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이학박사학위논문

**Systematic study on the Superfamily Majoidea
(Crustacea : Malacostraca : Decapoda)
from Korean waters**

한국산 물맞이게상과의 계통분류학적 연구

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생명과학부

이 상 휘

Abstract

Systematic study on the Superfamily Majoidea (Crustacea : Malacostraca : Decapoda) from Korean waters

Sang-Hui Lee

School of Biological Sciences

The Graduate School

Seoul National University

Majoid crabs belong to one of the most diverse brachyuran taxa, with more than 900 species reported globally. As many morphologically as many species were there, there was confusion in identifying species or analyzing phylogeny. The aims of this study were to 1) study the taxonomy of Korean majoid crabs using morphological and molecular characteristics, and 2) infer the phylogenetic relationships of selected majoid crab species using complete mitochondrial genomes.

Chapter 1 presents the results of literature surveys and specimen observations of majoid crab diversity in Korean waters. It includes an updated checklist, a key for identification of Korean majoid crabs, species descriptions including photographs of crab specimens, and distribution maps. The diversity survey confirmed the inhabit of 51 species of 29 genera belonging to 5 families, including nine species of six genera newly reported in Korea. The majoid crab diversity of Jejudo Island, where 33 species of 20 genera were collected, was the highest of the areas surveyed and included 20 species that were unique to the waters surrounding this island. A survey conducted in offshore waters (15 km or more from shore) identified majoid crab species that are rare or have not previously been reported in Korea.

Morphology and *COXI* molecular characteristics were analyzed and corrected for *Pugettia quadridens sensu lato*, which was frequently misidentified due to morphological similarity with each other. It has been confirmed that '빨물맞이게', which has been known as *P. quadridens* in Korea, is *P. ferox*. Furthermore, *P. quadridens sensu stricto* also discovered from Korean waters. In this study, it was not confirmed that *P. pellucens* inhabit the Korean waters, and further study is needed to investigate the existence of this species.

Chapter 2 presents the complete mitochondrial genomes of 10 majoid crab species which were determined to infer the phylogenetic relationships of Majoidea. Seven species of which were first reported in the Epiplatidae, Inachidae, and Inachoididae. Phylogenetic relationships were analyzed using the maximum likelihood and Bayesian inference methods applied to the complete mitochondrial genome sequences of 14 species, selected to represent all six majoid crab families. According to the analysis, Oregoniidae was the first to branch, followed by Inachidae and Inachoididae. Phylogenetic placement of the

genus *Micippa* of the Majidae requires further study. The Epialtidae was polyphyletic at the subfamily level, and the Mithracidae was located closest to the Epialtidae.

The diversity of gene order patterns in majoid crabs was found to be relatively high in comparison with other brachyurans. Brachyurans are known to have eighteen gene order patterns, with eight of these found only in majoid crabs. Generally, gene order patterns were known to be conservative at the family level, but in Majoidea, there was a tendency to be partially conservative at the genus level.

Key words: Taxonomy, Molecular taxonomy, Majoid crabs, Korean fauna, Phylogeny, Complete mitochondrial genome

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General introduction

Majoid crabs are one of the most diverse superfamilies of the infraorder Brachyura Latreille, 1802 (Ng et al., 2008; De Grave et al., 2009; Davie et al., 2015a) (Fig. 1). A total of 907 species from 189 genera belonging to six families of majoid crabs have been reported worldwide (Davie et al., 2015a). Majoid crabs have long and thin legs; therefore, they are called spider crabs, and they are also called decorator crabs because they possess efficient camouflage abilities (Poore, 2004). Majoid crabs generally have a carapace with pyriform, hooked setae on the carapace and legs, and well-developed pseudorostrum in various forms at the front of the carapace. The hooked setae on their carapace and legs enable them to camouflage with seaweed, sponges, and bryozoans (Guinot & Wicksten, 2015). Majoid crabs are the only superfamily of brachyurans that possess hooked setae and exhibit camouflage behavior (Guinot & Wicksten, 2015). They are distributed across a wide range of habitats, from intertidal zones to continental slopes (>1,000 m), from boreal to tropical regions, and they have evolved across these habitats.



Fig. 1. The morphological diversity of Majoidea.

There have been limited studies on majoid crabs in Korea. The study of Korean brachyuran species was initiated by British researcher Miers (1879); later, it was studied by Japanese researchers (Yokoya, 1933; Sakai, 1935, 1937, 1938, 1939; Kamita, 1941). The first academic study of brachyurans in Korea was initiated by Jung (1956), followed by a comprehensive review by Kim (1973). Ninety-seven genera and 168 species of Korean brachyurans were described by Kim (1973), and of these, majoid crabs consisted of 18 genera and 28 species. Recently, an updated study of Korean majoid crabs and larvae was reported by Ko and Lee (2015), and several additional species have been reported by other researchers; 5 families, 25 genera, and 43 species of majoid crabs have been identified in Korean waters. This is insufficient compared to the records of neighboring countries. It is therefore necessary to utilize more efficient survey methods, and to expand surveys/studies to previously unexplored waters.

As majoid crabs are of various species and occupy various habitats, their systematics and phylogeny have also been complicated (Garth, 1958; Griffin & Tranter, 1986; Ng et al., 2008; Marco-Herrero et al., 2013; Windsor & Felder, 2014). In order to solve the problem of phylogeny in majoid crabs, an analysis was attempted using not only the adult form but also the larval, and partial DNA sequencing (Hultgen & Stachowicz, 2008; Hultgen et al., 2009; Marco-Herrero et al., 2013; Windsor & Felder, 2014), but it was still ineffective. Recently, studies involving the use of complete mitochondrial genome have been conducted on various taxa to infer phylogeny (Cunha et al., 2009; Allcock et al., 2011; Shi et al., 2015; Basso et al., 2017; Bai et al., 2018; Palero et al., 2019). The mitochondrial genome is more informative than partial DNA sequencing because it considers variations in sequences as well as the gene order, making it suitable for more in-depth phylogenetic analysis. Therefore, a study using the complete mitochondrial genome will greatly help solve the problem of phylogeny in majoid crabs.

The aim of this study was (1) to review the updated fauna of Korean majoid crabs in terms of morphology and molecular taxonomy; to provide a list and a key of Korean majoid crabs, and (2) to infer the phylogeny of the majoid crabs using the complete mitochondrial genome.

Chapter 1.

***Morphological and molecular taxonomic study
of Korean majoid crabs***

1.1. Introduction

Historically, faunal studies of brachyurans in Far East Asia have been actively conducted (De Haan, 1833-1850; Ortmann, 1893; Balss, 1922; Stimpson, 1907; Miers, 1886), but very little research has been performed in the Korean waters. The taxonomic study of Korean brachyurans began with Miers (1879), reporting 64 species collected from Korea and Japan. 22 species in this article are marked as being collected from the Korean channel and the Korean seas. However, considering the location of the collection site, it was found that the only species collected in the Korean waters were *Pilumnus hirsutus* (= *P. minutus*), *Trichocarcinus dentatus* (= *Glebocarcinus amphioetus*), and *Arcania globate*. Later, Yokoya (1933) reported five species of crabs collected in the Korean Strait, including *Oregonia gracilis*. Sakai (1936) wrote "Crabs of Japan," with 29 species marked Korea in their distribution. Subsequently, Sakai (1937, 1938, 1939) published the "Studies on the Crabs of Japan" series, of which 55 species marked with distributions of Korea or Korea Strait, among which there were 4 majoid species. And Kamita (1941) provided descriptions and illustrations of 121 species of 71 genera, including majoid crabs 17 species of 11 genera, in the Korean waters in "Studies on the Decapod Crustaceans of Chosen". Jung (1956) wrote "Checklist of Crab from Gyeonggi-do" based on previous literature, and he reported 51 species of 32 genera belonging to 12 families which were named in Korean for the first time. It was at this point that research on brachyurans began independently in Korea. Kim (1973) recorded 168 species belonging to 97 genera of Korean brachyurans based on the results of the studies and reported a comprehensive record of the study history and distribution. Since then, brachyurans in Korea have been studied by several researchers in

Korea. Currently, 241 species of 166 genera belonging to 44 families have been recorded to have been found in Korean waters. In majoid crabs, after 28 species were organized by Kim (1973), 38 species including adults and larvae morphologies were described by Ko & Lee (2015). After which 3 species of 3 genera more were subsequently reported (Yang et al., 2015; Seo et al., 2017), and it is known that 42 species of 25 genera belonging to 5 families are currently inhabiting in Korean waters.

Despite the efforts of previous researchers, the species diversity of majoid crabs in Korea is lower than that of neighboring countries. Previous surveys of majoid crabs in Korea were mainly conducted at the intertidal zone, SCUBA diving within 30 m depth, fishing port, and market survey. The spatial limitations resulting from the constraints of these collection methods eventually led to a limited number of recorded species. Neighboring countries have expanded the range of survey areas for decapods by using the research vessel and ROV (remotely-operated vehicle), and have achieved results (Komai, 2011, 2014, 2017; Lee et al., 2015; Dong & Li, 2018; Chang & Chan; 2019). During the study period, the collection was carried out by a survey method (i.e., technical diving at 40 to 75 m and otter trawl) that has not been commonly used in Korea. As a result, a number of rarely reported or unreported species were found in Korean waters. Accordingly, an updated list of Korean majoid crabs and the description of the variations among these species reported in Korean waters are needed.

Majoid crabs are one of the most diversified taxa in the Brachyura (De Grave et al., 2009), resulting in high morphological similarity between species and high variation within the species. As a result, many misidentifications have been reported (see synonyms of Taxonomic accounts, this Chapter). Molecular-based species identification is helpful for identifying related species with similar morphology and for discovering cryptic species.

Among many genetic regions, the mitochondrial *COXI* gene has been used by many researchers because of its ability to discriminate between species (Hebert et al., 2003; Kim et al., 2012; Macpherson & Barcia, 2015). In addition, universal primers (Folmer et al., 1994) have been developed; they are relatively short (658 bp), easy to handle, and can identify most species. For this reason, applying the molecular identification technique using the *COXI* gene has a great potential of providing an answer to the exact identification of majoid crabs that have not been clearly understood.

The aims of this chapter are: (1) to re-examine all the majoid crabs discovered in Korean waters, and arrange them according to the recently approved classification system; and (2) to support accurate species identification of Korean majoid crabs by applying molecular identification using the *COXI* gene.

1.2. Materials and methods

Literature and specimen survey

The scope of Korean majoid crabs covered in this study is based on the literature previously recorded in Korean waters, specimens collected by the author and specimens deposited research institutes in Korea. In the literature search, the scientific literatures of taxonomy experts were used, and general reports (e.g., environmental survey reports etc.) were excluded. The spatial scope addressed in the study includes all territorial and Exclusive Economic Zones (EEZs) in the Republic of Korea, as permitted by the 1982 United Nations Convention on the Law of the Sea (UNCLOS).

A total of 331 individuals of Korean specimens were examined in this study and were collected from 1970 to 2020. Between August 2015 and January 2020, 274 individuals were collected, and the remaining specimens used in this study were obtained from the National Marine Biodiversity Institute of Korea (MABIK). Specimens were collected from the intertidal zone at a depth of 1,000 meters using hands, SCUBA diving, or otter trawl. All specimens collected in this study were preserved in 95% ethyl alcohol at the site for morphological and molecular studies. Uncollected species and additional observed specimens were borrowed from the National Marine Biodiversity Institute of Korea, Seocheon, Korea (MABIK), National Institute of Biological Resources, Incheon, Korea (NIBR), and the Marine Arthropod Depository Bank of Korea, Seoul, Korea (MADBK).

Morphological observation

In the laboratory, algae, bryozoans, sponges, etc., which were attached to the specimens were removed with forceps and a soft brush. The specimens were sorted using the naked eye. A stereomicroscope (Leica M205C) was used to observe the microscopic parts.

Photographs were taken with multiple foci using a digital camera (Nikon D810) and synthesized in a digital image processing tool (Helicon Focus v7.0.2). Illustrations were prepared using a camera lucida attached to a stereomicroscope.

All specimen measurements are given in millimeters (mm). Carapace length (cl) was measured as part of the total length, which includes the pseudorostral spines. Post-pseudorostral carapace length (pcl) was measured in the middle line from the base of the pseudorostral sinus to its posterior border. Carapace width (cw) was defined as the widest part of the carapace, excluding spines. The abbreviation G1 is for the male first gonopod. The major morphological features of majoid crabs are demonstrated in Figures 2 and 3.

The classification scheme that was followed was proposed by Davie et al. (2015a) and morphological terminology generally follows Griffin (1966a) and Ng & Richer de Forges (2015).

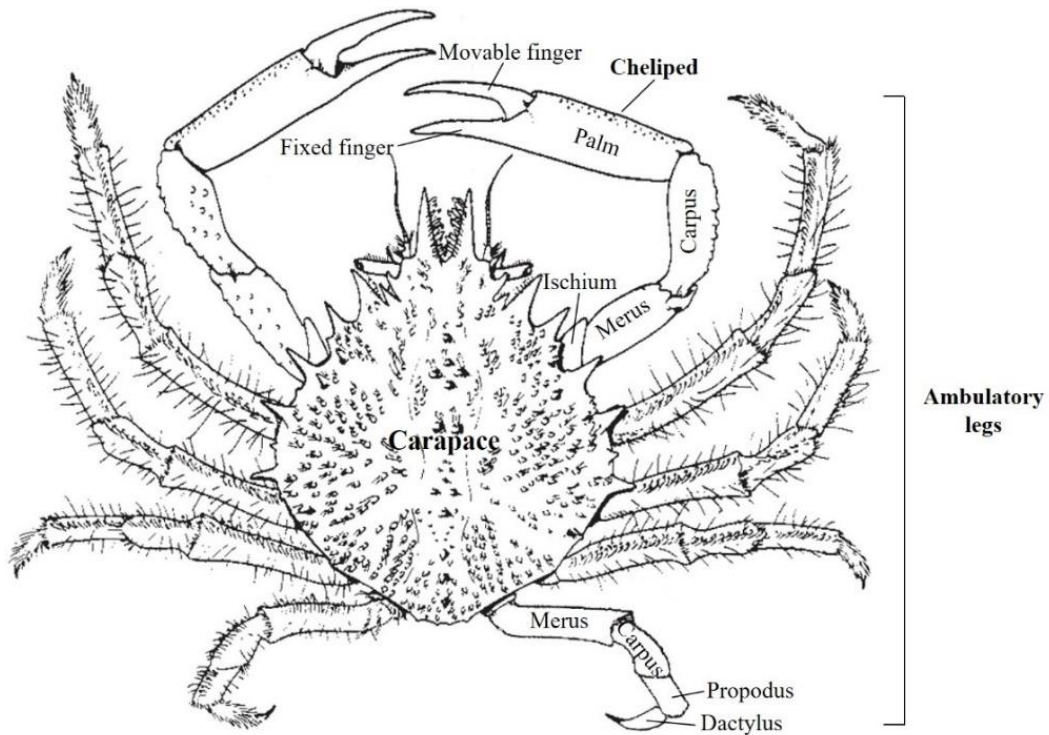


Fig. 2. Descriptive terms of the dorsal view of the carapace and associated part. Modified from Carpenter & Niem (1998).

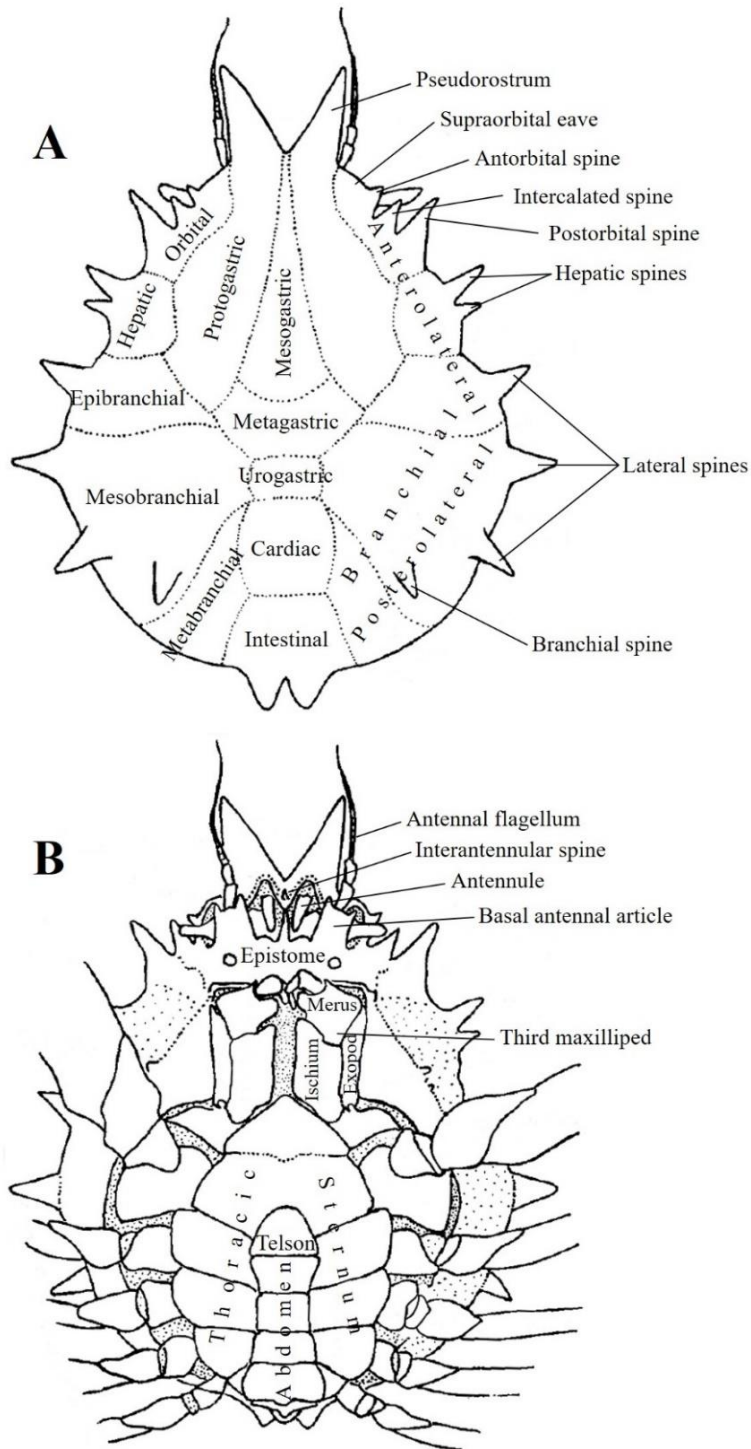


Fig. 3. Descriptive terms of the carapace and associated part; A, Dorsal view of carapace; B, Ventral view of carapace. Modified from Griffin (1966a).

DNA extraction, PCR amplification, and molecular analysis

DNA sequencing of the majoid crabs was conducted on specimens collected in Korea and Russia from 2001 to 2020. In most cases, DNA sequencing was performed on the morphologically identified specimens. However, in *Pugettia quadridens sensu lato* (*P. quadridens*, *P. pellucens*, *P. intermedia*, *P. ferox*, and *P. vulgaris*), many morphological variations depend on the size of the individual, and there are many shared characteristics between species, which makes it difficult to identify them (see remarks of *P. quadridens* and *P. pellucens*), so morphological characteristics were observed after the DNA sequencing of all individuals.

DNA sequencing was performed for a total of 246 specimens of majoid species. Tissues were extracted from the appendage or eggs. Total genomic DNA was extracted using the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. A partial sequence of the mitochondrial genes encoding cytochrome c oxidase subunit I (*COXI*) was amplified by polymerase chain reaction (PCR) using the universal primers, LCO 1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') and HCO 2198 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer et al., 1994). The conditions needed for PCR amplification were: heat at 95°C for 5 min, then rotate 40 cycles of 95°C for 20 s, heat at 50°C for 20 s, and 72°C for 5 s, followed by a final extension at 72°C for 7 min. The resulting PCR products were sequenced in both directions using an ABI PRISM 3730XL Analyzer (Applied Biosystems, Foster City, USA). All sequences were aligned using MAFFT v7.308 (Kato & Standley, 2013). Pairwise distances (P-distance) were calculated using the Kimura 2 parameter (K2P) model (Kimura, 1980). All datasets were analyzed using the Neighbor-joining method (NJ). A bootstrap value of 1,000 replications was applied to examine the NJ tree using MEGA ver. 6 (Tamura et al., 2013).

Table 1. Taxa and specimens used for molecular taxonomic analysis.

Species	Locality	Individuals
1. <i>Huenia heraldica</i>	Jeju-si, Jeju-do, Korea	1
2. <i>Menaethius monoceros</i>	Yeongdeok-gun, Gyeongsangbuk-do, Korea	2
	Jeju-si, Jeju-do, Korea	2
	Seogwipo-si, Jeju-do, Korea	1
3. <i>Pugettia ferox</i>	Taeon-gun, Chungcheongnam-do, Korea	1
	Gijang-gun, Busan-si, Korea	2
	Saha-gu, Busan-si, Korea	1
	Suyeong-gu, Busan-si, Korea	1
	Yeongdo-gu, Busan-si, Korea	2
	Seocheon-gun, Chungcheongnam-do, Korea	2
	Taeon-gun, Chungcheongnam-do, Korea	5
	Gangneung-si, Gangwon-do, Korea	6
	Goseong-gun, Gangwon-do, Korea	2
	Pohang-si, Gyeongsangbuk-do, Korea	3
	Uljin-gun, Gyeongsangbuk-do, Korea	4
	Geoje-si, Gyeongsangnam-do, Korea	2
	Tongyeong-si, Gyeongsangnam-do, Korea	7
	Jeju-si, Jeju-do, Korea	2
	Gunsan-si, Jeollabuk-do, Korea	1
	Wando-gun, Jeollanam-do, Korea	3
	Yeosu-si, Jeollanam-do, Korea	1
	Ulju-gun, Ulsan-si, Korea	1
	Andreyevka, Primorsky, Russia	3
4. <i>Pugettia incisa</i>	Gijang-gun, Busan-si, Korea	4
	Pohang-si, Gyeongsangbuk-do, Korea	1
	Seogwipo-si, Jeju-do, Korea	1
5. <i>Pugettia intermedia</i>	Gijang-gun, Busan-si, Korea	1
	Yeongdo-gu, Busan-si, Korea	1
	Boryeong-si, Chungcheongnam-do, Korea	5
	Seocheon-gun, Chungcheongnam-do, Korea	8
	Gunsan-si, Jeollabuk-do, Korea	7
	Yeosu-si, Jeollanam-do, Korea	6

Table 1. Continued.

Species	Locality	Individuals
6. <i>Pugettia marissinica</i>	Seogwipo-si, Jeju-do, Korea	1
7. <i>Pugettia nipponensis</i>	Seogwipo-si, Jeju-do, Korea	2
8. <i>Pugettia quadridens</i>	Gijang-gun, Busan-si, Korea	1
	Haeundae-gu, Busan-si, Korea	1
	Samcheok-si, Gangwon-do, Korea	2
	Uljin-gun, Gyeongsangbuk-do, Korea	2
	Ulleung-gun, Gyeongsangbuk-do, Korea	1
	Jeju-si, Jeju-do, Korea	5
	Seogwipo-si, Jeju-do, Korea	12
	Dong-gu, Ulsan-si, Korea	1
9. <i>Pugettia vulgaris</i>	Taeon-gun, Chungcheongnam-do, Korea	1
	Gijang-gun, Busan-si, Korea	1
	Saha-gu, Busan-si, Korea	1
	Pohang-si, Gyeongsangbuk-do, Korea	4
	Uljin-gun, Gyeongsangbuk-do, Korea	1
	Ulleung-gun, Gyeongsangbuk-do, Korea	1
	Jeju-si, Jeju-do, Korea	1
	Seogwipo-si, Jeju-do, Korea	4
	Sinan-gun, Jeollanam-do, Korea	1
	Ulju-gun, Ulsan-si, Korea	1
10. <i>Xenocarcinus conicus</i>	Seogwipo-si, Jeju-do, Korea	2
11. <i>Hyastenus elongatus</i>	Gijang-gun, Busan-si, Korea	1
	Pohang-si, Gyeongsangbuk-do, Korea	1
	Ulleung-gun, Gyeongsangbuk-do, Korea	1
	Seogwipo-si, Jeju-do, Korea	8
12. <i>Hyastenus pleione</i>	Boryeong-si, Chungcheongnam-do, Korea	1
13. <i>Naxioides robillardi</i>	Seogwipo-si, Jeju-do, Korea	3

Table 1. Continued.

Species	Locality	Individuals
14. <i>Scyra compressipes</i>	Gangneung-si, Gangwon-do, Korea	1
	Goseong-gun, Gangwon-do, Korea	8
	Pohang-si, Gyeongsangbuk-do, Korea	3
	Yeongdeok-gun, Gyeongsangbuk-do, Korea	1
	Nam-gu, Pohang-si, Korea	1
15. <i>Paratymolus pubescens</i>	Wando-gun, Jeollanam-do, Korea	1
16. <i>Achaeus japonicus</i>	Pohang-si, Gyeongsangbuk-do, Korea	3
	Seogwipo-si, Jeju-do, Korea	2
17. <i>Achaeus lacertus</i>	Tongyeong-si, Gyeongsangnam-do, Korea	1
	Wando-gun, Jeollanam-do, Korea	1
18. <i>Achaeus spinosus</i>	Seogwipo-si, Jeju-do, Korea	2
19. <i>Achaeus tuberculatus</i>	Seogwipo-si, Jeju-do, Korea	4
20. <i>Cyrtomaia platypes</i>	Seogwipo-si, Jeju-do, Korea	1
21. <i>Platymaia wyvillethomsoni</i>	Suyeong-gu, Busan-si, Korea	4
22. <i>Pyromaia tuberculata</i>	Pohang-si, Gyeongsangbuk-do, Korea	1
	Geoje-si, Gyeongsangnam-do, Korea	2
	Tongyeong-si, Gyeongsangnam-do, Korea	1
23. <i>Entomonox spinosus</i>	Seogwipo-si, Jeju-do, Korea	3
24. <i>Leptomithrax bifidus</i>	Jeju-si, Jeju-do, Korea	2
	Seogwipo-si, Jeju-do, Korea	1
25. <i>Leptomithrax edwardsii</i>	Seogwipo-si, Jeju-do, Korea	6
26. <i>Micippa platipes</i>	Jeju-si, Jeju-do, Korea	1
	Seogwipo-si, Jeju-do, Korea	2

Table 1. Continued.

