E, 26 Aug. 2021, collected by Jung J., Korea61, host: males, shield length 8 mm.

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

***Peltogasterella* sp.**

(Fig. 2B)

Material examined: on *Porcellanopagurus nihonkaiensis*: 2 individuals (single individual with 2 externae), Jeju, 33°25'17.44"N, 126° 9'38.96"E, Scuba, 24 Sep. 2011, collected by Lee SK., MADBK 160730_002, host: males, shield length 2 mm; 1 individual (3 externae), Seogwipo, 33°13'30.2"N, 126°34'11.9"E, Scuba 60m, 11 Nov. 2020, collected by Lee SH., KoreaPN1, host: shield length 1 mm.

Host species: *P. nihonkaiensis* (Anomura).

Distribution: Korea.

Diagnosis: Whole externa single to triple, smooth, and elongated oval in shape. Mantle aperture not well developed, and vertically small circular opening at the extremity.

Peltogastridae Lilljeborg, 1861

***Peltogaster* Rathke, 1842**

***Peltogaster lineata* Shiino, 1943**

(see Jung et al. 2019)

Host species: *Pagurus brachiomastus, Pagurus filholi, Pagurus nigrivittatus, Pagurus maculosus* (Anomura; Paguridae).

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

(see Jung et al. 2019)

Host species: *Pagurus filholi*, *P. minutus*, *P. nigrivittatus*, *Pagurus angustus* (Anomura; Paguridae).

Peltogaster reticulata **Shiino, 1943**

(see *P.* aff. *reticulata* and *Peltogaster* sp. 4 of Jung et al. 2019)

Material reexamined on *P. minutus*: 1 individual, Namhae, 34°52'40.83"N, 127°56'43.61"E, 14 Nov. 2012, collected by Jung J, MADBK 160706_065, host: female, shield length 4 mm; 1 individual (2 externae)., Namhae, 34°52'40.83"N, 127°56'43.61"E, 12 May 2018, collected by Jung J, MADBK 160706_125, host: female, shield length 3 mm.

On *P. proximus*: 1 individual, Shinan, 34°35'49.24"N 125°45'58.02"E, 16 Oct. 2008, collected by Hong J, MADBK 160718_040, host: female, shield length 3 mm.

Host species*: Pagurus constans*, *P. minutus*, *Pagurus proximus* (Anomura; Paguridae).

Distribution: Japan (type locality), Russia, Korea.

Peltogaster **sp. 1**

(Fig. 2C)

Material examined: on *P. lanuginosus*: 1 individual, Gangneung, 37°44'04.3"N 128°59'25.8"E, 23 Oct. 2021, collected by Jung J., DSEVIV0000000053. On *P. maculosus*: 1 individual, Sinan, 34°40'55.1"N 125°26'38.1"E, 26 Aug. 2021, collected by Jung J., DSEVIV0000000052, KoreaHS1-KoreaHS4, host: females, shield length 8 mm; Seogwipo, 33°14'05.1"N; 126°21'30.1"E, 6 Sep. 2021, DSEVIV0000000057, host: shield length 9 mm.

Host species: *P. lanuginosus*, *P. maculosus* (Anomura; Paguridae).

Distribution: Korea.

Diagnosis: Whole externa single, smooth, and irregular oval in shape. Mantle aperture slightly elevated or elevated tube, and vertically circular opening at the extremity.

***Peltogaster* sp. 2**

(see *Peltogaster* sp. 3 at Jung et al. 2019)

Host species: *Paguristes ortmanni* (Anomura; Diogenidae).