Species	Locality	Individuals
27. <i>Micippa thalia</i>	Nam-gu, Busan-si, Korea	1
	Saha-gu, Busan-si, Korea	1
	Yeongdo-gu, Busan-si, Korea	1
28. <i>Prismatopus longispinus</i>	Seogwipo-si, Jeju-do, Korea	1
29. <i>Pseudomicippe nipponica</i>	Seogwipo-si, Jeju-do, Korea	2
30. <i>Sakaija japonica</i>	Seogwipo-si, Jeju-do, Korea	6
31. <i>Sakaija sakaii</i>	Seogwipo-si, Jeju-do, Korea	1
32. <i>Schizophroida simodaensis</i>	Ulleung-gun, Gyeongsangbuk-do, Korea	1
	Seogwipo-si, Jeju-do, Korea	2
33. <i>Chionoecetes japonicus</i>	Goseong-gun, Gangwon-do, Korea	1
	Yeongdeok-gun, Gyeongsangbuk-do, Korea	1
34. <i>Chionoecetes opilio</i>	Goseong-gun, Gangwon-do, Korea	2
	Pohang-si, Gyeongsangbuk-do, Korea	1
35. <i>Hyas coarctatus</i>	Gangneung-si, Gangwon-do, Korea	2
	Goseong-gun, Gangwon-do, Korea	4
	Samcheok-si, Gangwon-do, Korea	1
	Sokcho-si, Gangwon-do, Korea	2
	Yangyang-gun, Gangwon-do, Korea	4
	Uljin-gun, Gyeongsangbuk-do, Korea	1
36. <i>Oregonia gracilis</i>	Suyeong-gu, Busan-si, Korea	3
37. <i>Pleistacantha oryx</i>	Seogwipo-si, Jeju-do, Korea	1
38. <i>Pleistacantha sanctijohannis</i>	Gyeongsangnam-do, Korea	1
	Seogwipo-si, Jeju-do, Korea	4

1.3. Results

List of Korean majoid crabs

The species name marked with an Asterisk (*) indicates newly reported species from Korea in this study.

Infraorder Brachyura Latreille, 1802 단미하목

Superfamily Majoidea Samouelle, 1819 물맞이게상과

Family Epialtidae MacLeay, 1838 빨물맞이게과

Subfamily Epialtinae MacLeay, 1838 빨물맞이게아과

Genus *Huenia* De Haan, 1837 외빨게속

1. *Huenia heraldica* (De Haan, 1837) 외빨게

Genus *Menaethius* H. Milne-Edwards, 1834 일각게속

2. *Menaethius monoceros* (Latreille, 1825) 일각게

Genus *Pugettia* Dana, 1851 빨물맞이게속

3. *Pugettia ferox* Ohtsuchi & Kawamura, 2019 빨물맞이게

4. *Pugettia incisa* (De Haan, 1839) 오늬이마물맞이게

5. *Pugettia intermedia* Sakai, 1938 중간빨물맞이게

*6. *Pugettia marissinica* Takeda & Miyake, 1972 애기빨물맞이게

7. *Pugettia minor* Ortmann, 1893 꼬마물맞이게

*8. *Pugettia nipponensis* Rathbun, 1932 긴다리빨물맞이게

9. *Pugettia pellucens* Rathbun, 1932 꼬마빨물맞이게

*10. *Pugettia quadridens* (De Haan, 1839) 매끈이빨물맞이게

11. *Pugettia vulgaris* Ohtsuchi, Kawamura & Takeda, 2014 잔털빨물맞이게

Genus *Xenocarcinus* White, 1847 물방울물맞이게속

12. *Xenocarcinus conicus* (A. Milne-Edwards, 1865) 물방울물맞이게

Subfamily Pisinae Dana, 1851 어리물맞이게아과

Genus *Hoplophrys* Hendersen, 1893 연산호빨게속

13. *Hoplophrys oatesii* Henderson, 1893 연산호빨게

Genus *Hyastenus* White, 1847 빨게속

14. *Hyastenus diacanthus* (De Haan, 1839) 빨게

15. *Hyastenus elongatus* Ortmann, 1893 박빨게

16. *Hyastenus pleione* (Herbst, 1803) 긴빨게

Genus *Naxioides* A. Milne-Edwards, 1865 긴가시빨게속

*17. *Naxioides robillardi* (Miers, 1882) 긴가시빨게

Genus *Oxypleurodon* Miers, 1886 세모뿔게속

18. *Oxypleurodon stimpsoni* Miers, 1885 세모뿔게

Genus *Pisoides* H. Milne-Edwards, 1843 어리물맞이게속

19. *Pisoides bidentatus* (A. Milne-Edwards, 1873) 어리물맞이게

Genus *Scyra* Dana, 1851 납작뿔게속

20. *Scyra compressipes* Stimpson, 1857 납작뿔게

Family Inachidae MacLeay, 1838 거미다리게과

Genus *Litosus* Loh and Ng, 1999

21. *Litosus sexspinosus* (Miers, 1884) 매끈콩알게

Genus *Paratymolus* Miers, 1879

22. *Paratymolus pubescens* Miers, 1879 콩알게

Subfamily Inachinae MacLeay, 1838

Genus *Achaeus* Leach, 1817 아케우스게속

23. *Achaeus japonicus* (De Haan, 1839) 아케우스게

24. *Achaeus lacertosus* Stimpson, 1858 가시이마아케우스게

25. *Achaeus spinosus* Miers, 1879 가시아케우스게

26. *Achaeus tuberculatus* Miers, 1879 가는다리아케우스게

Genus *Cyrtomaia* Miers, 1886 애기거미다리게속

*27. *Cyrtomaia platypes* Yokoya, 1933 애기거미다리게

Genus *Platymaia* Miers, 1885

28. *Platymaia wyvillethomsoni* Miers, 1885 거미다리게

Family Inachoididae Dana, 1851 한뿔두드럭게과

Subfamily Inachoidinae Dana, 1851

Genus *Pyromaia* Stimpson, 1871 한뿔두드럭게속

29. *Pyromaia tuberculata* (Lockington, 1877) 한뿔두드럭게

Family Majidae Samouelle, 1819 물맞이게과

Subfamily Majinae Samouelle, 1819 물맞이게아과

Genus *Entomonyx* Miers, 1884 가시뿔게속

30. *Entomonyx spinosus* Miers, 1884 가시뿔게

Genus *Holthuija* Ng and Richer de Forges, 2015

31. *Holthuija cognata* Ng & Richer De Forges, 2015 애기털다리게

Genus *Leptomithrax* Miers, 1876 두드럭게속

32. *Leptomithrax bifidus* (Ortmann, 1893) 가시두드럭게

33. *Leptomithrax edwardsii* (De Haan, 1835) 두드럭게

Genus *Micippa* Leach, 1817 누덕웃게속

- 34. *Micippa cristata* (Linnaeus, 1758) 가시누덕웃게
- 35. *Micippa philyra* (Herbst, 1803) 꼬마누덕웃게
- 36. *Micippa platipes* Rüppell, 1830 입술이마누덕웃게
- 37. *Micippa thalia* (Herbst, 1803) 누덕웃게

Genus *Paramaya* De Haan, 1837 털다리게속

- 38. *Paramaya spinigera* (De Haan, 1837) 털다리게

Genus *Prismatopus* Ward, 1933 뿔가시뿔게속

- 39. *Prismatopus longispinus* (De Haan, 1839) 뿔가시뿔게

Genus *Pseudomicippe* Heller, 1861 어리누덕웃게속

- 40. *Pseudomicippe nipponica* (Sakai, 1937) 제주어리누덕웃게
- 41. *Pseudomicippe okamotoi* (Sakai, 1938) 어리누덕웃게

Genus *Sakaija* Ng & Richer de Forges, 2015 애기물맞이게속

- *42. *Sakaija japonica* (Rathbun, 1932) 애기물맞이게
- *43. *Sakaija sakaii* (Takeda & Miyake, 1969) 날씬이애기물맞이게

Genus *Schizophroida* Griffin & Tranter, 1986 톱니물맞이게속

- *44. *Schizophroida simodaensis* Sakai, 1933 톱니물맞이게

Family Oregoniidae Garth, 1958 긴집게발게과

Subfamily Oregoniinae Garth, 1958

Genus *Chionoecetes* Krøyer, 1838 대게속

45. *Chionoecetes japonicus* Rathbun, 1932 홍게

46. *Chionoecetes opilio* (O. Fabricius, 1788) 대게

Genus *Hyas* Leach, 1814 두꺼비게속

47. *Hyas alutaceus* Brandt, 1851 바이올린두꺼비게

48. *Hyas coarctatus* Leach, 1815 두꺼비게

Genus *Oregonia* Dana, 1851 긴집게발게속

49. *Oregonia gracilis* Dana, 1851 긴집게발게

Subfamily Pleistacanthinae Števcíć, 2005

Genus *Pleistacantha* Miers, 1879 삼천가시게속

*50. *Pleistacantha oryx* Ortmann, 1893 사슴삼천가시게

51. *Pleistacantha sanctijohannis* Miers, 1879 삼천가시게

A key to Korean majoid crabs

1. Orbits absent or with narrow, weakly developed supraorbital eave and postorbital lobe; basal antennal article slender (at most twice as long as broad) 2
 - Orbits present, formed by supraorbital eave, nearby spines, and postorbital spine or lobe; basal antennal article broad (at most twice as long as broad) 31 (Majidae)

2. Abdomen of male not terminally broadened; telson subtriangular (in *Pyromaia tuberculata*, sixth segment and telson fused to appear hexagonal), not inserted deeply into sixth segment 3
 - Abdomen of male often broad; telson subquadrate, inserted deeply into sixth segment 45 (Oregoniidae)

3. Orbits with narrow, weakly developed supraorbital eave partially exposed eyes; basal antennal article not extremely slender, immovable 4 (Epialtidae)
 - Orbits absent; basal antennal article extremely slender, sometimes movable 23 (Inachidae and Inachoididae)

Epialtidae

4. Postorbital lobe absent or present but not cupped; intercalated spine absent 5 (Epialtinae)
 - Postorbital process prominent, often cupped to receive the retracted eyestalk; intercalated spine sometimes present 16 (Pisinae)

- 5. Carapace with frontal projection single or bifurcate at tip..... 6
 - Carapace with frontal projection two spines, divergent..... 8

- 6. Carapace elongated oval; rostrum stout, conical; preorbital spine absent.....
 - *Xenocarcinus conicus*
 - Carapace subtriangular (in female of *Huenia heraldica*, hepatic lobe extremely expanded); rostrum slender; preorbital spine prominent 7

- 7. Cross-section of the rostrum triangular; carpus and merus of the cheliped and ambulatory legs with crest; sexual dimorphism *Huenia heraldica*
 - Cross-section of the rostrum tetragonal; carpus and merus of the cheliped and ambulatory legs without crest..... *Menaethius monoceros*

- 8. Postorbital and hepatic spines distinctly separated 9
 - Postorbital and hepatic spines completely or incompletely fused 11

- 9. Cardiac and intestinal regions each with one prominent spine *Pugettia minor*
 - Cardiac and intestinal regions each with one tubercle 10

- 10. Carapace covered with short setae sparsely; epibranchial region without tubercle
 - *Pugettia marissinica*
 - Carapace covered with dense tomentum; epibranchial region with tubercles.....
 - *Pugettia nipponensis*

11. Postorbital and hepatic spines completely fused; in male, G1 with ventral lobe vestigial
 *Pugettia incisa*
- Postorbital and hepatic spines incompletely fused; in male, G1 with ventral lobe distinct
 12
12. Gastric and branchial regions without tubercles; supraorbital eave nearly horizontal.. 13
- Gastric and branchial regions with tubercles; supraorbital eave inclined..... 14
13. Pseudorostrum 0.4–0.5 times as long as pcl; hepatic spine distinctly larger than
 postorbital spine; ischium of cheliped with blunt ridge on mesial surface
 *Pugettia pellucens*
- Pseudorostrum 0.3–0.4 times as long as pcl; hepatic and postorbital spines subequal
 size or hepatic spine slightly larger than postorbital spine; ischium of cheliped rounded
 mesially..... *Pugettia vulgaris*
14. Mesobranchial region with two faint tubercles; metabranchial region smooth; carpus of
 cheliped with dorsal ridge unarmed *Pugettia quadridens*
- Mesobranchial region with two or three distinct tubercles; metabranchial region with
 one tubercle; carpus of cheliped with dorsal ridge dentate or tuberculate 15
15. Protogastric tubercles more separated from mesogastric tubercle than from metagastric
 tubercle; in male, G1 with mesial lobe as long as dorsal lobe; in female, gonopore
 elongated transversely *Pugettia intermedia*
- Protogastric tubercles separated equally from mesogastric tubercle than from
 metagastric tubercle; in male, G1 with mesial lobe shorter than dorsal lobe; in female,
 gonopore comma-shaped *Pugettia ferox*

16. Pseudorostrum very long (at least 0.33 times as long as pcl) and slender, beak-like or lyre-shaped 17
- Pseudorostrum short, various form 21
17. Carapace triangular, regions separated into distinct plates *Oxypleurodon stimpsoni*
- Carapace pyriform, regions separated by groove 18
18. Carapace covered with numerous, various size of spines; pseudorostrum with one accessory spine dorsally *Naxioides robillardi*
- Carapace unarmed or with spines rarely; pseudorostrum without accessory spine dorsally 19
19. Dorsal surface of branchial region with tubercles *Hyastenus pleione*
- Dorsal surface of branchial region without tubercles 20
20. Branchial region with a distinct epibranchial spine *Hyastenus diacanthus*
- Branchial region smooth, unarmed *Hyastenus elongates*
21. Dorsal surface carapace armed with distinct spines *Hoplophrys oatesii*
- Dorsal surface carapace with some granules 22
22. Carapace subcircular; pseudorostrum very short, tapered anteriorly *Pisoides bidentatus*
- Carapace triangular; pseudorostrum broad, tapered and acute anteriorly *Scyra compressipes*

Inachidae and Inachoididae

23. Carapace subcircular 24
- Carapace not subcircular..... 25
24. Eyestalk long, slender; basal antennal article immovable; second to fourth ambulatory legs with dactylus cylindrical *Cyrtomaia platypes*
- Eyestalk short, robust; basal antennal article movable; second to fourth ambulatory legs with dactylus flatten, slightly broaden distally..... *Platymaia wyvillethomsoni*
25. Carapace pentagonal; carpus of cheliped with long single spine 26
- Carapace pyriform; carpus of cheliped unarmed or with several spines or tubercles... 27
26. Carapace and posterolateral margin unarmed; cheliped with carpus having relatively short and stout spine *Litosus sexspinosus*
- Carapace and posterolateral margin tuberculated; cheliped with carpus having relatively long and slender spine *Paratymolus pubescens*
27. Carapace with frontal projection single, acute distally..... *Pyromaia tuberculata*
- Carapace with frontal projection very short, bifurcate 28
28. Carapace with dorsal surface unarmed..... 29
- Carapace with dorsal surface with prominent tubercles or spinules..... 30

29. Hepatic region moderately expanded laterally; third and the fourth ambulatory legs with dactyli slightly curved *Achaeus japonica*
- Hepatic region prominent expanded laterally; third and the fourth ambulatory legs with dactyli strongly curved *Achaeus lacertosus*
30. Carapace with gastric and cardiac regions each having one tubercle; third and the fourth ambulatory legs of dactyli slightly curved *Achaeus tuberculatus*
- Carapace with gastric and cardiac regions having one gastric, two cardiac, and two baranchial tubercles; the third and the fourth ambulatory legs with dactyli strongly curved *Achaeus spinosus*

Majidae

31. Basal antennal article broader than long 32
- Basal antennal article longer than broad or as long as broad 35
32. Pseudorostrum divided into two lobes 33
- Pseudorostrum divided into four lobes 34
33. Orbit closed below; pseudorostrum with lateral margin having numerous spines *Micippa cristata*
- Orbit open below; pseudorostrum with lateral margin unarmed *Micippa thalia*
34. Orbit open below; basal antennal article smooth; carapace with anterolateral border having eight to ten spines *Micippa platipes*
- Orbit open below; basal antennal article granulated; carapace with anterolateral border having eight to ten spines *Micippa philyra*

35. Antennal flagellum positioned outside of orbit	36
– Antennal flagellum positioned inside of orbit.....	42
36. Supraorbital eave with two preorbital spines; antorbital spine present.....	37
– Supraorbital eave unarmed; antorbital spine prominent	38
37. Pseudorostrum short, acute distally, straight, markedly deflexed··	<i>Entomonyx spinosus</i>
– Pseudorostrum long, curved outward, knobbed distally	<i>Prismatopus longispinus</i>
38. Dorsal surface of carapace with hooked setae; pseudorostrum deflexed, slightly curved outward.....	39
– Dorsal surface of carapace without hooked setae; pseudorostrum horizontal, straight	40
39. Pseudorostrum strongly deflexed; movable finger of cheliped serrated	
.....	<i>Pseudomicippe nipponica</i>
– Pseudorostrum slightly deflexed; movable finger of cheliped armed with a stout tooth near the middle	<i>Pseudomicippe okamotoi</i>
40. Carapace with dorsal surface nearly smooth	<i>Schizophroida simodaensis</i>
– Carapace granulated.....	41
41. Carapace subtriangular; postorbital spine bifid at the tip of the spine.....	
.....	<i>Leptomithrax bifidus</i>
– Carapace subcircular; postorbital spine single at the tip of the spine.....	
.....	<i>Leptomithrax edwardsii</i>

42. Merus of ambulatory legs with strong subdistal spine dorsally..... *Paramaya spinigera*
 – Merus of ambulatory legs unarmed dorsally 43
43. Suborbital margin distinctly separated from margin of postorbital tooth by clear deep fissures or cleft.....*Holthuija cognata*
 – Suborbital margin fused with margin of postorbital tooth, not separated by fissure or cleft 44
44. Carapace with more strongly inflated branchial region; ambulatory legs (particularly the merus) relatively shorter and stouter; in male, G1 strongly curved.....
 *Sakaija japonica*
 – Carapace with moderately inflated branchial region; ambulatory legs (particularly the merus) relatively slender and longer; in male, G1 gently curved.....*Sakaija sakaii*

Oregoniidae

45. Abdomen of male with fifth segment broader than sixth segment..... 46
 – Abdomen of male with sixth segment broader than fifth segment..... 49
46. Carapace subcircular; carapace and ambulatory legs almost unarmed; orbits incomplete; ambulatory legs flattened..... 47
 – Carapace pyriform; carapace and ambulatory legs covered with extremely numerous spines; orbits absent; ambulatory legs cylindrical..... 48
47. Posterior part of carapace with slope steep; live color dark red.....
 *Chionoecetes japonicus*
 – Posterior part of carapace with slope gentle; live color light brown.....
 *Chionoecetes opilio*

48. Pseudorostrum appressed in proximal half to three-quarters, strongly upward; carapace spinulose, with a few prominent spines dorsally and on anterior and posterior branchial margins *Pleistacantha sanctijohannis*
- Pseudorostrum separate and divergent from base, horizontal; carapace spinulose, with prominent dorsal spines, without prominent spines on anterior and posterior branchial margins *Pleistacantha oryx*
49. Pseudorostrum very slender and long, slightly outward distally *Oregonia gracilis*
- Pseudorostrum short, broad, tapered distally 50
50. Pseudorostrum relatively shorter and broader; width of anterior third of carapace wide *Hyas alutaceus*
- Pseudorostrum relatively long; width of anterior third of carapace narrow *Hyas coarctatus*

Taxonomic accounts

Infraorder Brachyura Latreille, 1802 단미하목

Superfamily Majoidea Samouelle, 1819 물맞이게상과

Family Epialtidae MacLeay, 1838 빨물맞이게과

Subfamily Epialtinae MacLeay, 1838 빨물맞이게아과

Genus *Huenia* De Haan, 1837 외빨게속

1. *Huenia heraldica* (De Haan, 1837) (Figs 4, 5) 외빨게

Maja (Huenia) heraldica De Haan, 1837: pl. 23, fig. 6.

Maja (Huenia) elongate De Haan, 1839: pl. 23, figs 4, 5.

Maja (Huenia) proteus De Haan, 1839: 95, fig. G.

Huenia proteus—Adams & White, 1848: 21, pl. 4, figs 4–7; Miers, 1886: 35; Henderson, 1893: 341; Ortmann, 1893: 40; De Man, 1902: 662; Sakai, 1938: 264, fig. 31, pl. 26, figs 4, 5; 1965: 75, pl. 34, figs 1, 2; 1976: 207, fig. 112a–c, pl. 71, fig. 1, 2; 1974: 14; Kim & Park, 1972: 62; Kim, 1973: 532, 665, fig. 249, pl. 104, fig. 195a–d; 1977: 208; Griffin, 1976: 190; Kim & Kim, 1982: 146; Kim & Chang, 1985: 49; Griffin & Tranter, 1986: 84, fig. 24c, d; Dai & Yang, 1991: 133, fig. 68(2), pl. 15(1, 2).

Huenia brevirostrate Dana, 1852: 134.

Huenia heraldica—Holthuis, 1987: 15; Ko & Lee, 2015: 13, pl. 1.

Material examined

Three males (pcl 18.3–20.8 mm), Seogwipo-si, Jeju-do, Korea, 8 Aug. 1970; 1 female (pcl 16.3 mm), 1 male (pcl 18.7 mm), Beophwan-dong, Seogwipo-si, Jeju-do, Korea, 22 Oct. 1991; 1 female (pcl 13.6 mm), Hallim-eup, Jeju-si, Jeju-do, Korea, 33°25'10.77"N, 126°13'27.02"E, 16 Oct. 2018, coll. by SCUBA diving.

Diagnosis of male

Carapace subtriangular, smooth. Gastric region with three tubercles forming inverted triangle. Cardiac region with one tubercle. Rostrum single, long, acute distally, with numerous setae on dorsal surface, cross-section triangular. Preorbital spine prominent, acute distally. Hepatic margin with rudimentary lobe. Branchial margin with triangular lobe. Cheliped stout, smooth, shorter than first ambulatory leg; carpus and merus crested. Ambulatory legs compressed, crested.

Diagnosis of female

Carapace broader than long. Hepatic margin with very large and broad lobe. Branchial margin with well developed lobe. Pseudorostrum single, shorter than that of male. Cheliped slender.

Type locality

Japan.

Habitat

Subtidal, weedy pebbles, up to 50 m deep.



Fig. 4. *Huenia heraldica* (De Haan, 1837). Male (pcl 18.3 mm), dorsal view.

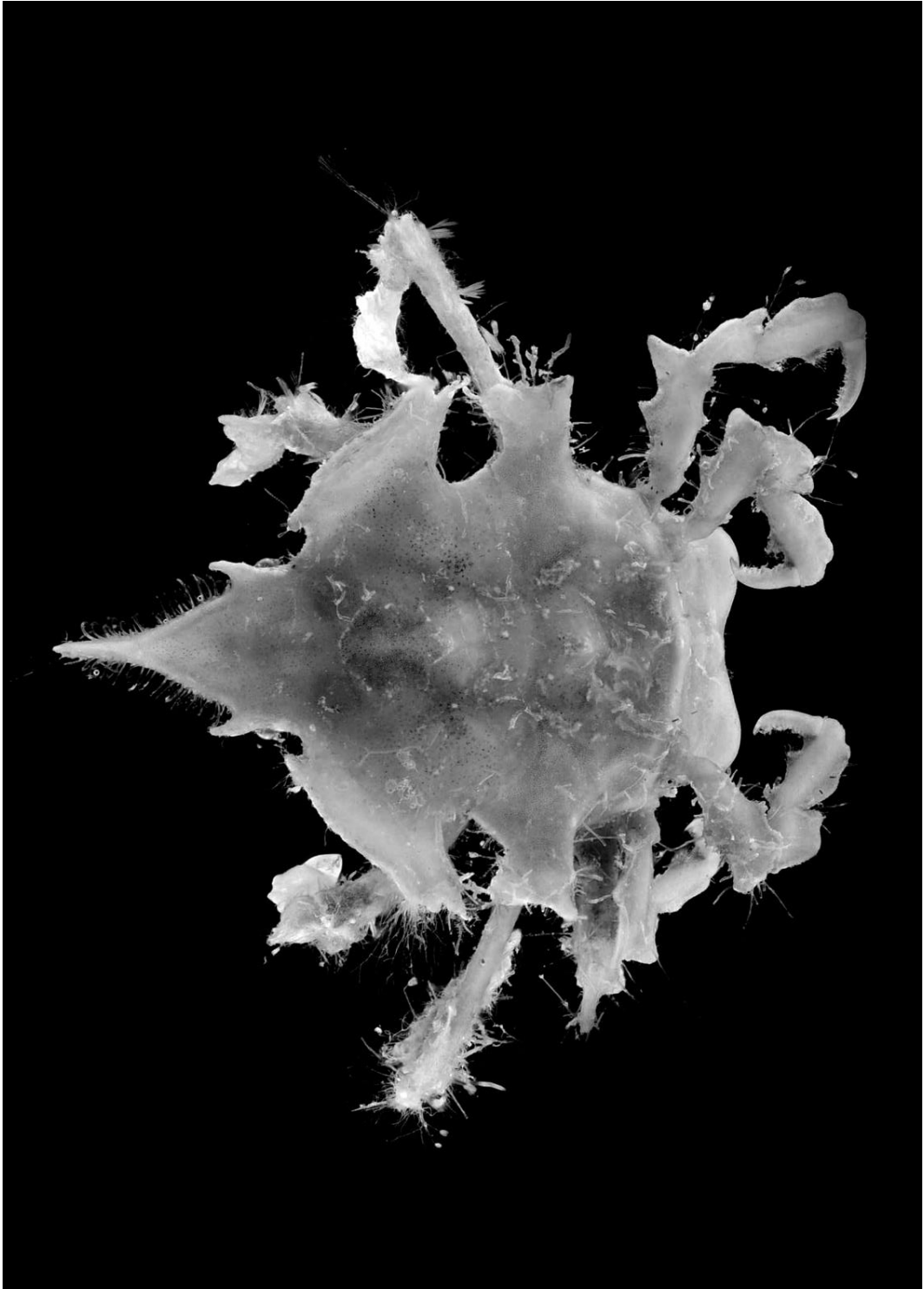


Fig. 5. *Huenia heraldica* (De Haan, 1837). Female (pcl 13.6 mm), dorsal view.

Distribution

This species is widely distributed in the Indo-Pacific region from the eastern coast of Africa to Hawaii (Fig. 6).

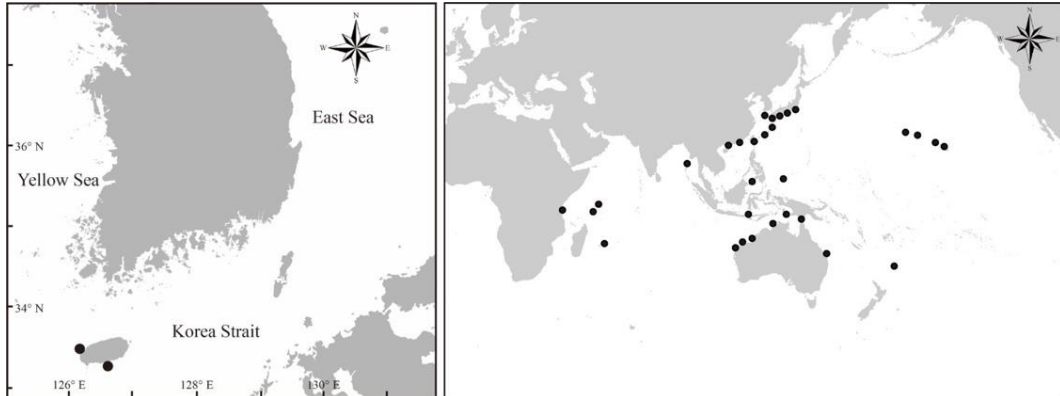


Fig. 6. Distribution of *Huenia heraldica* (De Haan, 1837).

Remark

Huenia heraldica (De Haan, 1837) exhibits very high sexual dimorphism. In males, the hepatic lobe is relatively small, while in females, it becomes much larger and broader.

In the Korean fauna, male *Huenia heraldica* is similar to *Menaethius monoceros* (Latreille, 1825). The differences between the two species are described under *M. monoceros*.

2. *Menaethius monoceros* (Latreille, 1825) (Fig. 8) 일각계

Pisa monoceros Latreille, 1825: 139.

Inachus arbutus Rüppell, 1830: 24, pl. 5, fig. 5, pl. 6, fig. 19.

Menaethius monoceros—H. Milne-Edwards, 1834: 339, pl. 15, figs 12, 13; 1862: 6; Ortmann, 1893: 41; Doflein, 1904: 78; Chopra, 1931: 324; Sakai, 1934: 294; 1938: 263, pl. 26, fig. 3; 1965: 74, pl. 33, fig. 4; 1976: 205, pl. 70, fig. 1; Buitendijk, 1939: 237; Griffin, 1974: 21; 1976: 200; Kim & Chang, 1985: 47, fig. 3; Griffin & Tranter, 1986: 89; Dai & Yang, 1991: 132, fig. 68(1), pl. 14(8); Ng et al., 2008: 101 (list); Ko & Lee, 2015: 15, pls. 2, 3.

Material examined

Two males (pcl 15.6 mm, 15.8 mm), Gujwa-eup, Jeju-si, Jeju-do, Korea, 33°32'21.6"N, 126°50'16.39"E, 8 Aug. 2018; 2 males (pcl 9.9 mm, 12.5 mm), Yeongdeok-gun, Gyeongsangbuk-do, Korea, 36°30'45.26"N, 129°26'56.84"E, 22 Nov. 2018; 13 males (pcl 16.1–9.8 mm), 9 females (pcl 14.3–8.9 mm), Seongsan-eup, Seogwipo-si, Jeju-do, Korea, 33°27'33.95"N, 126°56'8.45"E, 4 Jul. 2019; 1 male (pcl 8.6 mm), 1 female (pcl 12.5 mm), Yerae-dong, Seogwipo-si, Jeju-do, Korea, 33°14'25.68"N, 126°23'48.4"E, 4 Jul. 2019.

Diagnosis

Carapace subtriangular, smooth. Gastric region with three tubercles. Cardiac and intestinal regions each with one tubercle. Branchial region with one tubercle. Rostrum single, long, bifid at tip, with numerous hooked setae on dorsal surface, cross-section tetragonal.

Preorbital spine prominent, triangular. Hepatic margin with one blunt tubercle. Branchial margin with two blunt spines, anterior one weak, posterior one prominent. Cheliped long, smooth; fingers short. Ambulatory legs shorter than cheliped.

Type locality

Unknown.

Habitat

Intertidal rocky shore, weedy pebbles.

Distribution

This species is widely distributed in the Indo-Pacific region from the eastern coast of Africa to Tahiti (Fig. 7).

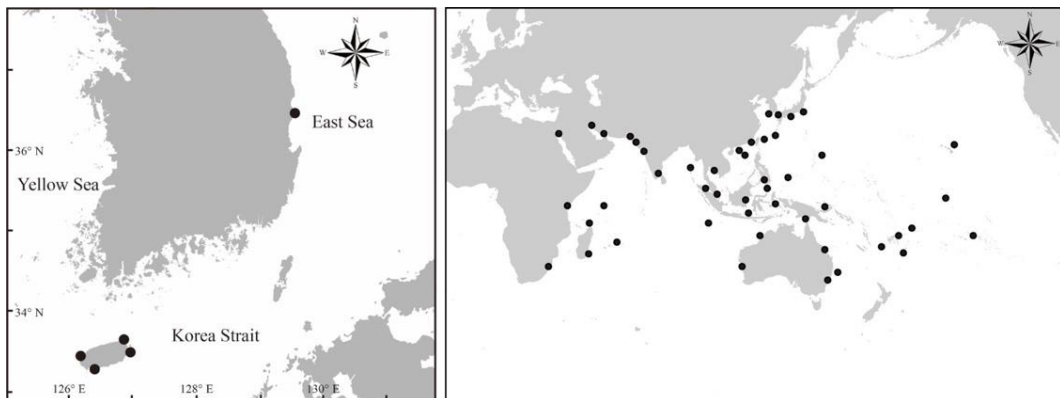


Fig. 7. Distribution of *Menaethius monoceros* (Latreille, 1825).



Fig. 8. *Menaethius monoceros* (Latreille, 1825). Male (pcl 14.9 mm), dorsal view.

Remark

Menaethius monoceros (Latreille, 1825) has very wide distribution range and large variations have been reported. Two specimens of *M. monoceros* were found in Yeongdeok. The region appears to be the northern limit of distribution of the species. Most of the species are observed in intertidal rocky shores and among algae at depths within 50 m, however, Chopra (1931) recorded a *M. monoceros* specimen sampled from the cloaca of a Holothurian. The examined specimens were found in the intertidal rocky shore and among weedy pebbles.

Menaethius monoceros is often misidentified for *Huenia heraldica* in Korea. However, *M. monoceros* can be distinguished from *H. heraldica* based on the following morphological characteristics: (1) cross-section of the pseudorostrum tetragonal (triangular in *H. heraldica*), (2) carpus and merus of the cheliped and ambulatory legs without crest (with crest in *H. heraldica*).

3. *Pugettia ferox* Ohtsuchi & Kawamura, 2019 (Fig. 9) 뿔물맞이게

Pugettia quadridens—Kamita, 1941: 65, text-fig. 28; Kim, 1973: 530, pl. 53 fig. 194; Griffin & Tranter, 1986: 97 (in part), fig. 28e, f; Dai & Yang, 1991: 129, pl. 14 (4), fig. 66 (2); Lee et al., 2014: 47, figs 3A, 4A; Ko & Lee, 2015: 19, figs 1B, 2A, B, pls. 11, 12. [Not *Pisa (Halimus) quadridens* De Haan, 1837]

Pugettia quadridens quadridens—Kim & Kim, 2001: 53, figs 45, 46. [Not *Pisa (Halimus) quadridens* De Haan, 1837]

Pugettia quadridens intermedia—Kim & Kim, 1998: 302, figs 1, 2. [Not *Pugettia quadridens intermedia* Sakai, 1938]

Pugettia ferox Ohtsuchi & Kawamura, 2019: 34, figs 26–38.

Material examined

One male (pcl 12.9 mm), Taean-gun, Chungcheongnam-do, Korea, 36°44'28.92"N, 126°8'1.8"E, 15 Oct. 2015; 1 male (pcl 14.9 mm), Gangneung-si, Gangwon-do, Korea 23 Oct. 2015; 1 male (pcl 11.8 mm), Taean-gun, Chungcheongnam-do, Korea 24 Feb. 2016; 1 male (pcl 15.4 mm), Uljin-gun, Gyeongsangbuk-do, Korea 6 Apr. 2017; 1 male (pcl 20.8 mm), Pohang-si, Gyeongsangbuk-do, Korea, 36°9'17.86"N, 129°24'2.01"E, 13 Jul. 2017; 1 male (pcl 22.3 mm), Goseong-gun, Gangwon-do, Korea, 10 Aug. 2017; 1 male (pcl 22.3 mm), Suyeong-gu, Busan-si, Korea, 35°8'16.72"N, 129°6'51.57"E, 21 Feb. 2018; 1 male (pcl 18.1 mm), Gangneung-si, Gangwon-do, Korea, 37°52'6.70"N, 128°51'26.40"E, 18 Apr. 2018; 3 males (pcl 15.4–18.2 mm), Tongyeong-si, Gyeongsangnam-do, Korea, 34°47'33.75"N, 128°22'54.56"E, 17 May 2018; 2 males (pcl 15.2, 15.2 mm), Wando-gun,

Jeollanam-do, Korea, 34°19'37.8"N, 126°48'54.24"E, 28 Aug. 2018; 1 male (pcl 29.6 mm), Pohang-si, Gyeongsangbuk-do, Korea, 36°12'27.2"N, 129°22'38.26"E, 27 Mar. 2019; 1 male (pcl 22.6 mm), Saha-gu, Busan-si, Korea, 35°3'17.37"N, 128°58'20.98"E, 10 Apr. 2019; 1 male (pcl 20.1 mm), Tongyeong-si, Gyeongsangnam-do, Korea, 34°45'30.86"N, 128°30'49.21"E, 21 May 2015; 1 female (pcl 28.9 mm), Seocheon-gun, Chungcheongnam-do, Korea, 36°44'28.92"N, 126°8'1.8"E, 1 Aug. 2019; 1 male (pcl 12.9 mm), Yeosu-si, Jeollanam-do, Korea, 34°35'32.42"N, 127°45'56.43"E, 22 Oct. 2019.

Comparative materials—Three males (pcl 18.0–22.5 mm), Andreyevka, Primorsky, Russia, 8 Oct. 2019.

Diagnosis

Carapace subtriangular, smooth, regions regularly distinct. Gastric region convex. Cardiac and intestinal regions separated. Mesobranchial region with 2–3 tubercles. Metabranchial region with one tubercle. Pseudorostrum acute distally, 0.2–0.3 times as long as pcl. Preorbital spine prominent, triangular. Supraorbital eave with lateral margin sinuous. Postorbital spine slightly smaller than hepatic spine, and incompletely fused with hepatic spine, both spines acute distally. Third maxilliped with exopod narrowed in distal two-fifth. Chela stout; merus with three to six low teeth on dorsal surface (increasing distally in size); carpus with dorsal ridge tuberculate. Ambulatory legs slender, long, with outer margin of merus having one moderate tubercle distally. In male, G1 with mesial lobe shorter than dorsal lobe, separated with dorsal lobe moderate wide hiatus. In female, gonopore comma-shaped, short transversely.



Fig. 9. *Pugettia ferox* Ohtsuchi & Kawamura, 2019. Male (pcl 22.3 mm), dorsal view.

Type locality

Akahama, Otsuchi Bay, Japan.

Habitat

Intertidal rocky shore, weedy pebbles, intertidal to 80 m deep.

Distribution

Sea of Okhotsk, Japan, North China, and Korea (Fig. 10).

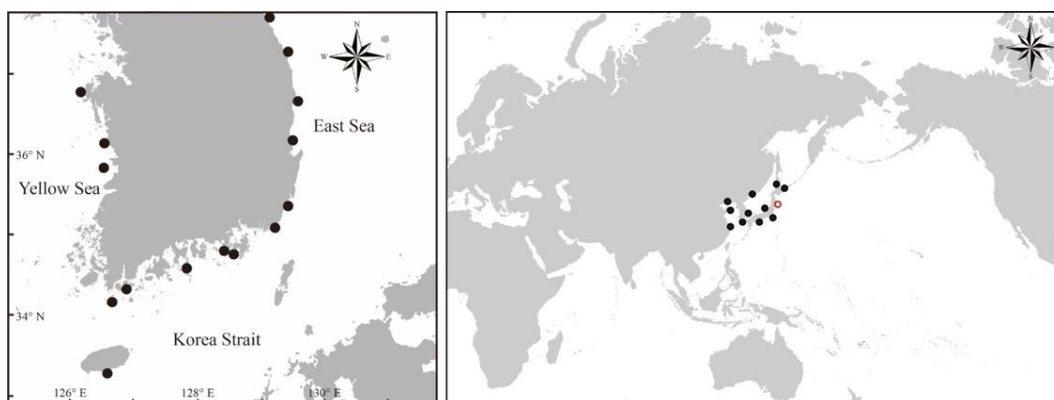


Fig. 10. Distribution of *Pugettia ferox* Ohtsuchi & Kawamura, 2019. Open circle=type locality.

Remark

Kamita (1941) reported the existence of *Pugettia quadridens* (De Haan, 1837) in Korea along with illustrations based on specimens collected from all waters of Korea. However, Ohtsuchi & Kawamura (2019) mentioned that *P. quadridens* reported by Kamita (1941) was similar to *P. ferox* and could potentially other species. The illustration by Kamita (1941) has the characteristics of *P. ferox* (protogastric tubercles separated equally from mesogastric tubercle than from metagastric tubercle), and the distribution he presented also consistent

with the distribution patterns of *P. ferox* in Korean waters. *Pugettia quadridens* reported by Kamita (1941) is considered *P. ferox* here. Most of the *P. quadridens* or *P. quadridens quadridens* reported in the Korean waters (Kim, 1973; Kim & Kim, 1998; Lee et al., 2014; Ko & Lee, 2015) after Kamita (1941) appear to be a misidentification of *P. ferox* (Ohtsuchi & Kawamura, 2019). Therefore, the Korean name ‘뿔물맞이게’, known as *P. quadridens* in Korea, is *P. ferox*.

The examined specimens were almost consistent with the original description (Ohtsuchi & Kawamura, 2019). Ohtsuchi & Kawamura (2019) mentioned that the pseudorostrum was 0.1–0.2 times as long as pcl. A morphological analysis 21 specimens (18 from Korea, 3 from Russia) revealed that *P. ferox* in the Korean waters ranged from 0.2–0.3 times as long as pcl except for one specimen.

Comparisons of DNA sequence of *COX1* among *Pugettia ferox*, *P. intermedia*, *P. quadridens*, and *P. vulgaris* (Table 2, Fig. 107) supported results of morphological examination.

4. *Pugettia incisa* (De Haan, 1839 [in De Haan, 1833-1850]) (Fig. 12)

오늬이마물맞이게

Pisa (Halimus) incisus De Haan, 1833–1849 (1837): pl. 24, fig. 3.

Pisa (Menoethius) incisus—De Haan, 1833–1849 (1839): 98.

Pugettia incisa—Miers, 1879: 23; 1886: 40; Ortmann, 1893: 44; Doflein, 1902: 656; Yokoya, 1928: 768; 1933: 148; Sakai, 1934: 294; 1936: 88, fig. 38; 1938: 254, fig. 27; 1965: 72, pl. 32, figs 1, 2; 1976: 195, fig. 102, pl. 68, fig. 3; Kamita, 1941: 63, fig. 27; Kim, 1970: 24; 1973: 529, 664, pl. 103, fig. 193; Kim & Chang, 1985: 45; Griffin & Tranter, 1986: 93, fig. 28g, h; Dai & Yang, 1991: 130, fig. 66(3), pl. 14(5); Kim & Kim, 1998: 302; Ko & Lee, 2015:16, pls. 4–6.

Pugettia cristata Gordon, 1931: 555, figs 33b, 34d, e.

Material examined

NIBRIV0000234296, 2 males (pcl 18.6–18.7 mm), Gijang-gun, Busan-si, Korea, 35°17'47.25"N, 129°17'31.36"E, 14 Jan. 2011; 1 female (pcl 11.5 mm), Gyeongju-si, Gyeongsangbuk-do, Korea, 35°47'47.25"N, 129°30'14.04"E, 11 Jul. 2018, coll. by SCUBA diving; 2 female (pcl 9.9 mm, 11.9 mm), Pohang-si, Gyeongsangbuk-do, Korea, 36°00'56.47"N, 129°35'23.23"E, 19 Sep. 2018, coll. by SCUBA diving at 18 m depth; 1 male (pcl 8.9 mm), Seogwipo-si, Jeju-do, Korea, 33°11'57.38"N, 127°11'44.83"E, 1 May 2019, coll. by otter trawl.

Diagnosis

Carapace subtriangular, smooth. Gastric region with one tubercle, with hooked setae. Cardiac region with one prominent tubercle. Intestinal region with one small tubercle. Branchial region with one epibranchial spine, projecting obliquely backward. Pseudorostrum acute distally, 0.3 times as long as cl, dorsal surface covered with hooked setae. Preorbital spine prominent, triangular. Postorbital spine and hepatic spine completely fused. Chela stout; merus with three crests; carpus with crest on upper margin. Ambulatory legs with merus having crest on anterior border. In male, G1 with mesial vestigial.

Type locality

Japan.

Habitat

Sand bottom or Sandy mud bottom.

Distribution

Japan, China (East China Sea, Yellow Sea), and Korea (Fig. 11).

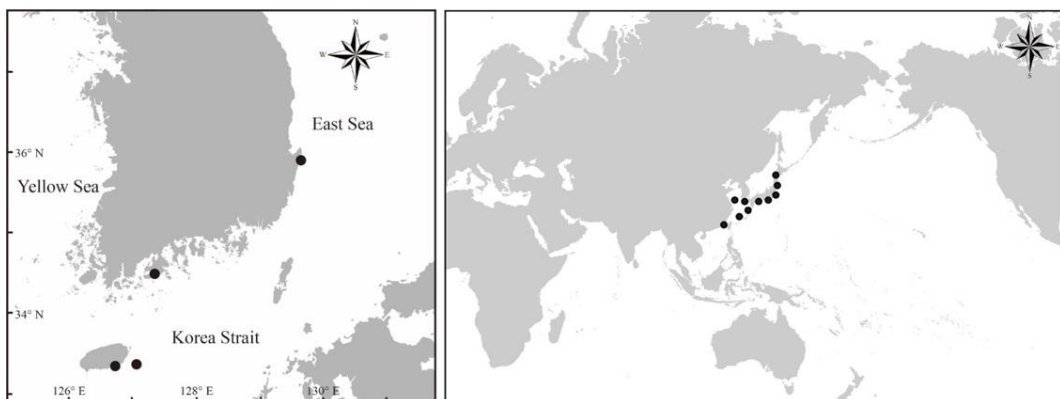


Fig. 11. Distribution of *Pugettia incisa* (De Haan, 1937).



Fig. 12. *Pugettia incisa* (De Haan, 1937). Male (pcl 18.7 mm) (NIBRIV0000234296), dorsal view.

Remark

Comparisons of DNA sequence of *COXI* between *Pugettia incisa* and *P. ferox* showed that very slightly differed from each other (Table 2). However, *P. incisa* forms a distinctly independent clade from *P. ferox* (Fig. 107), and there is a distinct difference in morphologically.

Pugettia incisa (De Haan, 1937) is easily distinguished from congeners based on the completely fused postorbital spine and the hepatic spine. This feature is observed in both males and females. In males, G1 has a small triangular ventral lobe.

In the figure of De Haan (1937), the epibranchial spine is projecting laterally, but in the observed specimens, it is projecting obliquely backward.

5. *Pugettia intermedia* Sakai, 1938 (Fig. 14) 중간뿔물맞이게

Pugettia quadridens intermedia Sakai, 1938: 258, pl. 36, fig. 2; 1965: 72, pl. 32, fig. 3; 1976: 197, text-fig. 103b.

Pugettia intermedia—Griffin & Tranter, 1986: 93, fig. 28a, b; Ng et al., 2008: 101 (list); Lee et al., 2014: 44, figs 1, 2; Ohtsuchi & Kawamura, 2019: 21, figs 2E, F, 14–24.

? *Pugettia quadridens intermedia*—Kim & Kim 1986: 325.

Material examined

NIBRIV0000192206, 2 females, 5 males (12.1–23.8 mm), Boryeong-si, Chungcheongnam-do, Korea, 21 Dec. 2001; NIBRIV0000261132, 1 female, Gijang-gun, Busan-si, Korea, 35°14'304"N, 129°14'28"E, 14 Jan. 2011; 1 female, 4 males (8.1–15.6 mm), Seocheon-gun, Chungcheongnam-do, Korea, 36°7'58.39"N, 126°30'12.26"E, 1 Aug. 2019, coll. from fishing port; 2 males (8.6, 9.1 mm), Seocheon-gun, Chungcheongnam-do, Korea, 2 Sep. 2019, coll. from fishing port; 1 female, 2 males (11.4–22.1 mm), Yeosu-si, Jeollanam-do, Korea, 34°41'29.4"N, 127°47'40"E, 22 Oct. 2019, coll. by SCUBA diving; 1 female, 2 males (8.2–10.2 mm), Yeosu-si, Jeollanam-do, Korea, 34°35'5.5"N, 127°47'25.1"E, 24 Oct. 2019, coll. by SCUBA diving.

Diagnosis

Carapace subtriangular, smooth, surface covered with tomentum, regions regularly distinct. Gastric region convex. Cardiac and intestinal regions separated. Mesobranchial region with 2 tubercles. Metabranchial region with one tubercle. Pseudorostrum acute distally, 0.2–0.3 times as long as pcl. Preorbital spine prominent, triangular. Supraorbital eave with lateral

margin nearly straight. Postorbital spine slightly slender, projecting anteriorly. Hepatic spine prominent, slender and acute distally. Third maxilliped with exopod narrowed in distal one-third. Chela stout; merus with three to six low teeth on dorsal surface (increasing distally in size); carpus with dorsal ridge dentate. Ambulatory legs slender, long, with club-shaped setae sparsely, with outer margin of merus having one distinct tubercle distally. In male, G1 with mesial lobe as long as dorsal lobe, separated with dorsal lobe moderate narrow hiatus. In female, gonopore elongated transversely.

Type locality

Simoda, Japan.

Habitat

Intertidal rocky shore, weedy pebbles, intertidal to 40 m deep.

Distribution

Japan, China (Qindao, Jiaozhou Bay), and Korea (Fig. 13).

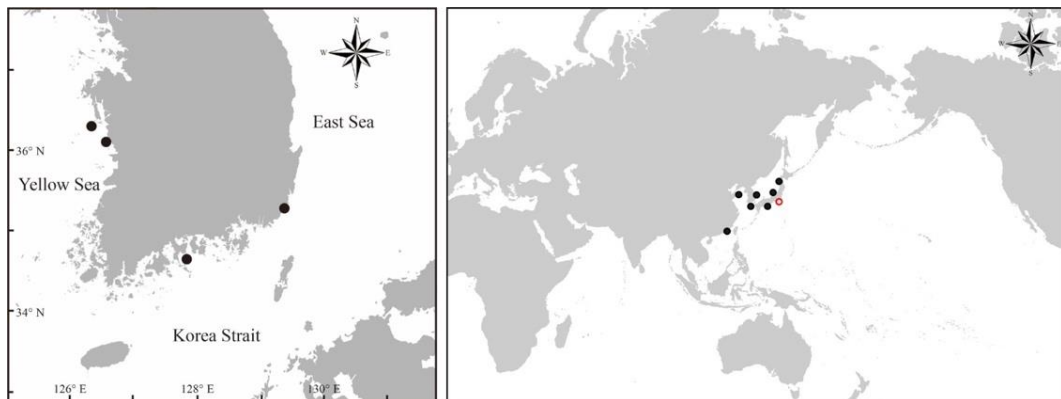


Fig. 13. Distribution of *Pugettia intermedia* Sakai, 1938. Open circle=type locality.



Fig. 14. *Pugettia intermedia* Sakai, 1938. Male (pcl 22.1 mm), dorsal view.

Remark

Pugettia intermedia Sakai, 1938 was first reported to the Korean waters by Kim & Kim (1986). Later, Kim & Kim (1998) was reported again with description and illustrations. Lee et al. (2014) also reported *P. intermedia* collected from Geojedo Island, noting that previously reported specimens of *P. intermedia* in Korea are *P. quadridens*. In a re-description, Ohtsuchi & Kawamura (2019) suggested that the described *P. intermedia* in Korea are different from *P. intermedia*, and they share some characteristics with *P. ferox* Ohtsuchi & Kawamura, 2019, and that they are potentially different species. However, the main characteristics of this species are considered as follows, and *P. intermedia* identified by Lee et al., (2014) is considered to be correct: (1) protogastric tubercles more separated from mesogastric tubercle than from metagastirc tubercle, (2) ambulatory legs covered with tomentum, having club-shaped hair sparsely, and (3) G1 with mesial lobe as long as dorsal lobe. Examined specimens almost agree with the re-description of Ohtsuchi & Kawamura (2019). Subsequently, comparative research with Japanese specimens is required to identify them.

Comparisons of DNA sequence of *COXI* among *Pugettia ferox*, *P. intermedia*, *P. quadridens*, and *P. vulgaris* (Table 2, Fig. 107) supported the present result of morphological examination.

* **6. *Pugettia marissinica* Takeda & Miyake, 1972 (Fig. 15)** 애기뿔물맞이게

Pugettia marissinica Takeda & Miyake, 1972: 260, fig. 4; Takeda, 1973b: 40; Griffin & Tranter, 1986: 95, fig. 28c, d.

Material examined

One male (pcl 10.1 mm, cw 7.1 mm), Seogwipo-si, Jeju-do, Korea, 33°31'44.84"N, 127°21'34.54"E, 6 May 2019, coll. by otter trawl.

Diagnosis

Carapace subtriangular, covered with short setae sparsely. Gastric region unarmed. Cardiac and intestinal regions each with one large tubercle. Pseudorostrum slender, with dorsal surface covered with hooked setae, acute distally, 0.33 times as long as cl. Preorbital spine prominent, triangular. Postorbital spine prominent, projecting anteriorly, curved downward. Hepatic spine prominent, slightly smaller than postorbital spine. Postorbital and hepatic spines distinctly separated. Branchial margin with one prominent spine. Anterior branchial margin covered with hooked setae. Mesobranchial region with one tubercle. Chela with merus having one strong spine distally, with four granulated ridges. Ambulatory legs slender. In male, G1 with mesial lobe as long as dorsal lobe.

Type locality

Tsushima, Japan, 34°42'N, 129°16'E, 207m deep.

Habitat

Sandy mud bottoms, 45 to 207 m deep.



Fig. 15. *Pugettia marissinica* Takeda & Miyake, 1972. Male (pcl 10.1 mm), dorsal view.

Distribution

Japan, Taiwan Strait, and Korea (Fig. 16).

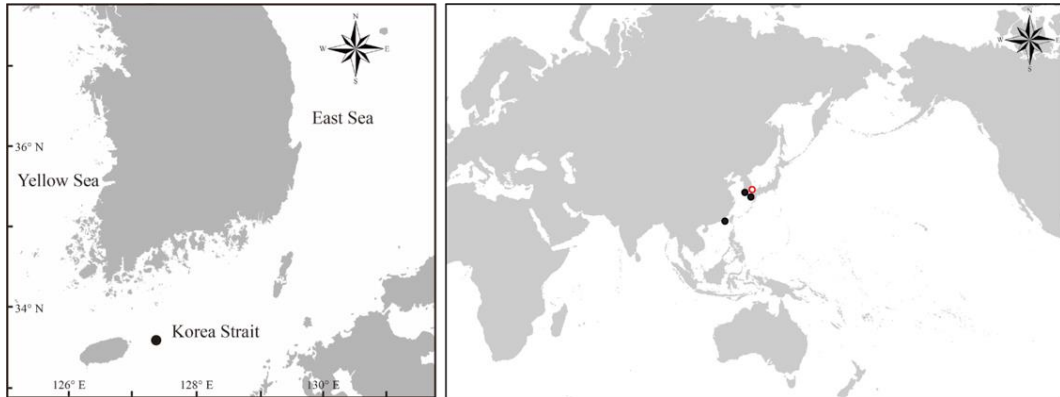


Fig. 16. Distribution of *Pugettia marissinica* Takeda & Miyake, 1972. Open circle=type locality.

Remark

Pugettia marissinica Takeda & Miyake, 1972 is similar to *P. nipponensis* Rathbun, 1932.

The differences between the two species are described under *P. nipponensis*.

Characteristics of examined specimens were consistent with the original description of Takeda & Miyake (1972). Griffin & Tranter (1986) noted that some specimens have some tubercles on the gastric region. The present specimen from Jeju Island has no tubercle on the gastric region.

7. *Pugettia minor* Ortmann, 1893 (Fig. 17) 꼬마물맞이게

Pugettia minor Ortmann, 1893: 44; Sakai, 1934: 294; 1938: 260, fig. 29, pl. 25, fig. 2; 1965: 72, pl. 31, fig. 4; 1976: 199, pl. 68, fig. 2; Kim & Chang, 1985: 47, fig. 2; Griffin & Tranter, 1986: 96; Dai & Yang, 1991: 131, fig. 67(2), pl. 14(7); Ko & Lee, 2015: 17.