Polyascidae Høeg & Glenner in Høeg, Noever, Rees, Crandall & Glenner, 2019

***Parasacculina* Høeg & Glenner in Høeg, Noever, Rees, Crandall & Glenner, 2019**

***Parasacculina imberbis* (Shiino, 1943)**

(Fig. 2D, see Jung et al. 2021)

Additional materials examined: on *Pachygrapsus crassipes*: 1 individual, Seogwipo, 33°14'09.6"N, 126°21'35.4"E, 6 Sep. 2021, collected by Jung J., Koreax8, host: ♀, caraface length 14 mm; 1 individual, Tongyeong, 34°45'31.3"N, 128°30'59.4"E, 29 Oct. 2021, collected by Jung J., Korearr54; 1 individual, Jeju, 33°30'57.3"N, 126°30'38.5"E, 23 Aug. 2022, collected by Jung J., Koreakr10.

Host species: *P. crassipes* (Brachyura; Grapsidae).

Diagnosis: Whole externa single, smooth or slightly wrinkled, and slightly bilobed with half-oval-shaped left and right lobes divided by a mid-notch. Mantle aperture slightly elevated as short tube shape and vertically circular opening at the extremity.

Color: yellow.

***Parasacculina pilosella* (Van Kampen & Boschma, 1925)**

(Fig. 2E, see Jung et al. 2021)

Additional materials examined: on *Pugettia intermedia*: 1 individual, Sokcho, 38°13'38.1"N 128°35'16.1"E, 8 Sep. 2020, Korearr1; 1 individual, Goseong, 38°27'01.3"N, 128°28'03.9"E, 25 Sep. 2021, GS 2381.

Host species: *P. intermedia*, *Pugettia* aff. *ferox* (Brachyura; Epialtidae).

***Parasacculina pinnotherae* (Shiino, 1943)**

(see Jung et al. 2021)

Additional materials examined: on *Arcotheres sinensis*: 3 individuals, Jindo, 34°23'16.9"N 126°17'20.8"E, 23 July 1994, KoreaJD1.

Host species: A. sinensis (Brachyura; Pinnotheridae).

***Parasacculina shiinoi* (Lützen, Itani, Jespersen, Hong, Rees & Glenner, 2016)**

(see Jung et al. 2021)

Additional materials examined: on *Upogebia major*: 1 individual, Namhae, 34°52'40.83"N 127°56'43.61"E, 26 Sep. 2021, collected by Jung J., Korea56.

Host species: *U. major* (Gebiidea; Upogebiidae).

iDiagnosis: Whole externa single, smooth, and irregular oval shape with a shallow median groove on dorsal margin. Mantle aperture vestigial and vertically large circular opening with radiated ridges at the extremity.

***Parasacculina yatsui* (Boschma, 1936)**

(Fig. 2F, see Jung et al. 2021)

Additional materials examined: on *Cyclograpsus intermedius*: 1 individual, Ulleung, 37°28'32.4"N, 130°53'51.5"E, 19 Sep. 2019, collected by Jung J., Korearr40.

On *Hemigrapsus penicillatus*: 1 individual, Goseong, 38°16'11.5"N, 128°33'27.2"E, 26 Sep. 2021, collected by Jung J., GS12, host: ♂, carapace length 20 mm; 1 individual, Gangneung, 37°44'04.3"N, 128°59'25.8"E, 23 Oct. 2021, collected by Jung J., Korearr10. On *Hemigrapsus sanguineus*: 1 individual, Goheung, 34°30'22.2"N 127°28'56.0"E, 9 Oct. 2022, collected by Jung J., KoreaN14; 1 individual, Goseong, 38°27'01.3"N 128°28'03.9"E, 25 Sep. 2021, collected by Jung J., Korea71, host: ♀, carapace length 19 mm; 1 ind, Tongyeong, 34°38'24.9"N 128°34'06.1"E, 19 Aug. 2019, collected by Jung J., Korea39, host: ♂, carapace length 14 mm. On *P. crassipes*: 1 individual, Yeongdeok, 36°16'22.0"N 129°22'44.3"E, 29 Aug. 2021, collected by Jung J., Korea72, host: ♀, carapace length 22 mm; 1 individual, Gangneung, 37°44'04.3"N 128°59'25.8"E, 23 Oct. 2021, collected by Jung J., Korearr9; 1 individual, Samcheok, 37°12'50.5"N 129°20'46.5"E, 19 May 2022, collected by Jung J., Korearr25; 1 individual, Jeju, 33°30'57.3"N 126°30'38.5"E, 23 Aug. 2022, collected by Jung J., Koreakr9.