Material examined

One male (pcl 7.5 mm), Beophwan-dong, Seogwipo-si, Jeju-do, Korea, 7 Feb. 1971.

Diagnosis

Carapace subtriangular, smooth. Gastric region with one low tubercle. Cardiac region with one prominent blunt spine. Intestinal region with one small spine. Pseudorostrum acute distally, 0.3 times as long as cl. Preorbital spine prominent, triangular. Postorbital spine larger than hepatic spine, curved downward. Postorbital and hepatic spines distinctly separated. Chela stout; merus with four crests; carpus with two crests. Ambulatory legs slender, long.

Type locality

Sagami Bay, Japan.

Habitat

Sandy, sandy mud bottoms, 35 to 540 m deep.

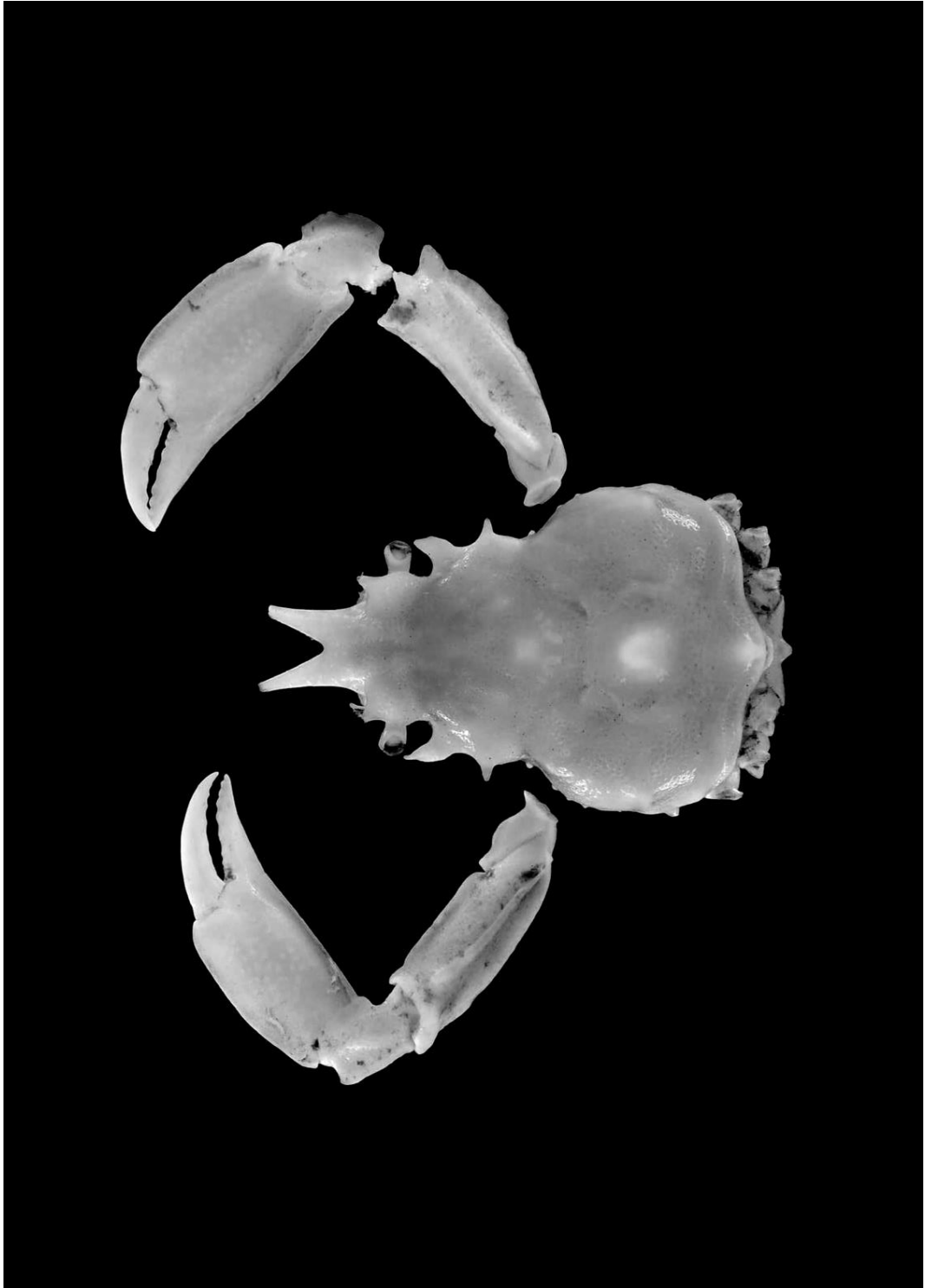


Fig. 17. *Pugettia minor* Ortmann, 1893. Male (pcl 7.5 mm), dorsal view.

Distribution

Japan, China (East China Sea, Yellow Sea), and Korea (Fig. 18).

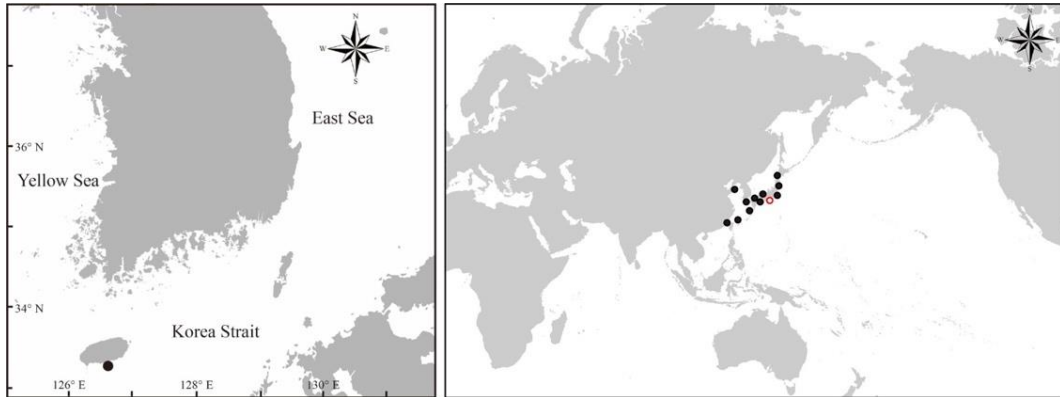


Fig. 18. Distribution of *Pugettia minor* Ortmann, 1893. Open circle=type locality.

Remark

Pugettia minor Ortmann, 1893, a very rare species found in Korean waters, has not been observed since a male species was reported by Kim & Chang (1985). *Pugettia minor* can be distinguished from congeners based on the following characteristics: (1) the hepatic and the postorbital spines separated, (2) the cardiac and the intestinal region with one spine.

* **8. *Pugettia nipponensis* Rathbun, 1932 (Fig. 19)** 긴다리뿔물맞이게

Pugettia nipponensis Rathbun, 1932: 31; Yokoya, 1933: 152; Sakai, 1936: 90, fig. 40, pl. 21, fig. 4; 1938: 261, figs 30a, b, pl. 26, fig. 2; 1965: 73, pl. 33, fig. 1; 1976: 200, fig. 108a, b, pl. 69, fig. 1; Griffin & Tranter, 1986: 96; Dai & Yang, 1991: 130, fig. 67(1), pl. 14(6); Takeda, 1997: 242.

Material examined

Two males (pcl 14.3 mm, 14.8 mm), Seogwipo-si, Jeju-do, Korea, 33°21'58.41"N, 127°11'44.83"E, 1 May 2019, coll. by otter trawl.

Diagnosis

Carapace subtriangular, covered with dense tomentum. Gastric region with three tubercles forming inverted triangle, posterior one larger. Cardiac region with one large tubercle. Intestinal region with one small tubercle. Epibranchial region with two tubercles. Mesobranchial region with one tubercle. Pseudorostrum slender, acute distally, 0.33 times as long as cl. Preorbital spine prominent, triangular. Postorbital spine prominent, projecting anteriorly. Hepatic spine prominent, smaller than postorbital spine. Postorbital and hepatic spines distinctly separated. Anterior branchial margin with four prominent tubercles. Posterior branchial margin with one tubercle. Chela stout, with merus having tubercles. Ambulatory legs slender, covered with tomentum.

Type locality

Doumiki Saki, Japan.



Fig. 19. *Pugettia nipponensis* Rathbun, 1932. Male (pcl 14.8 mm), dorsal view.

Habitat

50 to 604 m deep.

Distribution

Japan, China (East China Sea), Indonesia (Ambon), and Korea (Fig. 20).

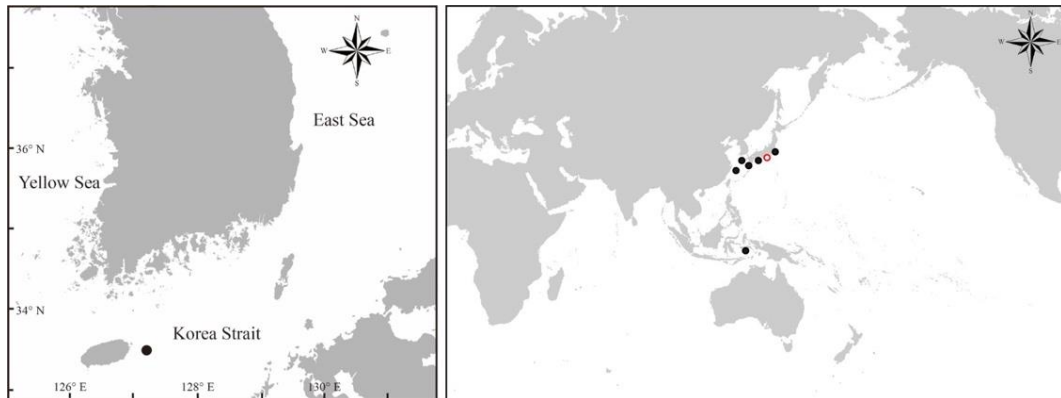


Fig. 20. Distribution of *Pugettia nipponensis* Rathbun, 1932. Open circle=type locality.

Remark

Pugettia nipponensis Rathbun, 1932 is similar to *P. marissinica* Takeda & Miyake, 1972. They share the following characteristics: postorbital and hepatic spines are distinctly separated, and cardiac and intestinal regions each have one tubercle. However, *P. nipponensis* can be distinguished from *P. marissinica* based on the following morphological characteristics: (1) carapace is covered with dense tomentum (covered with short setae sparsely in *P. marissinica*), (2) epibranchial region has tubercles (without tubercle in *P. marissinica*).

Sakai (1938) described that *Pugettia nipponensis* has a row of three tubercles on the anterior branchial margin and has three or four groups of tubercles on the dorsal surface of the branchial region. However, the observed specimen has a row of four tubercles on the anterior branchial margin and has only one tubercle on the dorsal surface of the branchial region.

9. *Pugettia pellucens* Rathbun, 1932 꼬마뿔물맞이게

Pugettia quadridens pellucens Rathbun, 1932: 31; Sakai, 1938: 258, pl. 36, fig. 3; 1976: 197, text-fig. 104; Griffin & Tranter, 1986: 92 (key).

Pugettia pellucens—Ng et al., 2008: 101 (list); Ohtsuchi et al., 2014: 558, figs 1–3, 6A–E.

? *Pugettia quadridens pellucens*—Kim & Kim, 1985: 200; Lee et al., 2014: 47, figs 3B, 4B; Ko & Lee, 2015: 18, pls. 9, 10.

Type locality

Omae-Zaki, Suruga Bay, Japan.

Habitat

Sandy, sandy mud bottoms, intertidal zone.

Distribution

Japan, and (?) Korea (Fig. 21).



Fig. 21. Distribution of *Pugettia pellucens* Rathbun, 1932. Open circle=type locality.

Remark

Pugettia pellucens Rathbun, 1932 is very rare species. In Korean waters, Kim & Kim (1985) first reported *P. pellucens* collected from Geomundo Island without description and illustrations. And the author could not observe the specimen reported by Kim & Kim (1985). *Pugettia pellucens* is closely related to *P. vulgaris* Ohtsuchi, Kawamura & Takeda, 2014. The differences between the two species are described under *P. vulgaris*. *Pugettia pellucens* reported in Korea (Lee et al., 2014; Ko & Lee, 2015) after Kim & Kim (1985) does not match the characteristics presented by Ohtsuchi et al. (2014) and Ohtsuchi & Kawamura (2019). And the author has not yet observed specimen of Korea. Therefore, further studies would be required to determine whether *P. pellucens* exists in Korean waters.

* **10. *Pugettia quadridens* (De Haan, 1837) (Fig. 23)** 매 끈이 빨물맞이게

Pisa (Halimus) quadridens De Haan, 1837: pl. 24, fig. 2.

Pisa (Menoethius) [sic.] quadridens—De Haan, 1839: 97 (in part); Yamaguchi & Baba, 1993: 353, fig. 113 (in part).

Pugettia quadridens—Sakai, 1936: 88 (in part), pl. 20, fig. 2, text-fig. 37; Griffin & Tranter, 1986: 97 (in part); Yamaguchi & Baba, 1993: 353, fig. 113 (in part); Ohtsuchi & Kawamura, 2019: 6, figs 2–13.

Pugettia quadridens quadridens—Sakai, 1976: 196 (in part), text-fig. 103a, pl. 68, fig. 1.

? *Pugettia quadridens*—Miers, 1879: 23 (in part); Sakai, 1934: 294; Kim, 1960: 342; 1962, 53; 1970, 24; Kim & Kim, 1982: 146; Kim & Chang, 1985: 45; Komai, 1999: 86.

? *Pugettia quadridens quadridens*—Kim, 1985: 79; Kim & Kim, 1986: 325.

Material examined

One male (pcl 14.0 mm), Jeju-si, Jeju-do, Korea, 33°29'17.38"N, 126°54'44.4"E, 11 Apr. 2017; 3 males (pcl 17.9–22.4 mm), Seongsan-eup, Seogwipo-si, Jeju-do, Korea, 33°27'33.95"N, 126°56'8.45"E, 12 Apr. 2017; 1 male (pcl 10.9 mm), Samcheok-si, Gangwon-do, Korea, 37°18'35.32"N, 129°17'28.71"E, 18 Oct. 2017; 1 male (pcl 21.0 mm), Daejeong-eup, Seogwipo-si, Jeju-do, Korea, 33°16'21.79"N, 126°10'19.21"E, 6 Mar. 2018; 3 males (pcl 18.3–22.2 mm), Gujwa-eup, Jeju-si, Jeju-do, Korea, 33°33'27.98"N, 126°44'21.66"E, 17 Apr. 2018, coll. from fishing port; 1 male (pcl 12.2 mm), Ulleung-gun, Gyeongsangbuk-do, Korea, 37°14'51.11"N, 131°51'48.17"E, 13 Sep. 2018, coll. by SCUBA diving; 1 female (pcl 10.4 mm), Seongsan-eup, Seogwipo-si, Jeju-do, Korea, 33°27'33.95"N, 126°56'8.45"E, 27 Feb. 2019; 1 male (pcl 11.1 mm), Haeundae-gu, Busan-si, Korea, 35°10'44.79"N, 129°12'20.66"E, 3 Apr. 2019.

Diagnosis

Carapace subtriangular, smooth, regions indistinct. Gastric region convex. Cardiac and intestinal regions almost fused. Branchial region almost smooth. Pseudorostrum acute distally, 0.2–0.3 times as long as pcl. Preorbital spine prominent, triangular. Supraorbital eave with lateral margin concave. Postorbital spine distinctly smaller than hepatic spine. Third maxilliped with exopod narrowed in distal half. Chela stout; merus with three low teeth on dorsal surface (diminishing distally in size); carpus with dorsal ridge unarmed. Ambulatory legs slender, long. In male, G1 with mesial lobe short, developed perpendicular to dorsal lobe. In female, gonopore comma-shaped, short transversely.

Type locality

Japan.

Habitat

Intertidal rocky shore, weedy pebbles.

Distribution

Japan, China (Fuzhou), and Korea (Fig. 22).

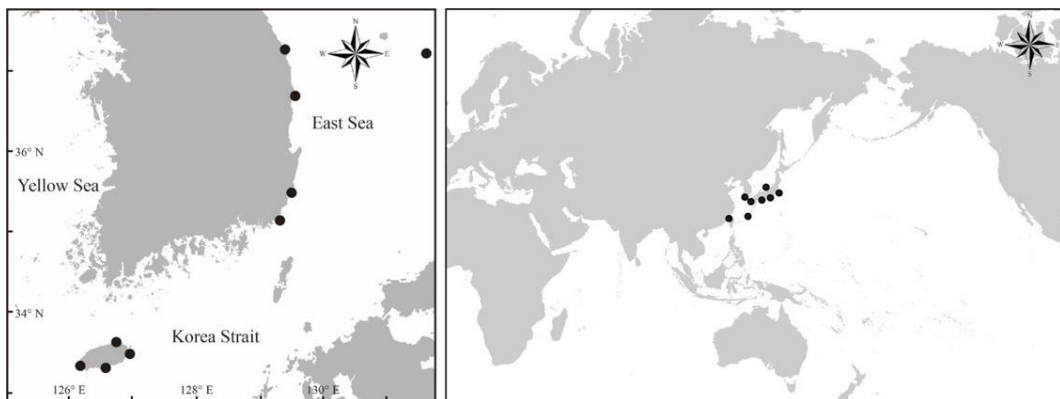


Fig. 22. Distribution of *Pugettia quadridens* (De Haan, 1837).



Fig. 23. *Pugettia quadridens* (De Haan, 1837). Male (pcl 22.4 mm), dorsal view.

Remark

De Haan (1837, 1839) described *Pugettia quadridens* as new species from Japan, subsequently, *P. quadridens intermedia* Sakai, 1938 and *P. q. pellucens* Rathbun, 1932 were reported from Japan as subspecies of *P. quadridens*. In addition, Ohtsuchi et al. (2014) newly described *P. vulgaris*, a relative of *P. pellucens*. They all have many variations or share numerous characteristics among allied species. Therefore, there have been frequent cases of misidentification of these species, and Ohtsuchi & Kawamura (2019) comprehensively revised *Pugettia quadridens sensu lato* with the release of an additional new species, *P. ferox*.

Ohtsuchi & Kawamura (2019) referred that *Pugettia quadridens*, previously reported in Korean waters, was misidentified and suggested examining whether the species exists in Korean waters. This study confirmed that *P. quadridens* inhabits Korean waters. In the examined specimens, smaller individuals had more distinct tubercles on the dorsal surface of the carapace.

Comparisons of DNA sequence of *COX1* among *Pugettia ferox*, *P. intermedia*, *P. quadridens*, and *P. vulgaris* (Table 2, Fig. 107) supported the present result of morphological examination.

11. *Pugettia vulgaris* Ohtsuchi, Kawamura & Takeda, 2014 (Fig. 25)

잔털빨물맞이게

Pugettia vulgaris Ohtsuchi, Kawamura & Takeda, 2014: 563, figs 4, 5, 6F–J, 7; Yang et al., 2015: 203, figs 1E, F, 3.

Material examined

Two males (pcl 14.5, 17.4 mm), Pohang-si, Gyeongsangbuk-do, Korea, 36°9'17.86"N, 129°24'2.01"E, 13 Jul. 2017; 1 male, Uljin-gun, Gyeongsangbuk-do, Korea, 20 Jul. 2017; 1 male (pcl 12.8 mm), Ulju-gun, Ulsan, Korea, 35°21'15.91"N, 129°20'29.65"E, 26 Apr. 2018; 1 female (pcl 8.9 mm), Gijang-gun, Busan, Korea, 35°18'36.12"N, 129°15'51.78"E, 27 Apr. 2018; 1 male (pcl 16.1 mm), Taean-gun, Chungcheongnam-do, Korea, 36°37'6.77"N, 125°34'38.94"E, 20 Jun. 2018; 1 male (pcl 17.3 mm), Ulleung-gun, Gyeongsangbuk-do, Korea, 37°14'51.11"N, 131°51'48.17"E, 13 Sep. 2018; 1 male, Sinan-gun, Jeollanam-do, Korea, 34°5'46.08"N, 125°5'37.28"E, 24 Nov. 2018, coll. by SCUBA diving at 24 m depth; 1 male (pcl 8.3 mm), Seongsan-eup, Seogwipo-si, Jeju-do, Korea, 16 Mar. 2019; 1 male (pcl 13.1 mm), Pohang-si, Gyeongsangbuk-do, Korea, 36°12'27.2"N, 129°22'38.26"E, 27 Mar. 2019, coll. by SCUBA diving at 28 m depth; 1 male (pcl 9.9 mm), Saha-gu, Busan, Korea, 10 Jul. 2019.

Diagnosis

Carapace elongated pyriform, dorsal surface sometimes covered with club-shaped setae, regions regularly distinct. Gastric region convex. Cardiac and intestinal regions separated. Pseudorostrum acute distally, 0.20–0.35 times as long as pcl. Preorbital spine prominent,

triangular. Supraorbital eave with lateral margin nearly straight. Postorbital spine projecting anterolaterally, triangular. Hepatic spine triangular. Postorbital spine slightly smaller than hepatic spine. Third maxilliped with exopod narrowed in distal half. Chela stout; merus with three low teeth on dorsal surface (increasing distally in size). Ambulatory legs slender, long, with outer margin of merus having one tubercle distally. In male, G1 with mesial lobe short, separated with dorsal lobe narrow hiatus. In female, gonopore comma-shaped, short transversely.

Type locality

Nagai, Yokosuka, Miura Peninsula, Japan.

Habitat

Weedy pebbles, shallow water from intertidal to 8 m deep.

Distribution

Japan, and Korea (Fig. 24).

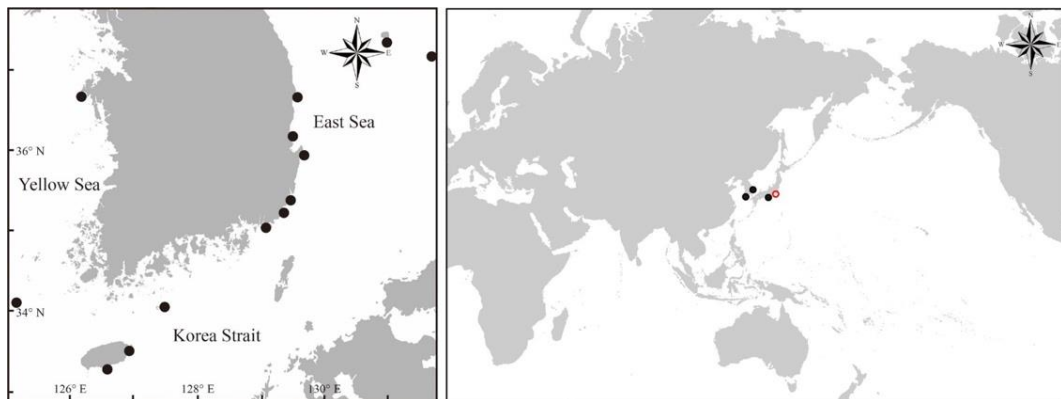


Fig. 24. Distribution of *Pugettia vulgaris* Ohtsuchi, Kawamura & Takeda, 2014. Open circle=type locality.



Fig. 25. *Pugettia vulgaris* Ohtsuchi, Kawamura & Takeda, 2014. Male (pcl 16.1 mm), dorsal view.

Remark

According to Ohtsuchi et al. (2014) and Ohtsuchi & Kawamura (2019), *Pugettia vulgaris* Ohtsuchi, Kawamura & Takeda, 2014 is closely related to *P. pellucens* Rathbun, 1932. They share the following characteristics: (1) carapace with elongated pyriform, (2) supraorbital eave compressed narrowly, and (3) cheliped with carpus having tridentated crest on dorsal margin, with carpus having two or three tuberculate. However, the *P. vulgaris* has the following characteristics: (1) pseudorostrum 0.3–0.4 times as long as pcl (0.4–0.5 times as long as in *P. pellucens*), (2) the hepatic and the postorbital spines subequal size or the hepatic spine slightly larger than the postorbital spine (the hepatic spine distinctly larger in *P. pellucens*), (3) buccal frame is moderate produced anterolaterally (distinct produced in *P. pellucens*), (4) anterolateral angle of buccal frame and anterolateral angle of merus of the third maxilliped overlaid (not overlaid in *P. pellucens*), and (5) ischium of cheliped is rounded on the mesial surface (with blunt ridge in *P. pellucens*) (Ohtsuchi et al., 2014).

Examined specimens are almost consistent with the original description of *Pugettia vulgaris*. However, in the examined specimens, many individuals were larger than the size of *P. vulgaris* presented by Ohtsuchi et al. (2014) and Ohtsuchi & Kawamura (2019). Examined specimens are very similar in morphologically to the specimens of Yang et al. (2015) and appear to be the same species. Ohtsuchi & Kawamura (2019) mentioned that *P. vulgaris* that Yang et al. (2015) reported in Korea were misidentification of *P. intermedia* for the following characteristics: (1) deep and rectangular orbital hiatus, (2) the rows of hooked setae on the gastric region is nearly connected to the rows of setae on the pseudorostrum, (3) relatively wide hiatus between mesial and dorsal lobes of G1 is deep and wide concavity, and (4) specimens quite larger than the previous record. However, the Korean specimens have the following characteristics that distinguish them from *P.*

intermedia: the gastric and branchial region smooth (with tubercles in *P. intermedia*), postorbital spines project anterolaterally (anteriorly in *P. intermedia*), postorbital and hepatic spines triangular and not slender distally (more slender and acute in *P. intermedia*), in females, gonopore is comma-shaped (elongated transversely in *P. intermedia*). In addition, comparisons of DNA sequence of *COXI* showed clearly divided clades with *P. intermedia* (Table 2, Fig. 107). Though careful, the author identifies the specimens observed as *P. vulgaris*.

Table 2. Minimum pairwise genetic distances (K2P distance) based on *COXI* sequences among *Pugettia ferox*, *P. incisa*, *P. intermedia*, *P. quadridens*, and *P. vulgaris*.

Species	<i>P. ferox</i>	<i>P. incisa</i>	<i>P. intermedia</i>	<i>P. quadridens</i>	<i>P. vulgaris</i>
<i>P. ferox</i>	-				
<i>P. incisa</i>	0.30	-			
<i>P. intermedia</i>	3.80	4.10	-		
<i>P. quadridens</i>	3.19	3.34	4.10	-	
<i>P. vulgaris</i>	12.16	12.16	11.70	12.91	-

12. *Xenocarcinus conicus* (A. Milne-Edwards, 1865) (Fig. 27)

물방울물맞이게

Huenioides conica A. Milne-Edwards, 1865: 145, pl. 4, fig. 3.*Xenocarcinus tuberculatus*—Alcock, 1895: 192; Alcock & Anderson, 1898, pl. 33, fig. 3, 3a; Rathbun, 1911: 248; Stephensen, 1945: 109, fig. 21C, D. [Not *Xenocarcinus tuberculatus* White, 1847]*Xenocarcinus tuberculatus* var. *alcocki* Laurie, 1906: 371.*Xenocarcinus conicus*—Gordon, 1934: 70; Griffin & Tranter, 1986: 100, fig. 30c, d; Lee et al., 2008: 152, fig. 1; Ko & Lee, 2015: 20.*Xenocarcinus nakazawai* Sakai, 1938: 325, fig. 52a–d; 1976: 213, fig. 116.*Xenocarcinus alcocki*—Sakai, 1965: 92.***Material examined***

MADBK 171905_001, 1 female (pcl 19.8 mm), Beophwan-dong, Seogwipo-si, Jeju-do, Korea, 33°13'40.86"N, 126°34'5.70"E, 19 Apr. 2002; 1 female (pcl 8.5 mm), Beophwan-dong, Seogwipo-si, Jeju-do, Korea, 33°13'42.54"N, 126°36'3.79"E, 31 Jan. 2016; 1 female (pcl 5.8 mm), Beophwan-dong, Seogwipo-si, Jeju-do, Korea, 33°13'32.66"N, 126°33'37.39"E, 28 Mar. 2018.