Host species: *P. crassipes* (Brachyura; Grapsidae), *H. sanguineus*, *H. penicillatus, C. intermedius* (Brachyura; Varunidae).

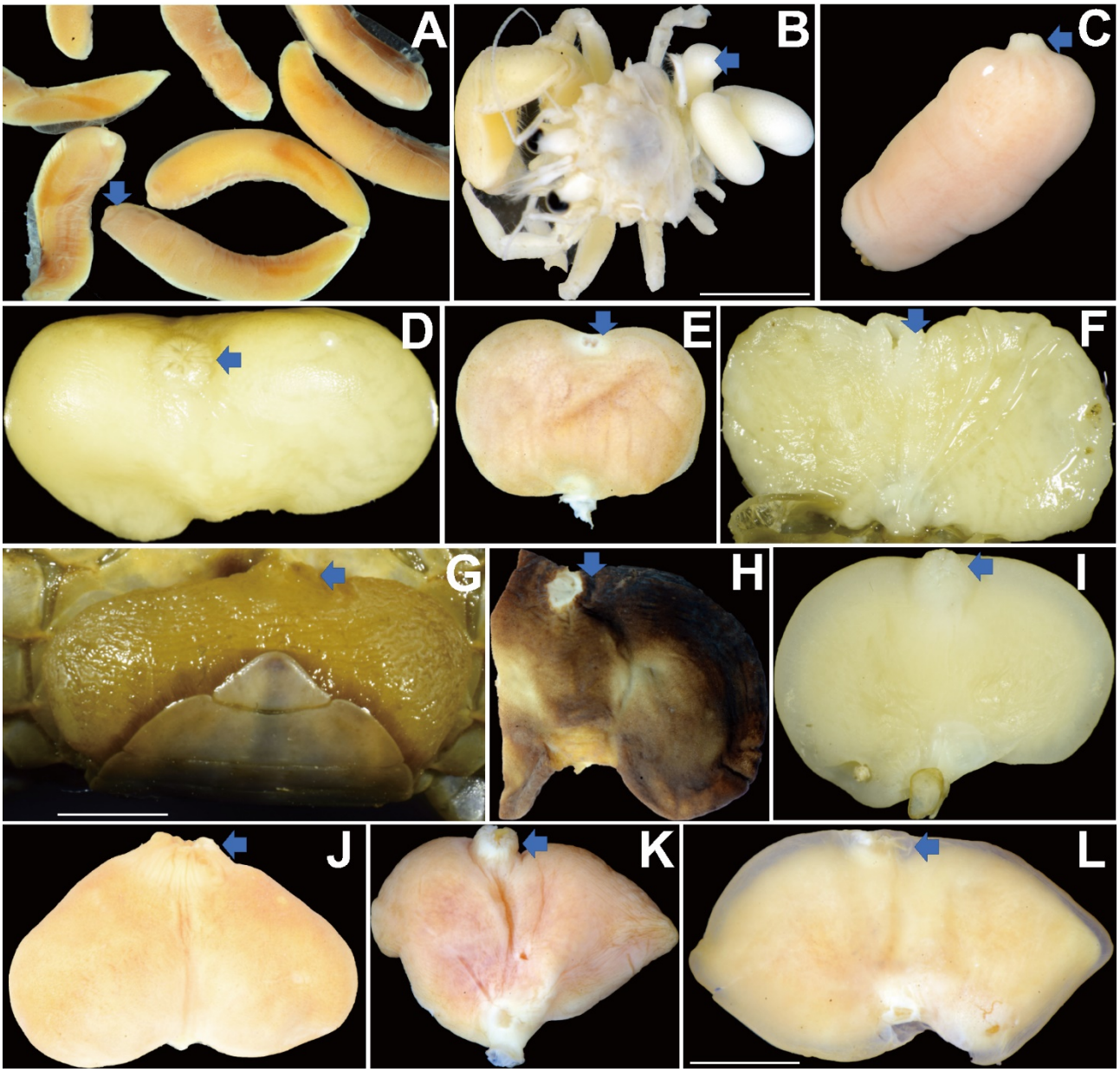

Fig. 2. Externae of Korean rhizocephalans in this study. Blue arrow: mantle aperture, scale bar: 2 mm for H and J, 1mm for A-G, I, K, L. A, *Peltogasterella gracilis*; B, *Peltogasterella* sp.; C, *Peltogaster* sp. 1; D, *Parasacculina imberbis*; E, *Parasacculina pilosella*; F, *Parasacculina yatsui*; G, *Parasacculina oblonga*; H, *Parasacculina* sp. 1; I, *Polyascus* cf. *gregarius*; J, *Heterosaccus papillosus*; K, *Sacculina angulata*; L, *Sacculina gracilis.* Externae of C and H were incomplete, in case they were used for molecular analysis.

***Parasacculina oblonga* (Lützen & Yamaguchi, 1999)**

(Korean name: Bi-Dan-Ge-Ju-Meo-Ni-Beol-Rae)

(Fig. 2G)

Material examined: on *C. intermedius*: 1 individual, Ulleung, 37°28'32.4"N, 130°53'51.5"E, 3 June 2021, collected by Jung J., DSEVIV0000000050 host: ♀, carapace length 12 mm; 1 individual, Ulleung, 37°28'32.4"N, 130°53'51.5"E, 3 June 2021, collected by Jung J., DSEVIV0000000051, host: ♀, carapace length 12 mm; 1 individual, Ulleung, 37°28'32.4"N, 130°53'51.5"E, 19 Sep. 2019, collected by Jung J., DSEVIV0000000054; 1 individual, Ulleung, 37°30'49.9"N, 130°47'45.0"E, 18 Sep. 2019, collected by Jung J., DSEVIV0000000055; 1 individual, Ulleung, 37°30'49.9"N, 130°47'45.0"E, 18 Sep. 2019, collected by Jung J., DSEVIV0000000056, host: ♂, carapace length 14 mm.

Host species: *C. intermedius* (Brachyura; Varunidae).

Distribution: Japan (type locality), Korea.

Diagnosis: Whole externa single, smooth or slightly wrinkled, and oval in shape. Mantle aperture large, elevated, and vertically Y-shape opening at the extremity.

***Parasacculina* sp. 1**

(Fig. 2H)

Material examined: on *H. sanguineus*: 1 individual, Goheung, 34°31'7.0"N, 127°26'12.2"E, 8 Oct. 2022, collected by Jung J and Park J-K., HVBNIV0000000005, host: ♀, carapace length 24 mm; 1 individual, Goheung, 34°30'22.2"N, 127°28'56.0"E, 9 Oct. 2022, collected by Jung J., Korea13N, host: ♀, carapace length 33 mm; 1 individual, Goheung, 34°30'22.2"N, 127°28'56.0"E, 9 Oct. 2022, collected by Jung J. and Park J-K, HVBNIV0000000006, host: ♀, carapace length 25 mm.

Host species: *H. sanguineus* (Brachyura; Varunidae).

Distribution: Korea.

Diagnosis: whole externa smooth, single, and cordiform with flat half-oval-shaped left and right lobes divided by outer mid-groove and inner mid-ridge. Mantle aperture slightly elevated, and slightly wrinkled with circular opening at extremity.