Diagnosis

Carapace elongated oval, covered with tomentum; regions not defined. Gastric region unarmed. Cardiac region with two spines transversely. Intestinal region with two spines.

Rostrum single, stout, conical, covered with tomentum, tapered and bifurcated distally. Preorbital and postorbital unarmed. Anterolateral and posterolateral margins with each one tubercle. Eyes large. Eyestalk short. Cheliped short, slender, with merus having three tubercles on outermargin. Ambulatory legs short, with tubercles.

Type locality

Indian Ocean.

Habitat

Collected from black coral, 13 to 80 m deep.

Distribution

The species is widely distributed in the Indo-Pacific region from the Red Sea to Japan (Fig. 26).

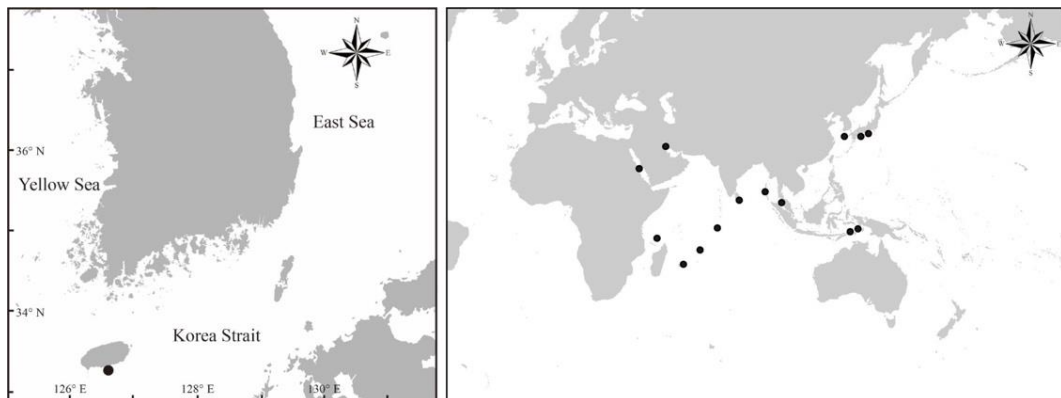


Fig. 26. Distribution of *Xenocarcinus conicus* (A. Milne-Edwards, 1865).



Fig. 27. *Xenocarcinus conicus* (A. Milne-Edwards, 1865). Female (pcl 5.8 mm), dorsal view.

Remark

Xenocarcinus conicus (A. Milne-Edwards, 1865) has an extremely wide distribution range. *Xenocarcinus conicus* was found on Jejudo Island in Korean waters, and the area is close to the northern limit of distribution of the species. The examined specimens were found in black corals. The illustration of A. Milne-Edwards (1865) showed that the rostrum is tapered extremely distally and the rostrum length is three-quarters the length of the postrostral carapace. Sakai (1938) presented female samples collected from Tanabe Bay in Japan as a new species, *X. nakazawai*, based on a rostrum with relatively short and wide and ambulatory legs, and merus with spines. Griffin & Tranter (1986) observed holotypes and additional specimens of *X. conicus*, and then synonymized *X. nakazawai* under *X. conicus*. The observed female specimens were consistent with the description of Sakai (1938).

Subfamily Pisinae Dana, 1851 어리물맞이게아과

Genus *Hoplophrys* Henderson, 1893 연산호뿔게속

13. *Hoplophrys oatesii* Hendersen, 1893 (Fig. 28) 연산호뿔게

Hoplophrys oatesii Henderson, 1893: 347, pl. 36, figs 1–4; Sakai, 1932: 48, pl. 2, fig. 4; 1936: 94, fig. 42; 1938: 294; Griffin & Tranter, 1974: 168; 1986: 119, fig. 37a; Lee & Kim, 2007: 103, fig. 1; Ko & Lee, 2015: 21.

Hoplophrys ogilbyi McCulloch, 1908: 51, pl. 12, figs 2, 2a; Buitendijk, 1939: 238; Sakai, 1976: 233, pl. 81, fig. 1.

Parazewa palauensis Miyake, 1939: 195, figs 12, 13; Takeda, 1973a: 97.

Material examined

MADBK 171912_001, 1 male (pcl 10.5 mm), 1 female (pcl 15.5 mm), Udo-myeon, Jeju-si, Jeju-do, Korea, 1996.

Diagnosis

Carapace subpyriform, as long as broad. Gastric region convex, with 9–10 spines. Cardiac region convex, with three spines transversely. Intestinal region with two spines. Pseudorostrum deflexed downwards, acute distally. Anterolateral region with two prominent, robust spines. Posterolateral margin with one low subdorsal spine. Preorbital spine distinct. Postorbital spine present, divided into two knobs distally. Cheliped short, slender, with tubercles on outermargin. Ambulatory legs short, with tubercles.

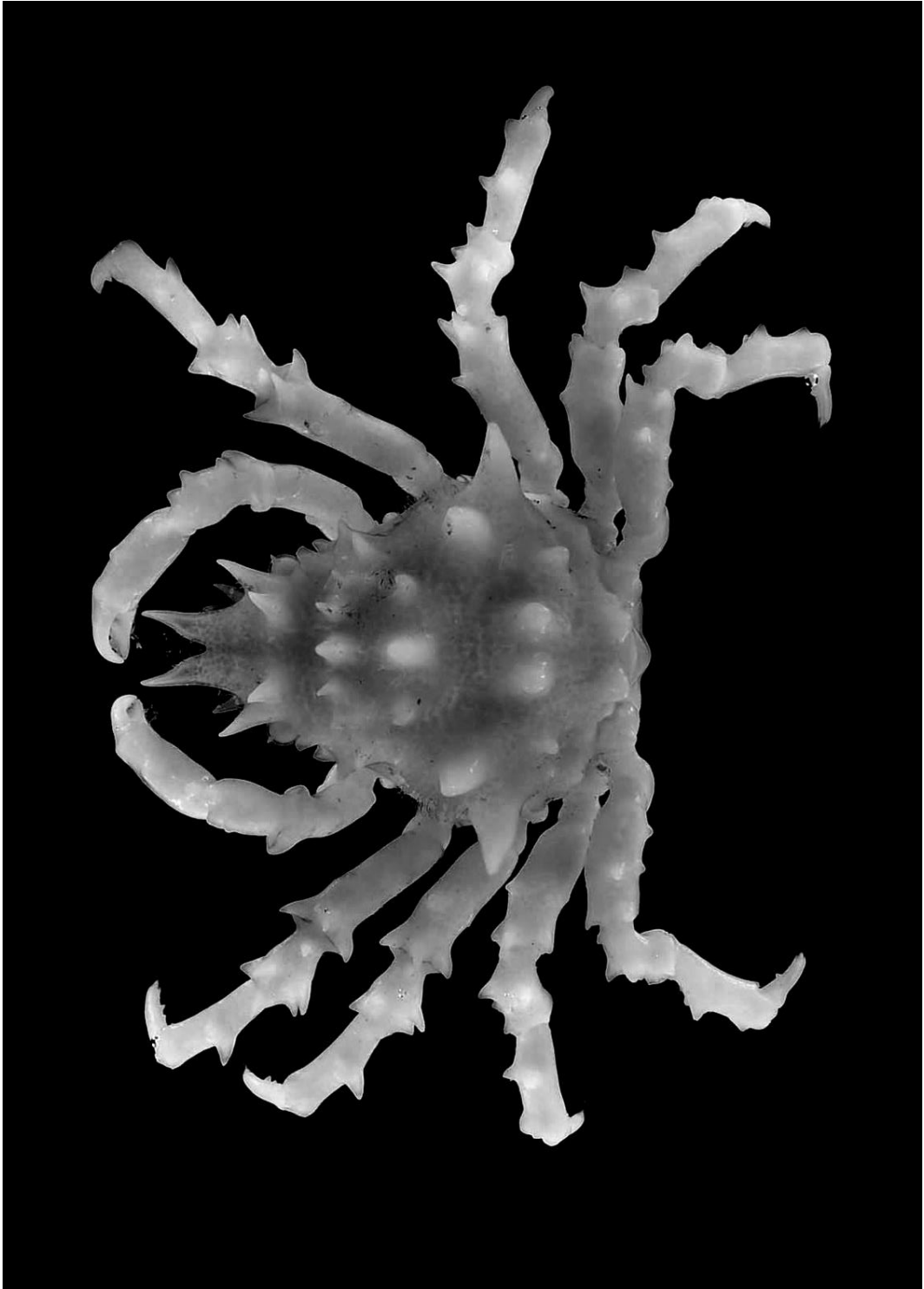


Fig. 28. *Hoplophrys oatesii* Hendersen, 1893. Male (pcl 10.5 mm) (MADBK 171912_001), dorsal view.

Type locality

Gulf of Martaban.

Habitat

Symbiosis with a soft coral.

Distribution

Indo-west Pacific, Western Indian Ocean (Fig. 29).

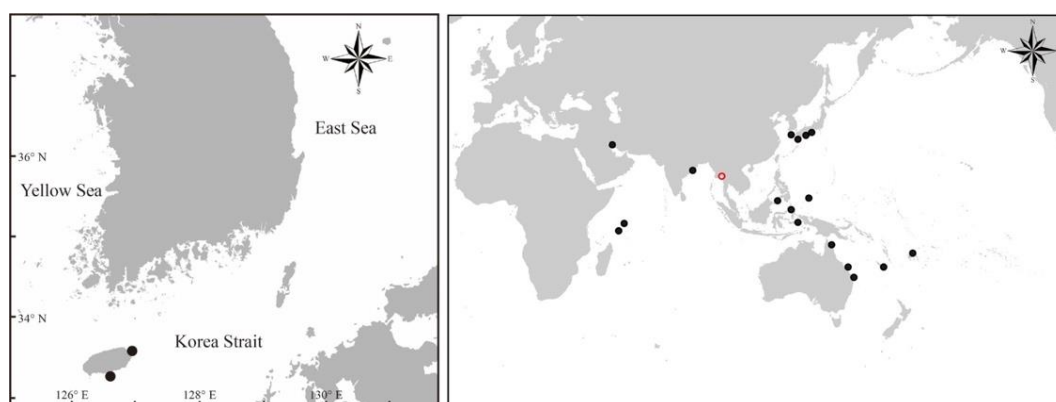


Fig. 29. Distribution of *Hoplophrys oatesii* Hendersen, 1893. Open circle=type locality.

Remark

Hoplophrys oatesii Hendersen, 1893 is the only species in the genus *Hoplophrys* Henderson, 1893. *Hoplophrys* is readily distinguished based on the following characteristics: (1) the carapace widens posteriorly, and has numerous acuminate spines, and (2) the intercalated spine does not exist. The examined specimens presented no unique features.

Genus *Hyastenus* White, 1847 빨게속

14. *Hyastenus diacanthus* (De Haan, 1839) 빨게

Pisa (Naxia) diacantha De Haan, 1833–1849 (1837): pl. 24, fig. 1; De Haan, 1833–1849 (1839): 96, pl. G; Yamaguchi, 1993: 585.

Naxia diacantha—Adams & White, 1848: 10.

Hyastenus diacanthus—Miers, 1879: 26; Terazaki, 1903: 46; Sakai, 1936: 95, pl. 24, fig. 2; 1938: 279, fig. 36, pl. 29, fig. 2; 1965: 81, pl. 36, fig. 1; 1976: 225, pl. 77, fig. 1; Buitendijk, 1939: 241, figs 5–8; Kamita, 1941: 76; Kim, 1970: 25; 1973: 535, 665, fig. 250, pl. 105, fig. 197a, b; Griffin, 1974: 14; Griffin & Tranter, 1974: 170; 1986: 140, figs 46c, 48a–c; Ko & Lee, 2015: 22.

Type locality

Japan.

Habitat

Muddy or sandy muddy bottoms, 12 to 180 m deep.

Distribution

The species is widely distributed in the Indo-Pacific region from the eastern coast of Africa to the eastern coast of Australia (Fig. 30).

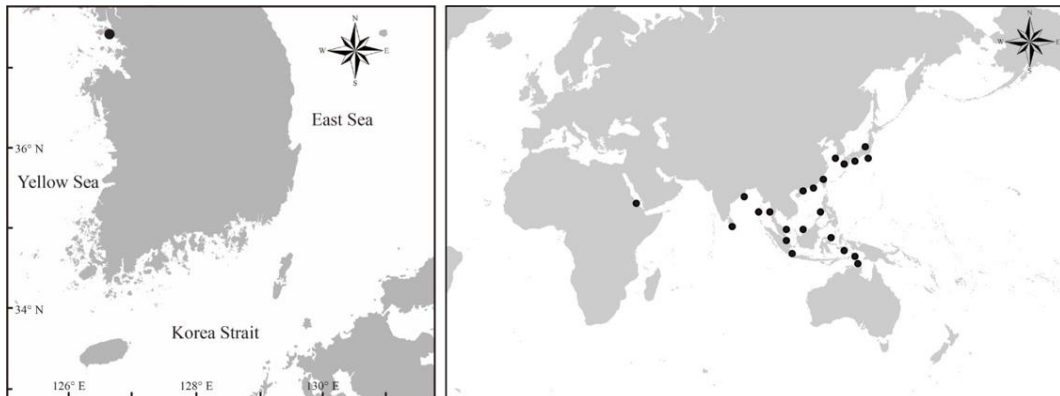


Fig. 30. Distribution of *Hyastenus diacanthus* (De Haan, 1839).

Remark

In Korean waters, Miers (1879) and Terazaki (1903) reported the collection of *Hyastenus diacanthus* (De Haan, 1839) on Jejudo Island and Incheon, respectively, and Kamita (1941) and Kim (1973) cited them. *Hyastenus diacanthus* has not been reported in Korean waters since 1903. The author has not yet encountered the species. Three *Hyastenus* White, 1847 species are known in Korean waters. The differences among the three species are described under *H. pleione* (Herbst, 1803).

15. *Hyastenus elongatus* Ortmann, 1893 (Fig. 32) 박뿔게

Hyastenus diacanthus var. *elongatus* Ortmann, 1893: 55.

Halimus elongatus—Rathbun, 1911: 251; Sakai, 1934: 295, fig. 9a, b.

Hyastenus elongatus—Sakai, 1936: 96, fig. 43; 1938: 281, pl. 36, fig. 6; 1965: 81, pl. 36, fig. 2; 1976: 226, pl. 77, fig. 2; Buitendijk, 1939: 242; Kim, 1970: 25, pl. 5, fig. 2; 1973: 536, 666, fig. 251, pl. 106, fig. 198a–d; Griffin & Tranter, 1974: 170; 1986: 143, figs 46e, f, 47a, b; Kim & Chang, 1985: 49; Ko & Lee: 23, pl. 14.

Material examined

One female (pcl 11.8 mm), Daejeong-eup, Seogwipo-si, Jeju-do, Korea, 15 Jul. 2016, coll. by SCUBA diving; 1 male (pcl 7.1 mm), Beophwan-dong, Seogwipo-si, Jeju-do, Korea, 29 Mar. 2018, coll. by SCUBA diving; 1 female (pcl 17.7 mm), Geonip-dong, Jeju-si, Jeju-do, Korea, 33°31'40.4"N, 126°32'39.5"E, 20 May 2019, coll. by SCUBA diving; 1 male (pcl 16.6 mm), Bomok-dong, Seogwipo-si, Jeju-do, Korea, 33°13'46.78"N, 126°36'6.73"E, 25 Jul. 2019, coll. by SCUBA diving at 27 m depth; MABIK CR00247308, 1 male (pcl 15.3 mm), Seogwi-dong, Seogwipo-si, Jeju-do, Korea, 33°13'36.36"N, 126°34'3.58"E, 27 Jul. 2019, coll. by SCUBA diving at 50 m depth.

Diagnosis

Carapace elongated pyriform, smooth, covered with tomentum. Gastric region convex, with one obtuse tubercle. Cardiac region slightly convex. Intestinal region with one blunt tubercle. Branchial region rounded, slightly convex. Pseudorostrum 0.6 times as long as pcl, covered with hooked setae, straight, acute distally. Supraorbital eave transversely

narrow. Antorbital lobe small, rounded. Postorbital lobe prominent, cupped. Basal antennal article narrow, distal margin unarmed. Cheliped short, slender, covered with tomentum. Ambulatory slender, covered with tomentum.

Type locality

Tokyo Bay and Sagami Bay, Japan.

Habitat

Sandy muddy bottoms, 30 to 180 m deep.

Distribution

Indo-west Pacific, Western Indian Ocean (Fig. 31).

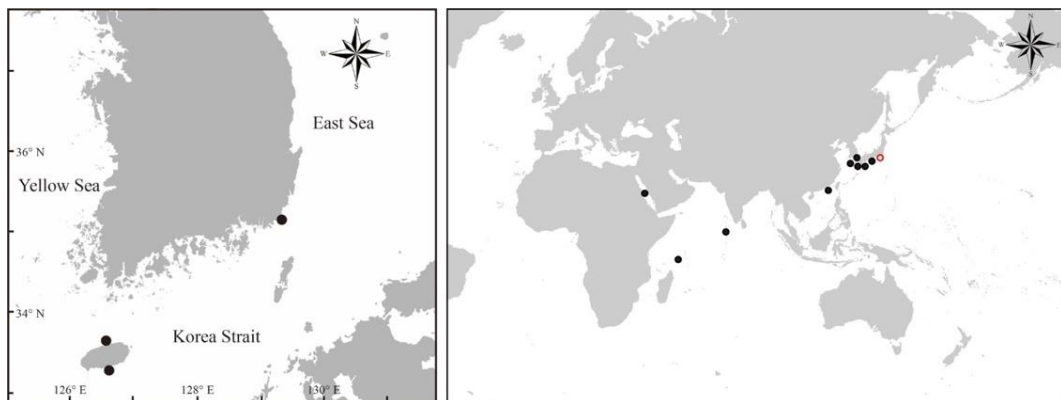


Fig. 31. Distribution of *Hyastenus elongatus* Ortmann, 1893. Open circle=type locality.



Fig. 32. *Hyastenus elongatus* Ortmann, 1893. Male (pcl 15.3 mm) (MABIK CR00247308), dorsal view.

Remark

Three species in the genus *Hyastenus* White, 1847 have been observed in Korean waters: *H. diacanthus* (De Haan, 1839), *H. elongatus* Ortmann, 1893, and *H. pleione* (Herbst, 1803). The differences among the three species are described under *H. pleione* (Herbst, 1803).

Sakai (1938) described that the gastric region of *Hyastenus elongatus* has an obtuse tubercle on the summit. However, some observed specimens have no tubercle in the gastric region.

16. *Hyastenus pleione* (Herbst, 1803) (Fig. 33) 긴빨게

Cancer pleione Herbst, 1803: 52, pl. 58, fig. 5.

Hyastenus pleione— A. Milne-Edwards, 1872: 250; Buitendijk, 1939: 247, fig. 14; Kamita, 1941: 74, fig. 34a, b; Shen & Dai, 1964: 41, fig.; Kim, 1970: 25; 1973: 538, 666, pl. 103, fig. 199; Griffin & Tranter, 1986: 153; Dai & Yang, 1991: 142, fig. 72(2), pl. 16(7, 8); Ko & Lee, 2015: 24, fig. 2C, D, pls. 15, 16.

Material examined

NIBRIV0000192007, 1 male (pcl 45.9 mm), Jung-gu, Incheon, Korea, 8 Jun. 2000; NIBRIV0000129716, 1 male (pcl 34.3 mm), Goheung-gun, Jeollanam-do, Korea, 24 Jun. 2008; MABIK CR00241008, 1 male (pcl 55.3 mm), Boryeong-si, Chungcheongnam-do, Korea, 13 Jul. 2008; NIBRIV0000753549, 1 female (pcl 44.6 mm), Mokpo-si, Jeollanam-do, Korea, 5 Mar. 2016.

Diagnosis

Carapace elongated pyriform, covered with tomentum, region well defined, dorsal surface convex. Proto gastric and mesogastric regions convex, with six tubercles arranged in form of 'Y'. Urogastric region with one tubercle. Cardiac region convex. Branchial region rounded, slightly convex, with three to four tubercles on anterior half. Pseudorostrum 0.33 times as long as pcl, covered with setae, straight. Supraorbital cave developed. Preorbital spine small, broad, projecting anteriorly. Antorbital lobe small, triangular. Postorbital lobe prominent, cupped. Basal antennal article narrow, distal margin unarmed. Pterygostomian region with three tubercles. Cheliped short, stout, covered with tomentum. Ambulatory stout, covered with tomentum.



Fig. 33. *Hyastenus pleione* (Herbst, 1803). Male (pcl 55.3 mm) (MABIK CR00241008), dorsal view.

Type locality

East Indies.

Habitat

Muddy bottom, 10 m deep.

Distribution

Pakistan, South India, Sri Lanka, Mergui Archipelago, China (Qingdao, Guangdong, Fujian, and Jiaozhou), Singapore, Indonesia (Ambon), and Korea (Fig. 34).

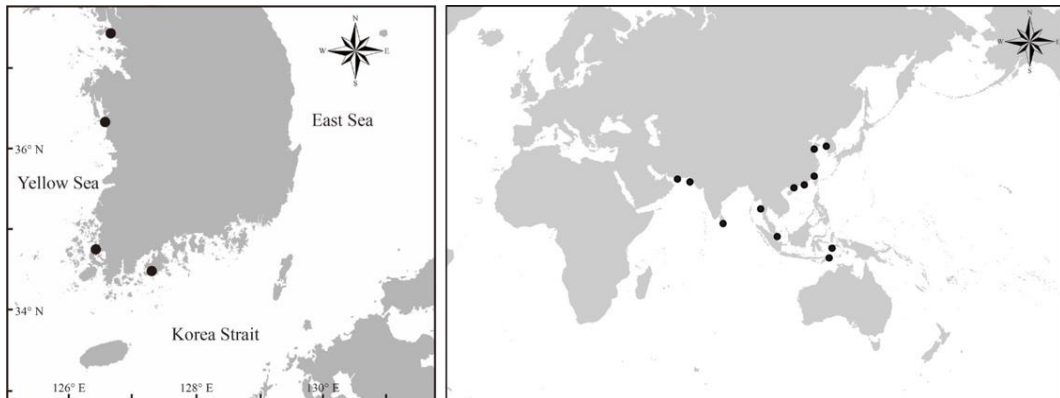


Fig. 34. Distribution of *Hyastenus pleione* (Herbst, 1803).

Remark

Hyastenus pleione (Herbst, 1803) has a wide distribution range. Incheon, one of the collection sites, is the northern limit distribution, and is the habitat of this species. Three species of *Hyastenus* White, 1847, have been reported in Korean waters. The three species have the following characteristics: *H. diacanthus* has an epibranchial spine; the branchial region of *H. elongatus* is unarmed; the mesogastric and protogastric regions of *H. pleione* have tubercles arranged in the form of a ‘Y’.

* 17. *Naxioides robillardi* (Miers, 1882) (Figs 36–38) 긴가시빨게

Naxia (*Naxioides*) *robillardi* Miers, 1882: 339, pl. 20, fig. 1.

Hyastenus elegans Miers, 1886: 58, pl. 6, fig. 3; Serène & Lohavanijaya, 1973:52.

Naxia mammillata Ortmann, 1893: 56, pl. 3 fig. 7.

Naxioides mamillata—Rathbun, 1911: 253; Sakai, 1938: 268, pl. 27, fig. 1; 1965: 78, pl. 35, fig. 1; 1976: 217, pl. 75, figs 1, 2; Serène & Lohavanijaya, 1973: 52, figs 98–103, pl. 9C–D.

Naxioides robillardi—Griffin, 1974: 21; Griffin & Tranter, 1986: 169 (key), 171; Poupin, 1995: 86, figs 7, 8a, b, 9a, b; Richer de Forges & Ng, 2013: 479 (list); Lee et al., 2017: 4, fig. 13A; Devi et al., 2019: 399, figs 2, 3.

Material examined

NIBRIV0000865951, 1 male (pcl 75.5 mm, cw 54.2 mm), Jocheon-eup, Jeju-si, Jeju-do, Korea, 8 Aug. 2015, coll. from fishing port; MABIK CR00247307, 1 male (pcl 5.5 mm, cw 3.6 mm), Seogwipo-si, Jeju-do, Korea, 32°41'26.97"N, 127°11'36.75"E, 5 May 2019, coll. by otter trawl; MABIK CR00247305–247306, 2 males (pcl 29.1, 18.5 mm, cw 17.1, 18.5 mm), Seogwipo-si, Jeju-do, Korea, 33°31'44.84"N, 127°21'34.54"E, 6 May 2019, coll. by otter trawl.

Diagnosis

Carapace elongated pyriform, covered with numerous, various spines and tomentum, regions well separated by grooves. Gastric region with three prominent spines transversely. Cardiac region slightly convex, with one prominent spine medially. Intestinal region with two spines transversely. Branchial region rounded, slightly convex. Pseudorostrum lyre-

shaped, 0.8 times as long as pcl, covered with hooked setae, with one accessory spine on distal one fourth dorsally. Supraorbital cave transversely narrow. Preorbital angle with prominent spine anteriorly. Intercalated spine prominent. Postorbital lobe prominent, cupped. Hepatic margin with one long spine. Branchial margin with numerous spines, posterior one largest. Basal antennal article with lateral margin having one short proximal spine projecting laterally. Cheliped short, slender; finger 0.5 times as long as palm. Ambulatory slender, covered with tomentum. In male, G1 gently curved, tapering distally, with distinct longitudinal groove.

Type locality

Mauritius.

Habitat

Rocky mud-shell bottoms, 38 to 260 m deep.

Distribution

The species is widely distributed in the Indo-Pacific region from the eastern coast of Africa to Australia (Norfolk Islands) (Fig. 35).

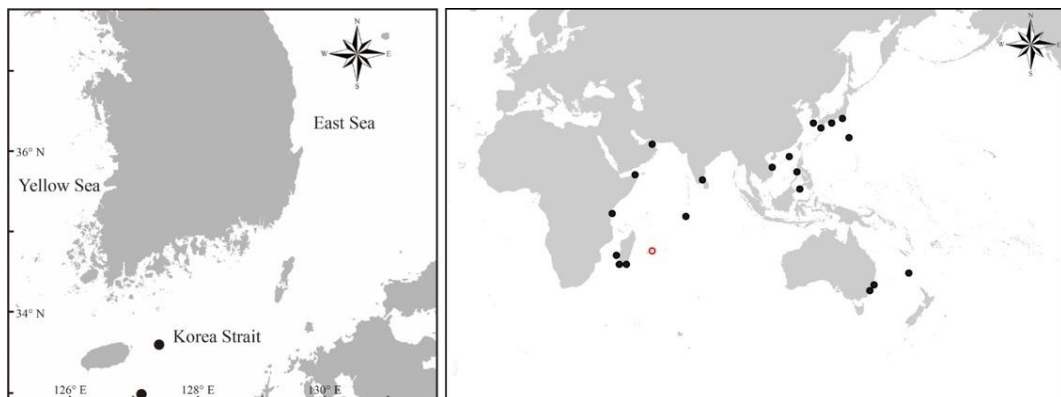


Fig. 35. Distribution of *Naxioides robillardi* (Miers, 1882). Open circle=type locality.