***Parasacculina* sp. 2**

(see *Parasacculina* sp. 1 of Jung et al. 2021)

Host species: *Macromedaeus distinguendus* (Brachyura; Xanthidae).

***Parasacculina* sp. 3**

(see *Parasacculina* sp. 2 of Jung et al. 2021)

Host species: *Macromedaeus distinguendus* (Brachyura; Xanthidae).

***Polyascus* Glenner, Lützen & Takahashi, 2003**

***Polyascus* cf. *gregarius* (Okada & Miyashita, 1935)**

(Fig. 2I, see *Polyascus* cf. *gregarius* of Jung et al. 2021)

Additional materials examined: on *H. sanguineus*: 1 individual, Yeosu, 34°29'22.4"N, 127°48'49.5"E, 11 May 2021, collected by Jung J., Korea45, 1 individual, Wando, 34°17'47.4"N 126°42'05.1"E, 24 May 2021, collected by Jung J., Korea47, host: ♂, carapace length 34 mm; 1 individual, Tongyeong, 34°45'31.3"N, 128°30'59.4"E, 29 Oct. 2021, collected by Jung J., Korearr56; 1 individual, Shinan, 24 May 2016, collected by Jung J., Korearr58; 1 individual, Busan, 13 May 2020, collected by Jung J., Korearr60; 1 ind, Jindo, 34°31'24.4"N, 126°12'56.5"E, 6 July 2022, collected by Jung J., Koreakr1; 1 individual, Goheung, 34°31'7.0"N, 127°26'12.2"E, 8 Oct. 2022, collected by Jung J., Korea1N.

Host species: *H. sanguineus, H. takanoi, Eriocheir japonica* (Brachyura; Varunidae).

Sacculinidae Lilljeborg, 1861

***Heterosaccus* Smith, 1906**

***Heterosaccus papillosus* (Boschma, 1933)**

(Fig. 2J)

Material examined: on *Charybdis* (*Charybdis*) *japonica*: 1 individual, Incheon, 37°15'54.2"N, 126°29'51.8"E, 23 Aug. 2012, NIBRIV0000895329; 1 individual, Incheon, 37°24'31.4"N, 126°38'41.0"E, 18 Aug. 1998, NIBRIV0000895330.

Host species: *Charybdis* (*Gonioneptunus*) *bimaculata*, *C.* (*C.*) *japonica* Brachyura; (Portunidae).

Distribution: Philippines (type locality), Japan, Korea.

Diagnosis: Whole externa single, smooth or slightly wrinkled, and reversed cordiform with left and right lobes divided by a mid-notch. Mantle aperture slightly elevated or elevated, radically wrinkled, and vertically large circular opening at the extremity.

Sacculina **Thompson, 1836**

Sacculina confragosa **Boschma, 1933**

(see Jung et al. 2021)

Additional materials examined: on *Gaetice depressus*: 1 individual, Goheung, 34°24'56.9"N, 127°29'36.5"E, 12 May 2021, collected by Jung J., Korea52, host: ♂, carapace length 18 mm.
on *P. crassipes*: 1 individual, Sokcho, 38°12'50.9"N, 128°36'05.5"E, 6 Sep 2021, collected by Jung J., Korea73, host: ♀, carapace length 17 mm; 1 individual, Jeju, 33°56'40.8"N, 126°20'03.5"E, 7 Sep 2021, collected by Jung J., Korea74, host: ♀, carapace length 14 mm; 1 individual, Gangneung, 37°44'04.3"N, 128°59'25.8"E, 23 Oct. 2021, collected by Jung J., Korearr8; 1 individual, Uljin, 37°03'32.7"N, 129°25'46.0"E, 24 Oct. 2022, collected by Jung J., Korearr28; 1 individual, Samcheok, 37°08'51.2"N, 129°21'48.9"E, 19 May 2022, collected by Jung J., Korearr53; 1 ind, Seogwipo, 33°12'28.3"N, 126°17'30.7"E, 21 Aug. 2022, collected by Jung J., Koreakr11.
on *H. sanguineus*: 1 individual, Gangneung, 37°44'04.3"N, 128°59'25.8"E, 18 May 2022, collected by Jung J., Korearr22; 1 individual, Pohang, 36°00'14.4"N, 129°34'32.1"E, 11 May 2020, collected by Jung J., Korearr59; 1 ind, Jindo, 34°31'25.0"N, 126°12'06.4"E, 6 July 2022, collected by Jung J., Koreakr2; 1 ind, Goheung, 34°31'7.0"N, 127°26'12.2"E, 8 Oct. 2022, collected by Jung J., Korea7N.