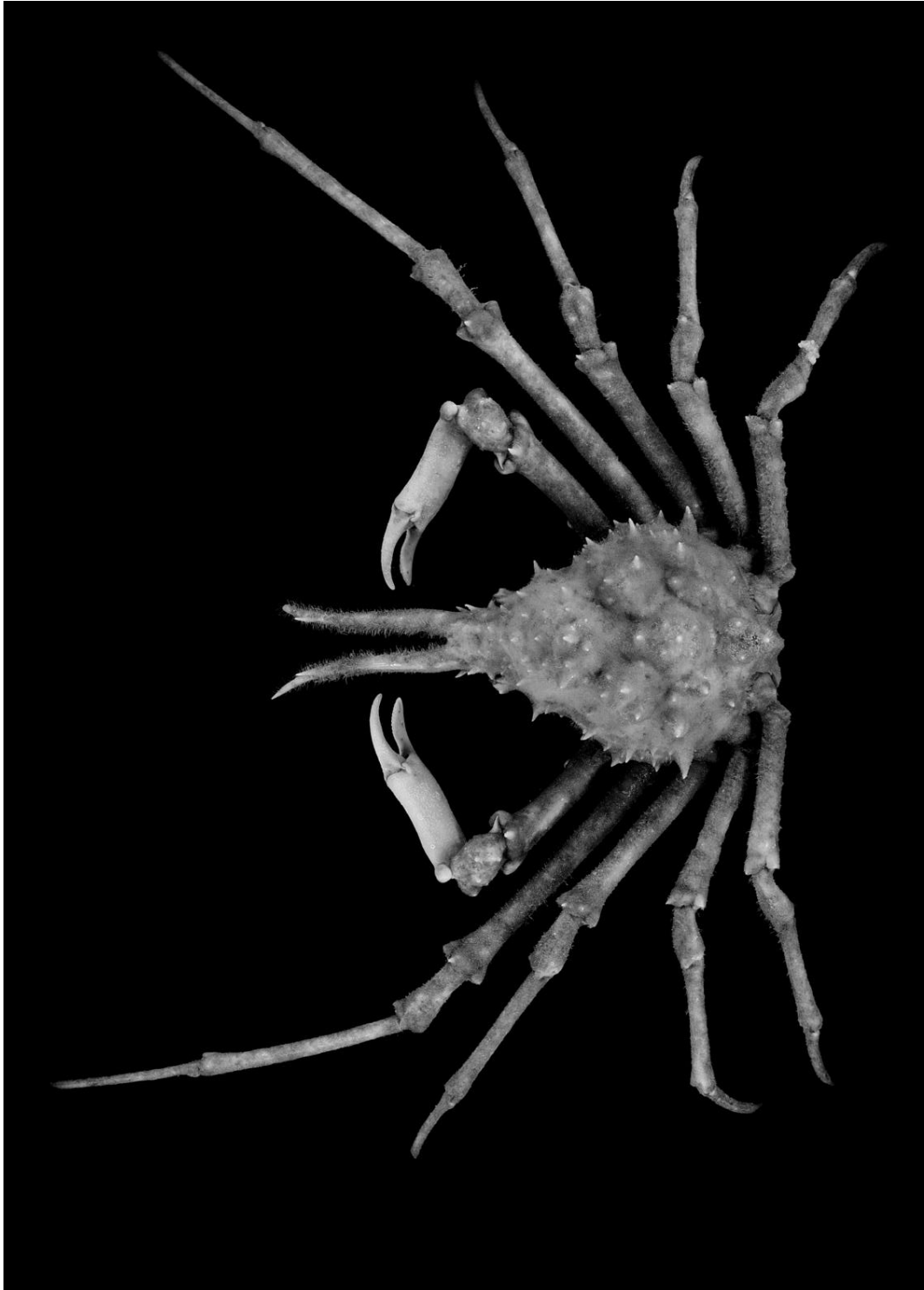


Fig. 36. *Naxioides robillardii* (Miers, 1882). Male (pcl 75.5 mm, cw 54.2 mm) (NIBRIV0000865951), dorsal view.



Fig. 37. *Naxioides robillardii* (Miers, 1882). Male (pcl 29.1 mm, cw 18.5 mm) (MABIK CR00247305), dorsal view.

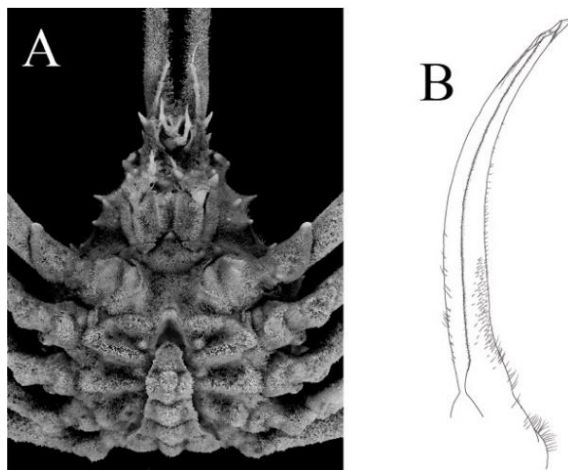


Fig. 38. *Naxioides robillardi* (Miers, 1882), Male (pcl 75.5 mm, cw 54.2 mm) (NIBRIV0000865951). A, Ventral view; B, left first gonopod, ventral view. Scale bar: B = 5 mm.

Remark

Naxioides robillardi (Miers, 1882) is the only species in the genus *Naxioides* A. Milne-Edwards, 1865 in Korea. The genus *Naxioides* can be distinguished from other epialtids based on the following characteristics: (1) a pseudorostrum with an accessory spine on the dorsal surface, and (2) a present of intercalated spine. Griffin (1974) synonymized *N. mammillata* Ortmann, 1893 under *N. robillardi*. Subsequently, however, Poupin (1995) detailed reviewed *N. robillardi* and recognized the presence of two forms. The characteristics of *N. robillardi* based on Griffin (1974) and Poupin (1995) are as follows: (1) the hepatic spine with one long spine, (2) the cardiac region with one medial spine, (3) pseudorostrum 0.86 times as long as pcl, and (4) basal antennal article with lateral margin having short proximal spine projecting laterally. And these two forms (typical and *mammillata* forms) feature presented by Poupin (1995) are as follows: (1) in the typical form, the posterior part of the carapace is a little convex (in *mammillata* form, more

convex), (2) the typical form with cw narrower than *mammillata* form when they are of similar size, (3) in the typical form, the gastric spines are well developed (in *mammillata* form, reduced), (4) in the typical form, the chela is more slender. Although these two forms are divided clearly, Poupin (1995) reported that the intermediate specimens were also found.

The observed specimens are generally consistent with the *mammillata* form. In this study, the authors identified the observed specimen as *N. robillardi* in line with the views of Griffin (1974). Specimens of various sizes (pcl 5.5–75.5 mm) were collected in Korean waters, and numerous small spines were observed in the carapace of a larger individual. This is consistent with the report of Poupin (1995) that spination of the carapace varies across individuals (e.g., juvenile, adult, and size).

Genus *Oxypleurodon* Miers, 1885 세모뿔게속

18. *Oxypleurodon stimpsoni* Miers, 1885 세모뿔게

Oxypleurodon stimpsoni Miers, 1885: 588; 1886: 38, pl. 6, figs 1, 1a–c; Richer de Forges, 1995: fig. 1A, pl. 1A; Richer de Forges & Ng, 2009: 248, 251, 523, fig. 7A; Lee et al., 2015: 1257, fig. 1A; Ko & Lee, 2015: 25; Lee et al., 2017: 5, figs 2A–C, 3A–C, 13B.

Sphenocarcinus stimpsoni—Alcock, 1899: 51; Sakai, 1934: 294; 1938: 286, pl. 29, fig. 3; 1976: 203, pl. 72, fig. 1, pl. 73, fig. 1; Kamita, 1941: 245; Kim, 1973: 534, pl. 103, fig. 196; Griffin, 1976: 215; Guinot & Richer de Forges, 1986: 136, figs 19C, D, 21A, B, pl. 8, figs G–I; 1986: 29; Richer de Forges, 1992: 4.

Rochinia stimpsoni—Griffin & Tranter, 1986: 187, fig. 63a, b.

Type locality

Ki Islands, Indonesia, 5°49'15"S, 132°14'15"E, 260 m.

Habitat

Muddy or sandy bottom, 221 to 580 m deep.

Distribution

Japan, Philippines, Indonesia, Taiwan, and Korea (Fig. 39).



Fig. 39. Distribution of *Oxypleurodon stimpsoni* Miers, 1885. Open circle=type locality.

Remark

In Korean waters, Sakai (1934) reported *Oxypleurodon stimpsoni* Miers, 1885, collected by Kaneko and Kamita (1941) and Kim (1973) cited it. *Oxypleurodon stimpsoni* has not been reported in Korean waters since 1934. The author has not yet observed the species.

19. *Pisoides bidentatus* (A. Milne-Edwards, 1873) (Fig. 40)

어리물맞이게

Libinia bidentata A. Milne-Edwards, 1873: 253.

Doclea orientalis Miers, 1879: 28, pl. 2, fig. 1.

Doclea bidentata—Ortmann, 1893: 48; Yokoya, 1928: 769; 1933: 154.

Pisoides bidentatus—Sakai, 1938: 290, fig. 39; 1976: 230, pl. 79, fig. 3; Kamita, 1941: 76, fig. 35; Kim, 1970: 25; 1973: 540, 667, fig. 253, pl. 107, 108, fig. 201a–d; Griffin & Tranter, 1986: 174 (list); Ko & Lee, 2015: 25.

Material examined

One male (pcl 31.9 mm), Samcheok-si, Gangwon-do, Korea, 25 Aug. 1970; MADBK 171914_001, 2 females (pcl 22.4 mm, 23.0 mm), 1 male (pcl 26.6 mm), Goseong-gun, Gangwon-do, Korea, 8 Feb. 1983.

Diagnosis

Carapace subcircular; dorsal surface granulated, covered with tomentum; regions well defined. Gastric region convex, with seven tubercles. Hepatic region with two tubercles. Cardiac region slightly convex, with two tubercles longitudinally. Intestinal region with one tubercle. Branchial region with six tubercles. Pseudorostrum short, slightly downwards, tapered anteriorly. Supraorbital cave developed. Preorbital spine prominent, projecting anteriorly, blunt. Postorbital spine prominent, small, acute. Hepatic spine prominent, broad, triangular, blunt. Postorbital spine and hepatic spine slightly fused. Branchial margin with one prominent spine, projecting laterally. Pterygostomial margin with three to four tubercles. Cheliped stout. Ambulatory legs long.



Fig. 40. *Pisoides bidentatus* (A. Milne-Edwards, 1873). Male (pcl 31.9 mm), dorsal view.

Type locality

Mouth of Amur River.

Habitat

Muddy or mud sandy bottoms, subtidal to 100 m deep.

Distribution

Russia (mouth of Amur River, Vladivostok), Japan, and Korea (Fig. 41).

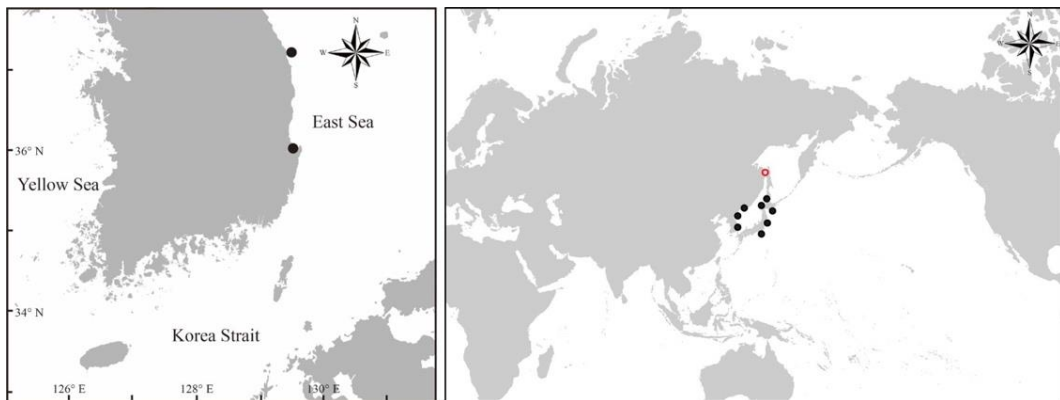


Fig. 41. Distribution of *Pisoides bidentatus* (A. Milne-Edwards, 1873). Open circle=type locality.

Remark

The genus *Pisoides* H. Milne-Edwards & Lucas, 1843 consists of three species: *P. bidentatus* (A. Milne-Edwards, 1873), *P. edwardsii* (Bell, 1836), and *P. ortmanni* (Bals, 1924). *Pisoides bidentatus* is the only species in the genus *Pisoides* H. Milne-Edwards & Lucas, 1843 in Korea. The genus *Pisoides* can be distinguished from other epialtids based on the following characteristics: (1) carapace subcircular, (2) intercalated spine absent, (3) pseudorostrum short, and (4) two to three tubercles on the pterygostomian margin.

Genus *Scyra* Dana, 1851 납작빨게속

20. *Scyra compressipes* Stimpson, 1857 (Fig. 43) 납작빨게

Scyra compressipes Stimpson, 1857: 218; Miers, 1886: 63, pl. 7, fig. 4; Yokoya, 1933: 155; Sakai, 1936: 97, fig. 44; 1938: 287, fig. 38; 1965: 82, pl. 37, fig. 2; 1976: 229, pl. 78, fig. 1; Kim, 1973: 538, 666, fig. 252, pl. 53, fig. 200; Dai & Yang, 1991: 144, pl. 17(2), fig. 73; Ko & Lee, 2015: 26, pls. 17, 18.

Material examined

Two males (pcl 17.0 mm, 26.6 mm), 2 females (pcl 17.0 mm, 20.5 mm) Pohang-si, Gyeongsangbuk-do, Korea, 36°00'1.0"N, 129°35'7.0"E, 31 May 2018, coll. by SCUBA diving; 1 female (pcl 18.8 mm), Pohang-si, Gyeongsangbuk-do, Korea, 36°00'1.0"N, 129°35'7.0"E, 20 Sep. 2018, coll. by SCUBA diving; 1 male (pcl 41.3 mm), Yeongdeok-gun, Gyeongsangbuk-do, Korea, 36°22'27.77"N, 129°24'50.25"E, 21 Nov. 2018, coll. by SCUBA diving at 15 m depth; 1 male (pcl 30.7 mm), Pohang-si, Gyeongsangbuk-do, Korea, 36°12'37.14"N, 129°23'6.12"E, 27 Mar. 2019, coll. by SCUBA diving.

Diagnosis

Carapace triangular, uneven, regions well defined. Gastric region convex, with four small tubercles, with hooked setae. Cardiac region slightly convex, with one tubercle. Intestinal region with one tubercle. Branchial region with one low but prominent tubercle, with few small tubercles irregularly. Pseudorostrum broad, flattened, tapered and acute anteriorly, with hooked setae on dorsal surface. Supraorbital eave developed. Preorbital spine prominent, triangular, acute anteriorly. Supraorbital eave and postorbital spine separated by

narrow slit. Postorbital spine and hepatic spine fused. Branchial margin with one strong spine, projecting laterally. Cheliped long, smooth, upper and inner margin parallel; with prismatic merus having crested margins; fingers about 0.6 times as long as palm. Ambulatory legs with carpus and merus having hooked setae on outer and inner margins.

Type locality

Hakodate Bay, Hokkaido, Japan.

Habitat

Subtidal rocky bottom.

Distribution

Japan, China (Yellow Sea), and Korea (Fig. 42).

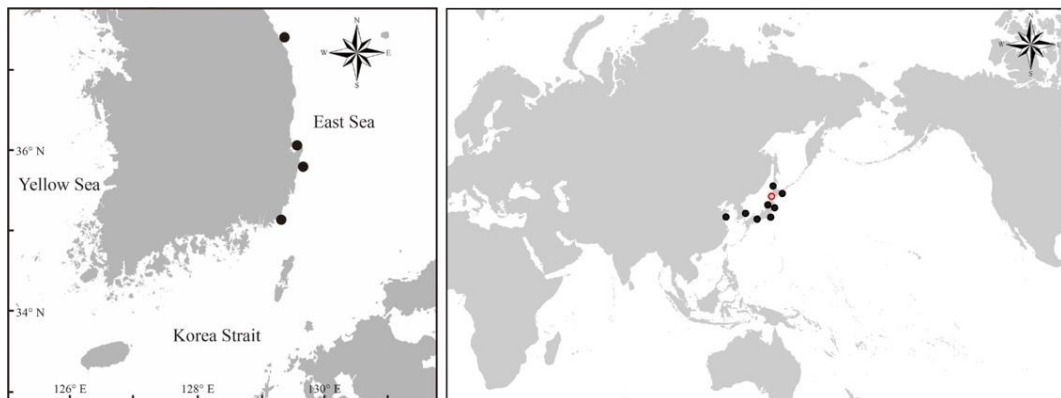


Fig. 42. Distribution of *Scyra compressipes* Stimpson, 1857. Open circle=type locality.



Fig. 43. *Scyra compressipes* Stimpson, 1857. Male (pcl 30.7 mm), dorsal view.

Remark

Scyra compressipes Stimpson, 1857 is commonly found at a depth of 20 to 30 m in the East Sea. The genus *Scyra* Dana, 1851 consists of three species: *S. acutifrons* Dana, 1851, *S. compressipes* Stimpson, 1857, and *S. tuberculata* Yokoya, 1933. *S. compressipes* can be distinguished from congeners based on the following characteristics: (1) the branchial margin has one strong and acute spine, and (2) a cheliped with a prismatic merus having crested margins.

Family Inachidae MacLeay, 1838

거미다리게과

Genus *Litosus* Loh & Ng, 1999

21. *Litosus sexspinosus* (Miers, 1884) 매끈콩알게

Paratymolus sexspinosus Miers, 1884: 261, pl. 27, fig. B; Henderson, 1893: 352; Calman, 1900: 33; Griffin & Tranter, 1986: 42, fig. 7f, g; Dai & Yang, 1991: 120.

Litosus sexspinosus—Loh & Ng, 1999: 399, figs 13, 14; Seo et al., 2017: fig. 2.

Type locality

Friday Island, Australia.

Habitat

Subtidal zone, Sandy bottoms, weedy pebbles, or coral rocks, up to 15 m deep.

Distribution

Australia, Indonesia, China, Singapore, India, and Korea (Fig. 44).

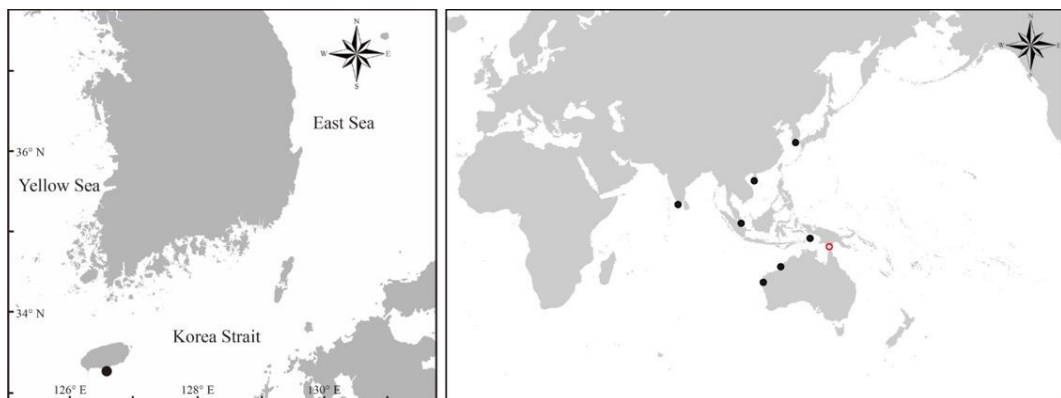


Fig. 44. Distribution of *Litosus sexspinosus* (Miers, 1884). Open circle=type locality.

Remark

Loh & Ng (1999) revised genus *Paratymolus* Miers, 1879 and separated genus *Litosus* Loh & Ng, 1999 from genus *Parayumolus*. The genus *Litosus* has the following features: (1) carapace without tubercles, (2) anterolateral margin of the carapace with one triangular tubercle projecting anteriorly, and (3) fused male abdominal segments 3–5 with concave lateral margins (Loh & Ng, 1999).

In Korean waters, Seo (2017) was reported to have collected *Litosus sexspinosus* (Miers, 1884) on Jejudo Island. The author has not yet observed the species.

Genus *Paratymolus* Miers, 1879

22. *Paratymolus pubescens* Miers, 1879 (Fig. 45) 콩알게

Paratymolus pubescens Miers, 1879: 45, pl. 2, fig. 6, 6a, b; Sakai, 1934: 293 (list); 1938: 208, text fig. 4, pl. 21, fig 1; 1965: 66, pl. 26, figs 3, 4; 1976: 156, pl. 48, fig. 3; Griffin & Tranter, 1986: 38, pl. 7c (part); Loh & Ng, 1999: 370, fig. 1; Ng et al., 2008: 112 (list); Takeda et al., 2011: 42, pl. 11, fig. 48; Seo et al., 2017: 746, fig. 1.

Paratymolus bituberculatus—Takeda, 1977; 121, pl. 12B. [Not *Paratymolus bituberculatus* Haswell, 1880c]

Material examined

One female (pcl 5.9 mm), Wando-gun, Jeollanam-do, Korea, 34°15'11.8"N, 126°46'45"E, 28 Aug. 2018, coll. from fishing port at 5 m depth; 1 female (pcl 6.4 mm), Tongyeong-si, Gyeongsangnam-do, Korea, 34°47' 7"N, 128°27'32.42"E, 27 Jun. 2019. coll. by van Veen grab sampler at 15.3 m depth.

Diagnosis

Carapace pentagonal, dorso-ventrally flattened. Anterior gastric region with two moderate height tubercles. Posterior gastric region with one weak or faint tubercle. Cardiac region with one broad and low tubercle. Branchial region with three tubercles on ridge. Pseudorostrum short, acute apically. Anterolateral margin with two prominent spines, posterior one larger. Posterolateral margin with one tubercle. Third antennal article 0.24 times pcl. Cheliped with merus having three small spines on posterior border; carpus with long, slender, and strong spine on flexor margin. Ambulatory legs long and slender; dactylus with denticle and one to two distinct spines on flexor margin.



Fig. 45. *Paratymolus pubescens* Miers, 1879. Female (pcl 6.4 mm), dorsal view.

Type locality

Matoya, Japan.

Habitat

Sandy bottoms or weedy pebbles, up to 50 m deep.

Distribution

Japan, and Korea (Fig. 46).

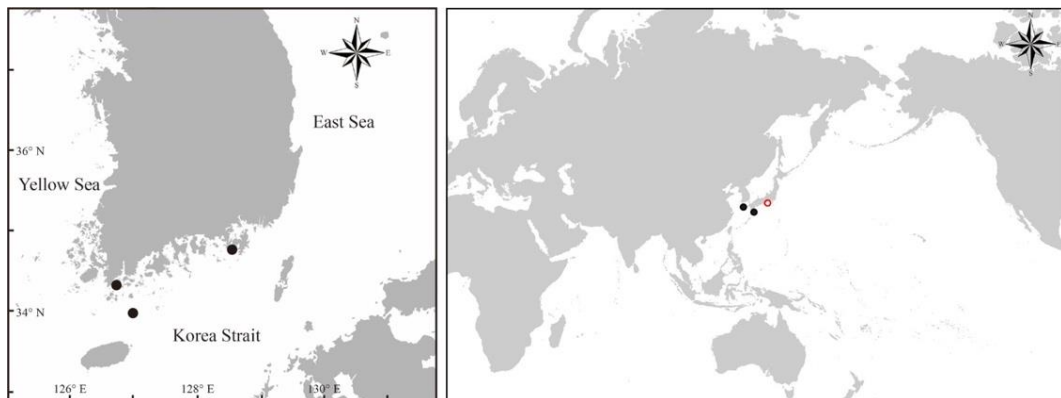


Fig. 46. Distribution of *Paratymolus pubescens* Miers, 1879. Open circle=type locality.

Remark

Ten species of the genus *Paratymolus* are recognized and they are distributed in the Indian and western Pacific Ocean: *P. apeli* Naderloo & Turkay, 2015, *P. barnardi* Loh & Ng, 1999, *P. bituberculatus* Haswell, 1880c, *P. coccus* Loh & Ng, 1999, *P. cygnus* Loh & Ng, 1999, *P. griffini* Loh & Ng, 1999, *P. hastatus* Alcock, 1895, *P. prolatus* Loh & Ng, 1999, *P. pubescens* Miers, 1879, and *P. vannus* Loh & Ng, 1999. Among these, *P. pubescens* Miers, 1879 is only reported in Japan and Korea.

Paratymolus pubescens is distinguished easily from its congeners based on the

following characteristics: (1) the third antenna segment is 0.2 times longer than pcl, (2) the post-gastric region has a weak tubercle, (3) the dorsal branchial region has three to four prominent tubercles, (4) posterior border of merus of cheliped has three to four small spines, (5) in male, the tip of the G1 is wide (Loh & Ng, 1999). All the examined specimens were female, but their characteristics were consistent with the description of Loh & Ng (1999).

Subfamily Inachinae MacLeay, 1838

Genus *Achaeus* Leach, 1817 아케우스게속

23. *Achaeus japonicus* (De Haan, 1839) (Fig. 48) 아케우스게

Inachus (Achaeus) japonicus De Haan, 1833–1849 (1839): 99, pl. 29, fig. 3, pl. H.

Achaeus japonicus—Miers, 1886: 9; Yokoya, 1933: 134; Sakai, 1934: 293, fig. 8; 1935: 65; 1936: 83, pl. 19, fig. 2; 1938: 211, fig. 5, pl. 22, fig. 1; 1965: 67, pl. 27, fig. 2; 1976: 158, pl. 49, fig. 1; Kamita, 1941: 59, fig. 24a–c; Kim, 1970: 23; 1973: 517, 661, fig. 238, pl. 50, fig. 185; Kim & Chang, 1985: 45; Griffin & Tranter, 1986: 10; Dai & Yang, 1991: 121, fig. 62, pl. 13(2); Ko & Lee, 2015: 28, fig. 2e, f, pl. 19.

Material examined

One individual, Uljin-gun, Gyeongsangbuk-do, Korea, 36°40'1.07"N, 129°25'41.66"E, 7 Jul. 2016, coll. by SCUBA diving; 1 ind., Pohang-si, Gyeongsangbuk-do, Korea, 35°58'9.74"N, 129°35'5.32"E, 24 Sep. 2016, coll. by SCUBA diving; 1 ind., Pohang-si, Gyeongsangbuk-do, Korea, 35°58'9.74"N, 129°35'5.32"E, 30 May 2018, coll. by SCUBA diving; 1 female (cl 15.2 mm), Pohang-si, Gyeongsangbuk-do, Korea, 36°00'20.59"N, 129°35'11.64"E, 19 Sep. 2018, coll. by SCUBA diving; 1 male (cl 15.4 mm), Seogwipo-si, Jeju-do, Korea, 33°11'43.85"N, 127°1'38.96"E, 1 May 2019, coll. by otter trawl; 1 female, 1 male (cl 15.6, 14.1 mm), Seogwipo-si, Jeju-do, Korea, 33°31'44.48"N, 127°21'34.54"E, 6 May 2019, coll. by otter trawl; 1 male (cl 13.2 mm), Geoje-si, Gyeongsangnam-do, Korea, 34°41'0.9"N, 128°46'6.06"E, 25 Jun. 2019, coll. by SCUBA diving at 20 m depth; 2 male (cl 16.4, 17.0 mm), Geoje-si, Gyeongsangnam-do, Korea, 34°43'52.04"N, 128°40'14.36"E, 26 Jun. 2019, coll. by SCUBA diving at 17 m depth.

Diagnosis

Carapace pyriform, with dorsal surface unarmed. Gastric, hepatic, cardiac and branchial regions clearly separated by grooves. Pseudorostrum short, each lobe with serrated on tip. Supraorbital cave unarmed. Hepatic lobe broad. Basal antennal article long, slender, with small granules distally. Cheliped robust, with scattered setae; with merus, carpus and propodus swollen, with merus and carpus having scattered tubercles on outer surface. Ambulatory legs extremely long and slender; first ambulatory leg longest; dactylus of third and fourth ambulatory legs slightly curved. Abdomen with five segments and telson.

Type locality

Japan.

Habitat

Subtidal rocky shore, weedy pebbles, sandy or muddy bottom, 20 to 100 m deep.

Distribution

Japan, China (Hong Kong), and Korea (Fig. 47).

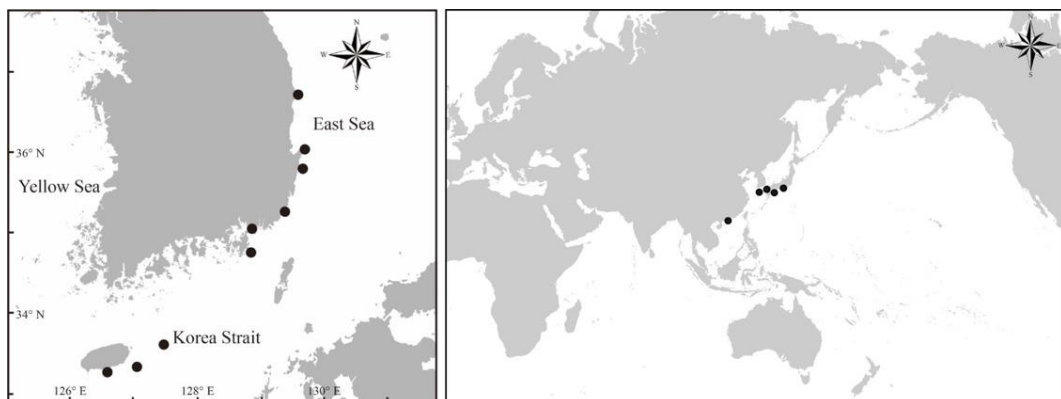


Fig. 47. Distribution of *Achaeus japonicus* (De Haan, 1839).



Fig. 48. *Achaeus japonicus* (De Haan, 1839). Male (cl 15.4 mm), dorsal view.

Remark

In the Korean fauna, in the genus *Achaeus* Leach, 1817, *A. japonicus* (De Haan, 1839) is similar to *A. lacertosus* Stimpson, 1857. The differences between the two species are described under *A. lacertosus*.

In Korean waters, *A. japonicus* is found in the subtidal zone of Jejudo Island, the southern part of the East Sea, and the eastern part of the Korea Strait. All the examined specimens had sponges on their carapaces and legs.

24. *Achaeus lacertosus* Stimpson, 1857 (Fig. 49) 가시이마아케우스게

Achaeus lacertosus Stimpson, 1857: 218; Griffin, 1966a: 38; 1970: 105, figs 1b, 5, 14a, d; 1972: 69; 1974: 6; Sakai, 1976: 159, fig. 82; Griffin & Tranter, 1986: 5 (key), 10; Ko & Lee, 2015: 29.

Achaeus breviceps Haswell, 1880b: 433; Haswell, 1880a: 146.

Achaeus spinifrons Sakai, 1938: 212, fig. 6; Kamita, 1941: 60, fig. 25; Kim, 1973: 518, 662, fig. 239, pl. 100, fig. 186.

Material examined

One female (cl 7.5 mm), Wando-gun, Jeollanam-do, Korea, 34°19'37.8"N, 126°48'54.24"E, 28 Aug. 2018; 1 female (cl 9.0 mm), Tongyeong-si, Gyeongsangnam-do, Korea, 34°47'50.7"N, 128°29'25.6"E, 26 Jun. 2019.

Diagnosis

Carapace pyriform, with dorsal surface unarmed, covered with hooked setae, regions indistinct. Epigastric region with dorsal surface having numerous spinules on midline. Pseudorostrum short, each lobe serrated distally. Supraorbital eave serrated on margin. Eyestalk long. Hepatic lobe broad, produced laterally, with margin serrated. Branchial margin serrated. Basal antennal article long, slender, with small granules near tip. Cheliped with scattered setae, shorter than ambulatory legs; with merus having row of spines on inner and outer margins; with carpus and palm having row of spines on inner margin. Ambulatory legs extremely long and slender; first ambulatory leg longest; dactylus of third and fourth ambulatory legs strongly falcate. Abdomen with five segments and telson.



Fig. 49. *Achaeus lacertosus* Stimpson, 1857. Female (cl 9.0 mm), dorsal view.

Type locality

Port Jackson, Australia.

Habitat

Subtidal rocky shore, weedy bottom, 6 to 90 m deep.

Distribution

The species is widely distributed in the Indo-Pacific region from the eastern coast of Africa to the eastern coast of Australia (Fig. 50).

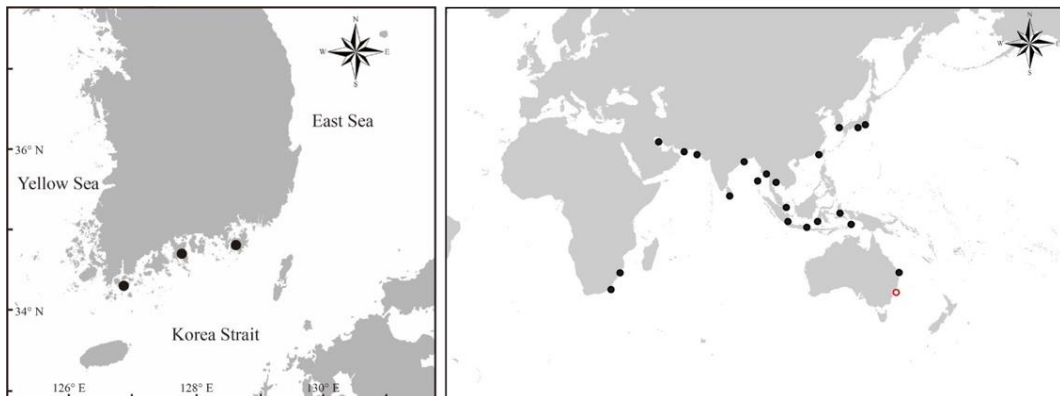


Fig. 50. Distribution of *Achaeus lacertosus* Stimpson, 1857. Open circle=type locality.

Remark

In the Korean fauna, in the genus *Achaeus* Leach, 1817, *A. lacertosus* Stimpson, 1857 is similar to *A. japonicus* (De Haan, 1839). These two species share the smooth carapace characteristic. However, *A. lacertosus* can be distinguished from *A. japonicus* based on the following morphological characteristics: (1) hepatic region is prominently expanded laterally (moderate expanded laterally in *A. japonicus*), (2) third and the fourth ambulatory legs with dactyli strongly curved (slightly curved in *A. japonicus*).

Achaeus lacertosus has an extremely wide range of distribution (see distribution).
Achaeus lacertosus was found on Hansando Island in Korean waters, and the area is close to the northern limit of distribution of the species.

25. *Achaeus spinosus* Miers, 1879 (Fig. 52) 가시아케우스케

Achaeus spinosus Miers, 1879: 25; Yokoya, 1933: 136; Sakai, 1938: 217, figs 9a–c; 1965: 67, pl. 27, fig. 3; 1976: 162, fig. 85; Kim, 1985: 78, fig. 3A; Kim & Chang, 1985: 45; Griffin & Tranter, 1986: 5 (key); Ko & Lee, 2015: 29.

Material examined

One female (cl 5.6 mm), Ulleung-gun, Gyeongsangbuk-do, Korea, 37°14'23.83"N, 131°52'21.75"E, 11 May 2018; 1 female (cl 3.2 mm), Seogwipo-si, Jeju-do, Korea, 33°13'39.28"N, 126°33'41.72"E, 13 Sep. 2018; 1 male, Seogwipo-dong, Seogwipo-si, Jeju-do, Korea, 33°27'11"N, 126°56'30"E, 14 Mar. 2019, coll. by SCUBA diving; 1 female (cl 7.8 mm), 1 male (cl 6.2 mm), Seongsan-eup, Seogwipo-si, Jeju-do, Korea, 33°13'30.5"N, 126°33'58.23"E, 24 Jul. 2019; 1 female (cl 7.1 mm), Seogwipo-dong, Seogwipo-si, Jeju-do, Korea, 33°13'39.28"N, 126°33'41.72"E, 26 Jul. 2019; 1 female (cl 6.1 mm), Seogwipo-dong, Seogwipo-si, Jeju-do, Korea, 33°13'7.25"N, 126°31'12.45"E, 28 Jul. 2019.

Diagnosis

Carapace pyriform, regions distinct. Gastric region convex, with dorsal surface having hooked setae on midline, with one prominent tubercle. Hepatic region with dorsal surface having hooked setae, produced laterally. Cardiac region strongly convex, with two tubercles side by side. Branchial region strongly convex, with two tubercles, with hooked setae medially. Intestinal region with one tubercle. Pseudorostrum short, each lobe rounded, with one or two spinules, with dorsal surface having hooked setae. Supraorbital cave

serrated on anterior half. Eyestalk long, with one tubercle on anterior margin. Postorbital region slightly concave. Hepatic lobe produced laterally, with anterior margin having small spines. Branchial margin with one spine laterally, posterolateral margin with row of spines. Basal antennal article long, slender, with row of small spines longitudinally. Cheliped robust, with scattered setae, shorter than ambulatory legs; with merus having row of spines on inner and outer margins; with carpus and palm having row of spines on inner margin. Ambulatory legs extremely long and slender; first ambulatory leg longest; dactylus of third and fourth ambulatory legs falcate. Abdomen with five segments and telson.

Type locality

off coast of Mie Prefecture, Japan, 34°10'N, 136°47'E, 55 m.

Habitat

Subtidal rocky shore, weedy bottom, 5 to 187 m deep.

Distribution

Persian Gulf, Maldives, Japan, and Korea (Fig. 51).

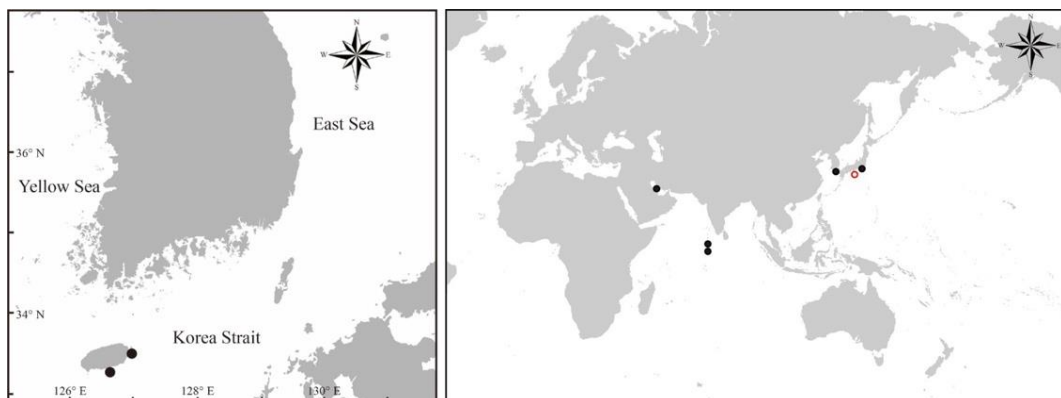


Fig. 51. Distribution of *Achaeus spinosus* Miers, 1879. Open circle=type locality.



Fig. 52. *Achaeus spinosus* Miers, 1879. Male (cl 7.8 mm), dorsal view.

Remark

In the Korean fauna, in the genus *Achaeus* Leach, 1817, *A. spinosus* Miers, 1879 is similar to *A. tuberculatus* Miers, 1879. The differences between the two species are described under *A. tuberculatus*.

26. *Achaeus tuberculatus* Miers, 1879 (Fig. 53) 가는다리아케우스게

Achaeus tuberculatus Miers, 1879: 25; Yokoya, 1933: 135; Sakai, 1934: 293; 1935: 65; 1936: 83, pl. 19, fig. 1; 1938: 214, fig. 7a–c, pl. 22, fig. 3; 1976: 160, figs 83a, b, pl. 49, fig. 2; Kamita, 1941: 61, fig. 26; Kim, 1970: 24; 1973: 520, 662, fig. 240, pl. 51, fig. 187; Kim & Chang, 1985: 45; Griffin & Tranter, 1986: 17; Dai & Yang, 1991: 122, pl. 13(3); Ko & Lee, 2015: 30.

Material examined

One male (cl 10.5 mm), Seogwipo-si, Jeju-do, Korea, 33°21'58.41"N, 127°11'44.83"E, 1 May 2019, coll. by otter trawl; 1 male (cl 10.7 mm), Seogwipo-si, Jeju-do, Korea, 33°11'37.09"N, 126°51'41.16"E, 2 May 2019; 1 male (cl 6.6 mm), Seogwipo-si, Jeju-do, Korea, 32°12'21.81"N, 126°41'59.52"E, 4 May 2019, coll. by otter trawl; 1 female (cl 10.3 mm), Seogwipo-si, Jeju-do, Korea, 32°42'7.76"N, 127°21'34.54"E, 5 May 2019, coll. by otter trawl; 1 female (cl 9.1 mm), Seogwipo-si, Jeju-do, Korea, 32°51'51.85"N, 127°1'22.81"E, 5 May 2019, coll. by otter trawl.

Diagnosis

Carapace pyriform. Gastric, hepatic, cardiac and branchial regions separated by shallow grooves. Gastric region with one prominent tubercle medially. Cardiac region with bifurcated tubercle medially. Pseudorostrum short, with tip rounded. Supraorbital eave unarmed. Hepatic lobe broad; with lateral margin having tubercles. Cheliped robust, with scattered setae; with merus, carpus and propodus swollen, with scattered teeth on outer surface. Ambulatory legs extremely long and slender; first ambulatory leg longest; dactylus of third and fourth ambulatory legs slightly curved. Abdomen with five segments and telson.

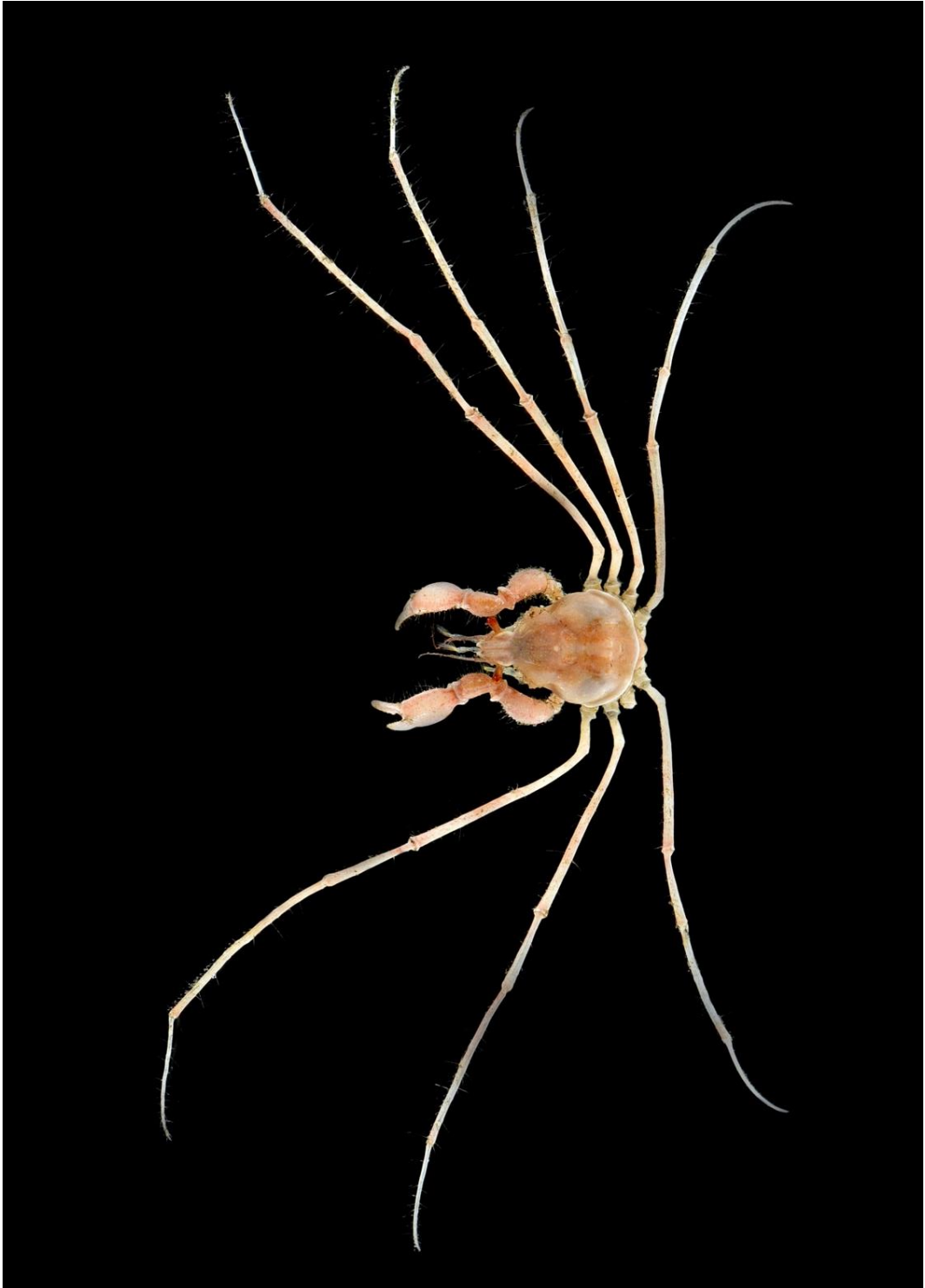


Fig. 53. *Achaeus tuberculatus* Miers, 1879. Male (cl 10.5 mm), dorsal view.

Type locality

Korea Strait.

Habitat

Muddy, sand muddy or broken shell bottoms, 20 to 200 m deep.

Distribution

Korea Strait, Japan, China (Jiaozhou Bay), East China Sea, and Korea (Fig. 54).

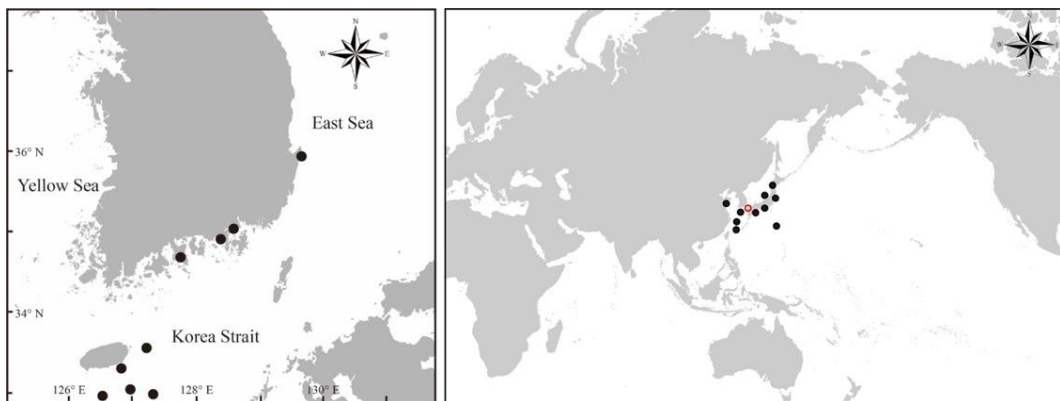


Fig. 54. Distribution of *Achaeus tuberculatus* Miers, 1879. Open circle=type locality.

Remark

The original description in Miers (1879) reported that the cardiac region with one non-bifurcated tubercle. Later, Sakai (1938) mentioned that bifurcated tubercle is often found. The examined specimens had bifurcated tubercles in the cardiac region.

In the Korean fauna, in the genus *Achaeus* Leach, 1817, *A. tuberculatus* Miers, 1879 is similar to *A. spinosus* Miers, 1987. *Achaeus tuberculatus* can be distinguished from *A. spinosus*, however, based on the following morphological characteristics: (1) carapace with gastric and cardiac regions each having one tubercle (with one gastric, two cardiac, and two branchial tubercles in *A. spinosus*), and (2) the third and the fourth ambulatory legs have slightly curved dactyli (strongly curved in *A. spinosus*).

Genus *Cyrtomaia* Miers, 1886

애기거미다리게속

*** 27. *Cyrtomaia platypes* Yokoya, 1933 (Fig. 55)** 애기거미다리게

Cyrtomaia platypes Yokoya, 1933: 145, fig. 52; Takeda & Miyake, 1969: 501, fig. 11f, g;
Guinot & Richer de Forges, 1982: fig. 47, 48A, B, 49C–E.

Cyrtomaja platypes—Sakai, 1938: 242.

Material examined

One male (cl 10.2 mm, cw 10.2), South of Jeju-do, Korea, 32°41'26.97"N, 127°11'36.75"E,
5 May 2019, coll. by otter trawl.

Diagnosis

Carapace subcircular; dorsal surface finely granulated. Gastric region convex, with two protogastric spines transversely, one median gastric spine. Hepatic region with one prominent spine. Cardiac region convex, with two spines transversely. Branchial region with anterior region having one prominent spine; posterior region with one row of four spines, size diminishing posteriorly. Intestinal region with one low spine. Rostrum slender. Pseudorostrum prominent. Eyestalk slender, long, with two spines terminally. Postorbital spine prominent, lateral margin serrated anteriorly. Fourth and fifth antennal articles foliate. Cheliped shorter than ambulatory legs; with row of long spines on outer margin; palm long and slender, with row of spines. Ambulatory legs very long and slender. First and second ambulatory legs with merus having row of spines on outer margin.

Type locality

near Tanabe, Wakayama Prefecture, Japan.



Fig. 55. *Cyrtomaia platypes* Yokoya, 1933. Male (cl 10.2 mm), dorsal view.

Habitat

100 to 210 m deep.

Distribution

Japan, (?) New Caledonia, and Korea (Fig. 56).

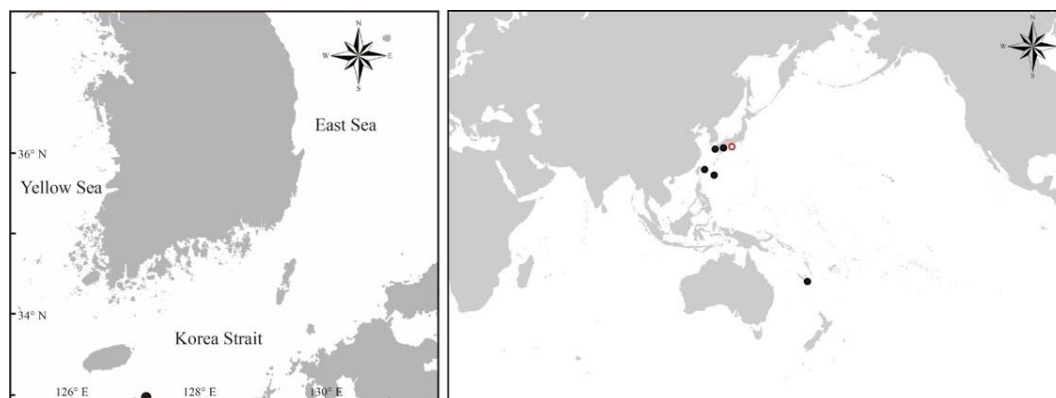


Fig. 56. Distribution of *Cyrtomaia platypes* Yokoya, 1933. Open circle=type locality.

Remark

Cyrtomaia platypes Yokoya, 1933 is closely related to *C. hispida* (Borradaile, 1916) and *C. lamellata* Rathbun, 1906. Guinot & Richer de Forges (1982) reviewed the taxonomy of the genus *Cyrtomaia* Miers, 1886 and recognized 21 species, including *C. hispida*, *C. lamellata* and *C. platypes*. Afterward, Griffin and Transter (1986) limited them to 17 species, questioning the validity of the species recognized by Guinot & Richer de Forges (1982). According to Griffin and Transter (1986), *C. hispida*, *C. lamellata* and *C. platypes* are one species because the features suggested by Guinot & Richer de Forges (1982) examined only a few specimens and geographical variations influences species identification. Richer de Forges & Ng (2007) noted that the differences between these species mentioned above are hardly normal variation.

The characteristics of a single male specimen collected from Jejudo Island were as follows: (1) eyestalk with two tubercles distally, (2) posterior branchial region with one row of four spines, and (3) a rostrum slender. The author identified the observed specimen as *C. platypes* in line with the views of Guinot & Richer de Forges (1982).

28. *Platymaia wyvillethomsoni* Miers, 1885 (Fig. 57) 거미다리게

Platymaia wyvillethomsoni Miers, 1886: 13, pl. 2, figs 1, 1a–e; Kim, 1970: 24; 1973: 515, pl. 50, fig. 184; Guinot & Richer de Forges, 1986: 90, fig. 2A–C, pl. I, fig. A, B; Ko & Lee, 2015: 31, pls. 20–22.

Platymaia alcocki—Seno & Konno, 1954: 85, fig. 1, pl. 2; Sakai, 1976: 176, fig. 94a, pl. 57. [Not *Platymaia alcocki* Rathbun, 1916]

Material examined

Two females (cl 26.8 mm, 35.4 mm), 3 males (cl 37.8–39.6 mm), Suyeong-gu, Busan, Korea, 11 Apr. 2019, coll. by gill net at 100 m depth.

Diagnosis

Carapace subcircular; dorsal surface finely granulated. Gastric region slightly convex, with four spines. Hepatic region with two spines. Cardiac region slightly convex, with two spines transversely. Branchial region with two spines. Rostrum short, slightly lower. Pseudorostrum short. Eyestalk short, robust. Postorbital spine prominent. Branchial margin with six spines. Basal antennal article slender, movable, with one tubercle near tip. Cheliped shorter than ambulatory legs; with merus very slender, with row of spines on outer and inner margin; palm very swollen, with spines on outer and inner margin. Ambulatory legs very long and slender. First ambulatory leg with long and prominent row of spines on outer and inner margin. Second to fourth ambulatory legs with propodus flatten, having row of long soft setae on inner margin; dactylus flatten, slightly broaden distally. Second and third ambulatory legs with meri having small row of spines on inner margin. Fourth ambulatory leg unarmed.