Host species: *G. depressus*, *P. crassipes* (Brachyura; Grapsidae), *C. intermedius*, *H. sanguineus* (Brachyura; Varunidae).

Sacculina 17ngulate **Van Kampen & Boschma, 1925**

(Korean name: O-Gak-Ge-Ju-Meo-Ni-Beol-Rae)

(Fig. 2K)

Material examined: on *Thalamita sima*: 1 individual (3 externae, 1 externa removed for molecular analysis), Busan, 35°9'6.4"N, 129°10'43.1"E, 25 Apr. 2018, collected by SH Kim, NIBRIV0000895328 host: ♂, carapace length 23 mm; 1 individual, Sacheon 34°53'2.0"N, 128°4'34.6"E, 16 July 2014, collected by SH Kim, NIBRIV0000895331 host: ♀, carapace length 25 mm.
Host: *Xiphonectes longispinosus*, *C.* (*G.*) *bimaculata*, *T. sima* (Brachyura; Portunidae).

Distribution: Indonesia (type locality), Thailand, Taiwan, Korea.

Diagnosis: Whole externa single or triple, smooth or slightly wrinkled, and irregular pentagonal in shape. Mantle aperture large, elevated, radically wrinkled, and vertically large circle opening at the extremity.

***Sacculina gracilis* Boschma, 1931**

(Korean name: Mae-Kkeun-Ge-Ju-Meo-Ni-Beol-Rae)

(Fig. 2L)

Material examined: on *T. sima*: 1 individual, Seogwipo, 33°12'38.6"N, 126°15'35.5"E, 12 Aug. 2010, collected by HS Ko, NIBRIV0000895332, host: ♂, carapace length 21 mm; 1 individual, Tongyeong, 34°50'14.5"N, 128°9' 29.9"E, 9 June 2013, collected by HY Suk, NIBRIV0000895334, host: ♂, carapace length 16 mm.

Host species: *Xiphonectes longispinosus, T. sima*, *Thalamita picta*, *Thranita danae*, (Brachyura; Portunidae) *Heteropilumnus setosus*, *Ser fukiensis*, (Brachyura; Pilumnidae) *Notonyx vitreu* (Brachyura; Goneplacidae).

Distribution: Thailand (type locality), Indonesia, Singapore, Philippines, China, Korea.

Diagnosis: Whole externa single, smooth, and round fusiform in shape. Mantle aperture small, slightly elevated, and vertically Y-shape opening at the extremity.

***Sacculina upogebiae* Shiino, 1943**

(see Lützen et al. 2016)

Materials examined: on *U. major*: 1 individual, Boryeong, 36°21'19.7"N, 126°32'40.2"E, 6 June 2012, NIBRIV0000453552; 1 individual, Incheon, 37°13'50.9"N 126°31'56.9"E, 21 Mar. 2014, NIBRIV0000453567.

Host species: *U. major* (Gebiidea; Upogebiidae).

DISCUSSION

In this study, we compared morphological and molecular information of Korean Rhizocephala species with previously published studies and discussed details of their morphological features and sequence divergences, and taxonomic consideration.

Peltogasterella sp.: The absence of a chitinous shield on the externa which is the main morphological characteristic of *Peltogasterella* indicates that this species belongs to the genus *Peltogasterella*. In addition, the elongated externae on the present specimens are similar to the characteristics of *P. gracilis*. However, a mantle aperture is not elevated, the number of externa is 1 to 3, and the *cox1* sequence (OR481994) is different from the *P. gracilis* and the similarity is below 74.4%. Moreover, this species is found only on the abdomen of *P. nihonkaiensis*. Therefore, we declare that these specimens are new species candidates of the genus *Peltogasterella*.

Peltogaster reticulata: MADBK 160718_040 has morphological characteristics such as banana-shaped single externa, an elevated mantle aperture, and an X-shape mantle aperture opening, which correspond with the original description (Shiino 1943). In addition, the hosts of these specimens were identical to previous studies of *P. reticulata* in Russia (Kashenko and Korn 2003; Korn et al. 2020). Furthermore, the *cox*1 sequence of MADBK 160706_065 has high DNA sequence similarity of Russian *P. reticulata* (98.9–99.4% to MN193580-MN193582, Korn et al. 2020). Therefore, the Korean *P*. aff. *reticulata* and *Peltogaster* sp. 4 in Jung et al. (2019) were identified as *P. reticulata.*

Peltogaster sp. 1: This species is regarded as *Peltogaster* species because of the presence of a chitinous shield on the externa which is the main morphological characteristic of *Peltogaster* and *cox1* sequences of this species nested within *Peltogaster* species. In addition, this species has single oval externa identical to *P. lineata*, another parasite of *P. maculosus* in Japan. However, this species has irregular oval externa and a well development mantle aperture differs from *P. lineata* which has regular oval externa and a vestigial mantle aperture. In addition, *cox1* sequences of this species (OR481985-OR481991) significantly differ from those of *P. lineata* and other *Peltogaster* species and the similarity is below 78.2%. Therefore, we declare that these specimens are new species candidates of the genus *Peltogaster*.

Parasacculina imberbis: The morphological character of externa of Korean *P. imberbis* which could not be observed due to immature specimens in Jung et al. (2021), was observed through additional specimens in this study. These morphological characters such as yellow and bilobed single externa and a slightly elevated mantle aperture tube are identical to the original description (Shiino 1943).

Parasacculina shiinoi: The morphological character of externa of Korean *P. shiinoi* which could not be observed due to immature specimens in Jung et al. (2021), was observed through additional specimens in this study. These morphological characteristics such as irregular oval externa and a vestigial mantle aperture tube are identical to the original description (Lützen et al. 2016).

Parasacculina yatsui: Jung et al. (2021) noted that Korean *P. yatsui* infects only *H. sanguineus*. The study revealed that Korean *P. yatsui* also infects *P. crassipes*, *H. penicillatus*, and *C. intermedius.* This is the first report that *P. yatsui* is parasitized on *H. penicillatus*.

Parasacculina oblonga: These samples are identical in the host species (*C. intermedius*) and morphological characters to the original description (Lützen and Yamaguchi 1999) such as single round externa, and large and elevated mantle aperture. Furthermore, the BLAST result showed that the sequences of this specimen (OR481965-OR481969) have very high sequence similarity to the sequences of the same GenBank species (DQ059780) at 99.4-99.8%. Therefore, we identified these specimens as *P. oblonga*. The distribution of *P. oblonga* expanded northward by this study. *Parasacculina* sp. 1: *Parasacculina yatsui* and *Polyascus* cf. *gregarius* have been reported to be parasites of *H. sanguineus*. However, these specimens differ in morphology and molecular sequences from *P. yatsui* and *P.* cf. *gregarius*. This species has single smooth externa, whereas *P.* cf. *gregarius* has 1-2 smooth externae and *P. yatsui* has single externa with a wrinkled outermost part (Jung et al. 2021). In addition, this species has a circular mantle aperture opening whereas *P. yatsui* and *P.* cf. *gregarius* have slit mantle aperture openings (Jung et al. 2021). BLAST result showed that *cox1* sequences of this species (OR481970-OR481972) are different from those of *P. yatsui* and *P.* cf. *gregarius* and all other polyasids and the similarity is below 74.9%. Therefore, we considered this species to be a new species candidate of the genus *Parasacculina*.

Heterosaccus papillosus: This species parasite on the *C.* (*C.*) *japonica* was first reported in Korea by Kim and Hong (2002). However, the morphology and the reference specimen of Korean *H. papillosus* were not presented in Kim and Hong (2002). In this study, the morphology and molecular characteristics of Korean *H. papillosus* were presented for the first time. The host (*C.* (*C.*) *japonica*) and morphological characteristics of these specimens such as single reversed heart shape externa and well-elevated pillar shape mantle aperture were consistence with the original description (Boschma 1933). In addition, the *cox1* sequence of Korean *H. papillosus* (OR481955) was separated from *cox1* sequences of other *Heterosaccus* species but similar to *Heterosaccus* species (94.9% similar to *Heterosaccus lunatus* DQ059778) than other genera in the BLAST result.

Sacculina confragosa: Jung et al. (2021) mentioned that Korean *S. confragosa* infects only *G. depressus*. This study revealed that Korean *S. confragosa* also infects *P. crassipes* and *H. sanguineus*. This is the first report that *S. confragosa* is parasitized on *H. sanguineus*.

Sacculina angulata: Morphological characteristics of the examined specimen such as irregular pentagonal externa and elevated large mantle aperture correspond with the original description of *S. angulata* (Van Kampen and Boschma 1925). In addition, the host of these specimens (*T. sima*) is

identical to the host of the previous study (Boschma 1931). Furthermore, the BLAST result showed that the sequence of this species (OR482032) is similar to *Sacculina* sp. (EF521402) at 83.0%. Therefore, we identified these specimens as *S. angulata*. The distribution of *S. angulata* expanded northeastward by this study.

Sacculina gracilis: The morphological characteristics of the examined specimen such as single fusiform externa and slightly elevated small mantle aperture correspond with the original description of *S. gracilis* (Boschma 1931). In addition, the host (*T. sima*) of these specimens was identical to the previous study of Boschma (1955). However, the BLAST result showed that the sequences of this species (OR482063-OR482064) are most similar to *Parasacculina beauforti* (KX426583) at 80.2%. A taxonomical revision of the genus of *S. gracilis* is required by further molecular analysis using additional DNA markers. This is the third report on *S. gracilis* after the original description (Boschma 1931) and Boschma (1955) and the distribution expanded eastward by this study.

CONCLUSIONS

Through this study, a checklist of 16 Korean parasitic barnacles was presented and three rhizocephalans were found to have an expanded distribution range and three new species candidates in Korea were identified. In addition, we noted brief remarks on Korean parasitic barnacles that were not reported in previous studies. This study suggests that further biodiversity studies of Rhizocephala should be conducted by examining more diverse hosts beyond those previously reported. In addition, this study will be a reference for examining the fauna of East Asian Rhizocephala and conducting related further studies on parasitic barnacles.

List of abbreviations

mitochondrial cytochrome c oxidase subunit I, *cox*I.

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Authors' contributions: Jibom Jung contributed to the study design, field works, acquisition, data analysis, interpretation of the sequence data, and manuscript draft.
Joong-Ki Park contributed to the study design, acquisition, data analysis, interpretation of the sequence data, and drafting the manuscript.

Competing interests: JJ and J-KP declare that they have no conflict of interest.

Availability of data and materials: The *cox1* data in this study were deposited in GenBank (Table 1). Voucher specimens in this study were deposited in the National Institute of Biological Resources (NIBR) and the Honam National Institute of Biological Resources (HNIBR).

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