Fig. 57. *Platymaia wyvillethomsoni* Miers, 1885. Male (cl 37.8 mm), dorsal view.

Type locality

Admiralty Islands, 1°54'S, 146°39'40"E, 270 m

Habitat

Muddy or sand muddy bottoms, 150 to 400 m deep.

Distribution

Japan, East China Sea, Philippines, Papua New Guinea (Admiralty Islands), and Korea (Fig. 58).

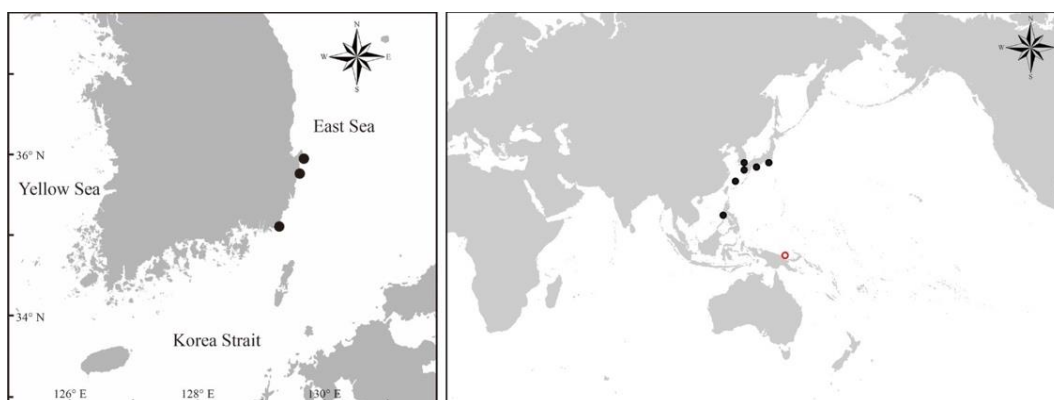


Fig. 58. Distribution of *Platymaia wyvillethomsoni* Miers, 1885. Open circle=type locality.

Remark

Platymaia wyvillethomsoni Miers, 1885, has been collected from Pohang in Korean waters. This region appears to be the northern limit of distribution of the species.

Family Inachoididae Dana, 1851 한뿔두드럭게과

Genus *Pyromaia* Stimpson, 1871 한뿔두드럭게속

Subfamily Inachoidinae Dana, 1851

29. *Pyromaia tuberculata* (Lockington, 1877) (Fig. 60) 한뿔두드럭게

Inachus tuberculatus Lockington, 1877: 30; Miers, 1886: 19.

Dasygyius tuberculatus—Rathbun, 1898: 570; Rathbun, 1904: 172, fig. 92, pl. 10, figs 3, 3a.

Inachoides tuberculatus—Schmitt, 1921: 199, figs 123a, b.

Pyromaia tuberculata—Rathbun, 1925: 133, pl. 40, fig. 3, pl. 218, figs 1–4; Sakai, 1971: 142, figs 4, 5; 1976: 168, fig. 92a, b, pl. 51, fig. 2; Kim, 1985: 78; Ko & Lee, 2015: 33, pls. 23, 24.

Material examined

MADBK 172201_003, 1 male (cl 19.6 mm), Changwon-si, Gyeongsangnam-do, Korea, 35°11'40.1"N, 128°34'47.63"E, 9 Jul. 2012, coll. from fishing port; 1 female (cl 11.9 mm), Geoje-si, Gyeongsangnam-do, Korea, 34°43'49.54"N, 128°37'26.82"E, 15 Aug. 2018, coll. from fishing port; 1 female (cl 13.6 mm), Pohang-si, Gyeongsangbuk-do, Korea, 35°57'58.7"N, 129°32'56.9"E, 18 Sep. 2018, coll. from fishing port; 1 female (cl 14.9 mm), Geoje-si, Gyeongsangnam-do, Korea, 34°46'36.66"N, 128°35'31.8"E, 25 Jun. 2019; 1 female (cl 14.8 mm), Tongyeong-si, Gyeongsangnam-do, Korea, 34°47'50.7"N, 128°29'25.6"E, 26 Jun. 2019, coll. from fishing port.

Diagnosis

Carapace pyriform, regions distinct, with dorsal surface having tubercles. Gastric region convex; anterior region with row of tubercles transversely; posterior region with four tubercles mesially. Cardiac region convex, with some tubercles longitudinally, with one prominent tubercle. Branchial region convex, with tubercles longitudinally. Intestinal region slightly convex, with some tubercles mesially. Rostrum single, acute distally, with dorsal surface having setae. Supraorbital eave well developed. Postorbital spine prominent, acute. Hepatic margin with tubercles. Anterolateral margin with prominent tubercles. Cheliped robust; with merus and carpus having row of tubercles on inner and outer border; chela swollen, with row of tubercles on dorsal surface. Ambulatory legs long and slender. Abdomen with six segments (sixth segment and telson fused).

Type locality

San Diego Bay, California.

Habitat

Muddy bottom of shores, up to 80 m deep.

Distribution

From California to the Bay of Panama, Western Australia, Japan, and Korea (Fig. 59).

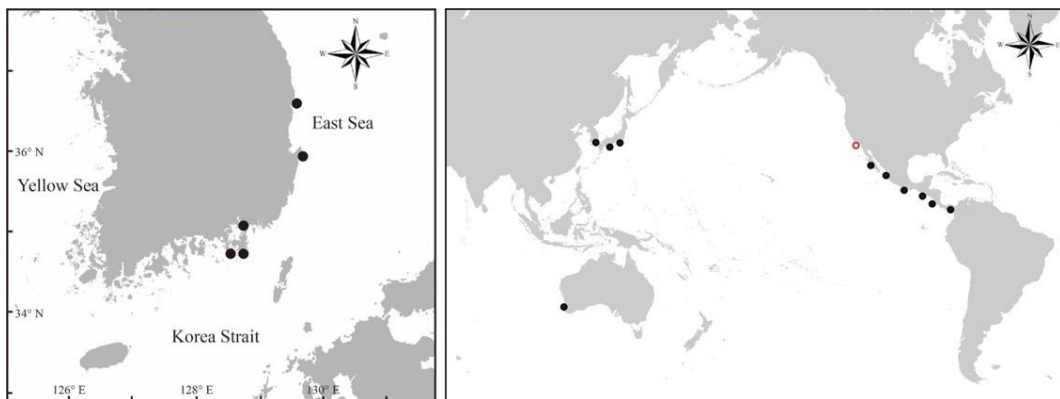


Fig. 59. Distribution of *Pyromaia tuberculata* (Lockington, 1877). Open circle=type locality.



Fig. 60. *Pyromaia tuberculata* (Lockington, 1877). Male (cl 19.6 mm) (MADBK 172201_003), dorsal view.

Remark

Pyromaia tuberculata (Lockington, 1877) is the only species in the family Inachoididae Dana, 1851 in Korea. It seems that the species inhabited Western Central America (from San Francisco to the Panama Canal), but migrated to the Northwest Pacific Region after World War II (Sakai, 1976), potentially because the larvae were carried by ballast water (McLay, 2009; Ahyong & Wilkens, 2011; McLay, 2015). In Korean waters, a collection from Uljin in 1982 was first reported by Kim (1985).

Family Majidae Samouelle, 1819 물맞이게과

Subfamily Majinae Samouelle, 1819 물맞이게아과

Genus *Entomonyx* Miers, 1884 가시뿔게속

30. *Entomonyx spinosus* Miers, 1884 (Fig. 62) 가시뿔게

Entomonyx spinosus Miers, 1884: 526, pl. 47, fig. B; Griffin, 1966a: 81; 1966b: 287 (key); 1974: 11; Kim, 1973: 545, 668, fig. 256, pl. 111, 112, fig. 105a–c; Griffin & Tranter, 1974: 166; 1986: 205; Sakai, 1976: 253, pl. 87, fig. 2; Kim & Chang, 1985: 49; Ko & Lee, 2015: 35.

Material examined

One male (pcl 16.9 mm), Seogwipo-si, Jeju-do, Korea, 32°52'5.42"N, 127°12'1"E, 5 May 2019, coll. by otter trawl; 2 female (pcl 23.5 mm, 20.2 mm), Seogwipo-si, Jeju-do, Korea, 32°41'26.97"N, 127°11'36.75"E, 5 May 2019, coll. by otter trawl; 1 male (pcl 22.9 mm), Seogwipo-si, Jeju-do, Korea, 33°31'44.84"N, 127°21'34.54"E, 6 May 2019, coll. by otter trawl; 1 male (pcl 23.2 mm), Seogwipo-si, Jeju-do, Korea, 33°31'51.56"N, 127°32'53.14"E, 6 May 2019, coll. by otter trawl.

Diagnosis

Carapace pyriform; dorsal surface covered with small tubercles and hooked setae. Gastric region convex, with two spines on midline. Cardiac region with two spines side by side. Intestinal region with one small spine. Branchial region with two long lateral spines. Pseudorostrum acute distally, straight, markedly deflexed, 0.2 times as long as pcl, covered with hooked setae. Supraorbital eave strongly expanded, with two preorbital spines and one

antorbital spine. Intercalated spine prominent. Postorbital spine bilobed distally. Hepatic margin with three or four distinct tubercles. Posterior carapace margin with one prominent spine medially. Cheliped robust, covered with small tubercles. Ambulatory legs slender, with numerous hooked setae, with merus having one distal spine on outer margin.

Type locality

Providence Islands, Seychelles.

Habitat

Muddy, sandy, and shell bottoms, 60 to 150 m deep.

Distribution

The species is widely distributed in the Indo-Pacific region from the eastern coast of Africa to Japan (Fig. 61).

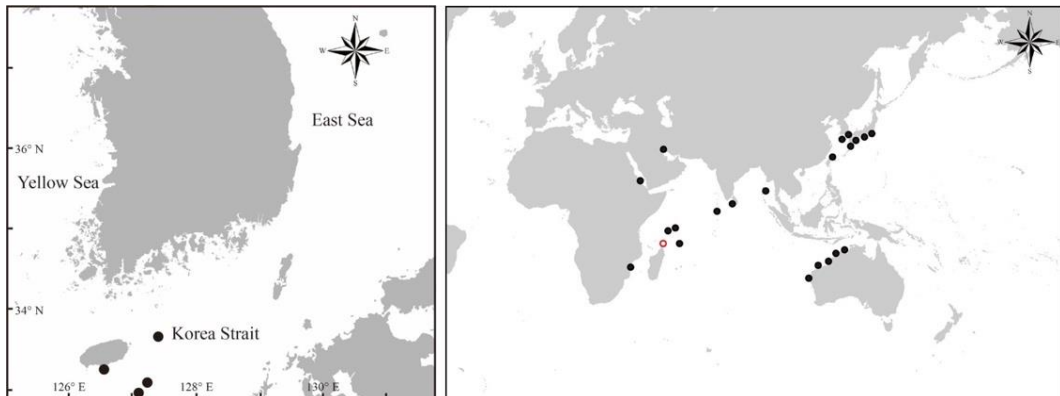


Fig. 61. Distribution of *Entomonyx spinosus* Miers, 1884. Open circle=type locality.



Fig. 62. *Entomonyx spinosus* Miers, 1884. Male (pcl 23.2 mm), dorsal view.

Remark

Entomonyx spinosus Miers, 1884 is the only species of the genus *Entomonyx* Miers, 1884.

The genus *Entomonyx* has the following features: (1) supraorbital eave strongly expanded, and (2) posterior carapace margin with one spine medially. *Entomonyx spinosus* has a wide distribution from eastern Africa to western Pacific Ocean. The species is mostly found in waters off Jeju Island in Korean waters, close to the northern limit of distribution of this species.

Genus *Holthuija* Ng & Richer de Forges, 2015

31. *Holthuija cognata* Ng & Richer de Forges, 2015 애기털다리개

Maja miersii—Muraoka, 1998: 27.

Maja miersi—Yokoya, 1933: 157; Sakai, 1938: 298, pl. 38 fig. 2; 1976: 237, pl. 82, fig. 3;
Kamita, 1941: 245; Kim, 1973: 544; Miyake, 1983: 47, pl. 16 fig. 1.

Holthuija cognata Ng & Richer de Forges, 2015: 161, figs 25A, 27I–K, 37H, 46D, 50H,
54G, 56E.

Type locality

Off Minabe, Kii Peninsula, 10 to 20 m deep, Japan.

Habitat

Muddy and shell bottom, 15 to 50 m deep.

Distribution

Japan, East China Sea, and Korea (Fig. 63).



Fig. 63. Distribution of *Holthuija cognata* Ng & Richer de Forges, 2015. Open circle=type locality.

Remark

In Korean waters, Yokoya (1933) reported the collection of *Maja miersi* Walker, 1887 on Jeju Island, without a description and without pictures, and Sakai (1938), Kamita (1941), and Kim (1973) cited it. The species has not been reported in Korean waters since 1933.

Ng & Richer de Forges (2015) revised the genus *Maja* Lamarck, 1801 and separated genus *Holthuija* Ng & Richer de Forges, 2015 from genus *Maja*. *Holthuija miersii* (Walker, 1887) is designated as the type specimen of the genus *Holthuija*. However, Ng & Richer de Forges (2015) recognized that specimens from the type locality (Singapore) and Japan have differences in the G1. They then identified the Japanese specimen, identified as *M. miersi*, as a new species, *H. cognata* Ng & Richer de Forges, 2015. Although the author did not observe the Korean specimen, the species that was identified as *M. miersi* in Korean waters is considered *H. cognata* according to Ng & Richer de Forges (2015).

32. *Leptomithrax bifidus* (Ortmann, 1893) (Fig. 65) 가시두드럭계

Paramithrax (*Leptomithrax*) *bifidus* Ortmann, 1893: 52, pl. 3, fig. 6; Yokoya, 1933: 161.

Leptomithrax bifidus—Sakai, 1934: 298; 1935: 66; 1936: 101, pl. 25, fig. 1; 1938: 303, pl. 31, fig. 1; 1965: 86, pl. 39, fig. 1; 1976: 243, pl. 87, fig. 1; Kim, 1970: 25; 1973: 549, 668, fig. 258, pl. 54, fig. 207a, b; Kim & Chang, 1985: 49; Griffin & Tranter, 1986: 209; Ko & Lee, 2015: 36, pl. 25.

Material examined

One male (pcl 32.9 mm), Seogwi-dong, Seogwipo-si, Jeju-do, Korea, 33°13'37.71"N, 126°34'6.07"E, 23 Jul. 2018, coll. by SCUBA diving at 55 m depth; 2 males (pcl 31.0 mm, 33.7 mm), Gujwa-eup, Jeju-si, Jeju-do, Korea, 33°33'27.98"N, 126°44'21.66"E, 17 Oct. 2018, coll. by gill net at 30 m depth; 1 male (pcl 40.4 mm), Seogwipo-si, Jeju-do, Korea, 33°31'51.56"N, 127°32'53.14"E, 6 May 2019, coll. by otter trawl.

Diagnosis

Carapace subtriangular; dorsal surface covered with ununiformed tubercles. Gastric region convex, with two spines on midline. Cardiac region with two spines side by side with their fused proximally. Intestinal region with one small spine. Branchial region with one long mesobranchial spine. Pseudorostrum slightly outward, acute distally, 0.3 times as long as pcl, covered with hooked setae. Supraorbital eave with one antorbital spine. Intercalated spine prominent, as long as half of postorbital spine. Postorbital spine bilobed. Hepatic margin with two distinct spines, anterior one prominent. Branchial margin with three long spines. Posterior carapace margin with two prominent spines side by side. In male, cheliped

robust; merus and carpus with row of small tubercles; palm smooth. Ambulatory legs longer than cheliped, slender.

Type locality

Sagami Bay, Japan.

Habitat

Muddy bottoms, 50 to 150 m deep.

Distribution

Japan, and Korea (Fig. 64).

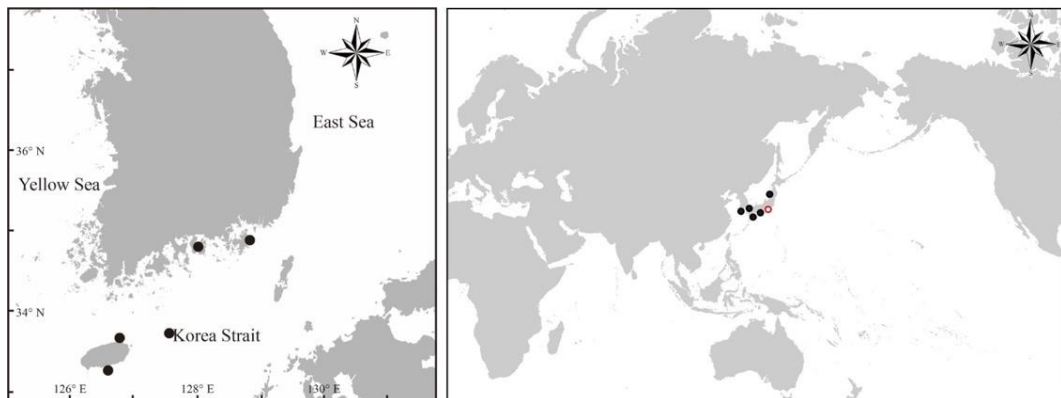


Fig. 64. Distribution of *Leptomithrax bifidus* (Ortmann, 1893). Open circle=type locality.

Remark

Two species of the genus *Leptomithrax* Miers, 1876 have been observed in Korean waters: *L. bifidus* (Ortmann, 1893), and *L. edwardsii* (De Haan, 1835). The differences between the two species are described under *L. edwardsii*. The examined specimens presented no unique features.



Fig. 65. *Leptomithrax bifidus* (Ortmann, 1893). Male (pcl 40.4 mm), dorsal view.

33. *Leptomithrax edwardsii* (De Haan, 1835) (Fig. 66) 두드럭게

Maja (*Paramithrax*) *edwardsii* De Haan, 1833–1849 (1839): 92, pl. G.

Paramithrax edwardsii—Adams & White, 1848: 14.

Paramithrax (*Leptomithrax*) *edwardsii*—Ortmann, 1893: 52; Yokoya, 1933: 160.

Leptomithrax edwardsii—Sakai, 1934: 298; 1936: 100, pl. 26, fig. 3; 1938: 302, pl. 30, fig. 4; 1965: 86, pl. 39, figs 2, 3; 1976: 242, pl. 86; Kamita, 1941: 78, fig. 36; Kim, 1970: 25; 1973: 547, 668, fig. 257, pl. 54, fig. 206; Miyake, 1983: 47, pl. 16, fig. 3; Kim & Chang, 1985: 49; Griffin & Tranter, 1986: 210; Ko & Lee, 2015: 37, figs 1A, 3A, 3B, 4, pls. 26, 27.

Leptomithrax edwardsii—Sakai, 1935: 66.

Material examined

One male (pcl 40.7 mm), 1 female (pcl 46.7 mm), Seogwipo-si, Jeju-do, Korea, 33°11'57.38"N, 127°11'44.83"E, 1 May 2019, coll. by otter trawl.

Diagnosis

Carapace subcircular; dorsal surface covered with ununiformed tubercles. Gastric region convex, with two spines on midline. Cardiac region with two prominent tubercles side by side. Intestinal region with three tubercles. Branchial region with one mesobranchial spine. Pseudorostrum slightly outward, acute distally, 0.14 times as long as pcl. Supraorbital eave with one antorbital spine. Intercalated spine prominent, as long as half of postorbital spine. Postorbital spine triangular, acute apically. Hepatic margin with two distinct spines, anterior one prominent. Branchial margin with three spines. Posterior carapace margin with two spines side by side. Cheliped robust; merus and carpus with row of small tubercles; palm smooth. Ambulatory legs longer than cheliped, slender.



Fig. 66. *Leptomithrax edwardsii* (De Haan, 1835). Male (pcl 46.7 mm), dorsal view.

Type locality

Japan.

Habitat

Sandy or muddy bottoms, 50 to 150 m deep.

Distribution

Japan, East China Sea, and Korea (Fig. 67).

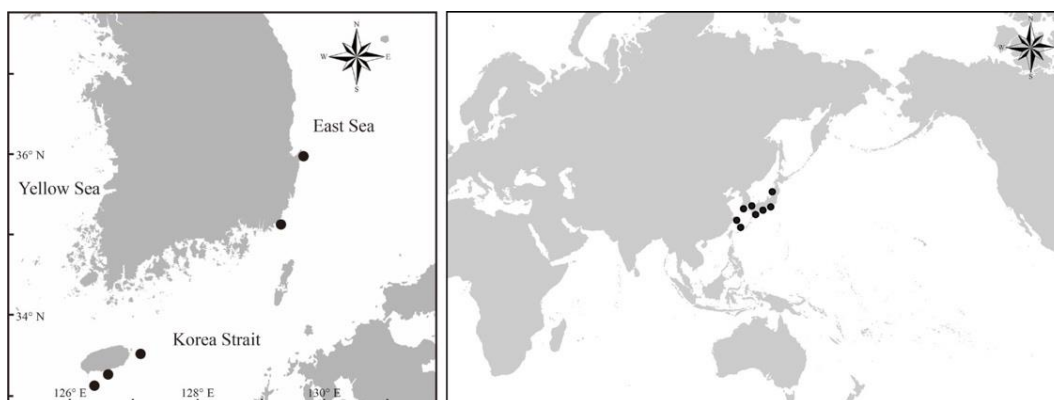


Fig. 67. Distribution of *Leptomithrax edwardsii* (De Haan, 1835).

Remark

Two species of *Leptomithrax* Miers, 1876 have been observed in Korean waters, *L. bifidus* (Ortmann, 1893), and *L. edwardsii* (De Haan, 1835). *Leptomithrax edwardsii* can be distinguished from *L. bifidus* based on the following characteristics: (1) the carapace is subcircular (subtriangular in *L. bifidus*), and (2) the postorbital spine single at the tip of the spine (bifid at the tip of the spine in *L. bifidus*). The examined specimens presented no unique features. The examined specimens presented no unique features.

Genus *Micippa* Leach, 1817 누덕옷게속

34. *Micippa cristata* (Linnaeus, 1758) 가시누덕옷게

Cancer cristatus Linnaeus, 1758: 629.

Micippe cristata—H. Milne-Edwards, 1834: 330; 1836–1844 (1839): pl. 31, figs 2, 2a; De Haan, 1833–1849 (1839): 99, pl. G.

Micippa cristata—Adams & White, 1848: 16; Buitendijk, 1939: 252, fig. 20; Griffin, 1976: 202; Griffin & Tranter, 1986: 275; Ko & Lee, 2015: 43.

Micippa cristata granulipes Zehntner, 1894; Sakai, 1932: 51, fig. 6; 1936: 105, figs 49a, b; 1938: 313; 1976: 255, figs 136, 137a; Kamita, 1941: 81; Kim, 1970: 26; 1973: 553, 669, fig. 261.

Type locality

Oceans in Asia.

Distribution

Japan, Philippines, Palau, Indonesia, and Korea (Fig. 68).



Fig. 68. Distribution of *Micippa cristata* (Linnaeus, 1758). Open circle=type locality.

Remark

In Korean waters, Sakai (1938) reported the collection of *Micippa cristata* (Linnaeus, 1758) on Jejudo Island, and Kim (1973) cited it. *Micippa cristata* has not been reported in Korean waters since 1938. The author has not yet observed the species. In the Korean fauna, in the genus *Micippa* Leach, 1817, *M. cristata* is similar to *M. thalia* (Herbst, 1803). For a detailed discussion of the two species, see remark for *M. thalia*.

35. *Micippa philyra* (Herbst, 1803) (Figs 69, 73A) 꼬마누덕웃게

Cancer philyra Herbst, 1803: 51, pl. 58, fig. 4.

Micippa philyra—H. Milne-Edwards, 1834: 330; Sakai, 1934: 298; 1935: 67; 1938: 315, fig. 45, pl. 38, fig. 6; 1954: 74; 1965: 90, pl. 42, fig. 1; 1976: 257, figs 138a, a', pl. 90, fig. 3; Kamita, 1941: 79, fig. 37a–d; Kim, 1970: 25; 1973: 552, 669, fig. 260, pl. 112, fig. 209; Kim & Chang, 1985: 49; Griffin & Tranter, 1986: 277; Dai & Yang, 1991: 157, fig. 80A(1, 2), pl. 19(3); Ko & Lee, 2015: 43, fig. 3C, 3D, pls. 33–35.

Material examined

One male (pcl 20.5 mm), Domioka, Asakusa, Japan, 6 Sep. 1934, coll. by Miyake.

Diagnosis

Carapace subquadrate, dorsal surface tuberculate, covered with numerous hooked setae. Hepatic region strongly depressed. Pseudorostrum with dorsal surface tuberculate, covered with numerous hooked setae, vertically deflexed, divided into four lobes. Anterolateral margin with six spines. Posterior margin with two small spines medially. Orbit closed below. Basal antennal article extremely broad, tuberculate. Cheliped smooth, short. Ambulatory legs with numerous hooked setae.

Type locality

East Indies.



Fig. 69. *Micippa philyra* (Herbst, 1803). Male (pcl 20.5 mm), dorsal view.

Distribution

The species is widely distributed in the Indo-Pacific region from the eastern coast of Africa to Hawaii (Fig. 70).

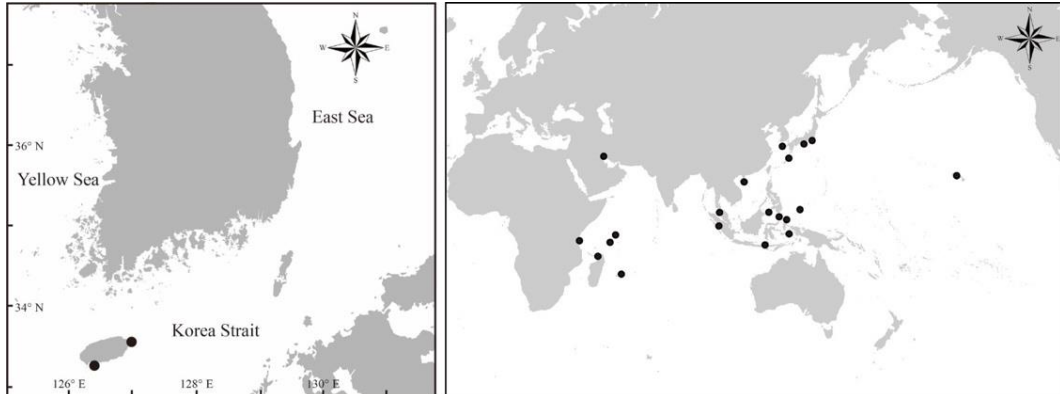


Fig. 70. Distribution of *Micippa philyra* (Herbst, 1803).

Remark

In Korean waters, Kamita (1941) and Ko & Lee (2015) reported collecting *Micippa philyra* (Herbst, 1803) on Jeju Island, but the author has not yet obtained the Korean specimen and described the Japanese specimen as a reference.

Micippa philyra is closely related to *M. platipes* Rüppell, 1830. The differences between the two species are described under *M. platipes*.

36. *Micippa platipes* Rüppell, 1830 (Figs 71, 73B) 입술이마누덕옷게

Micippa platipes Rüppell, 1830: 8, pl. 1, fig. 4; Sakai, 1938: 316, fig. 46, pl. 32, fig. 2, pl. 38, fig. 4; 1976: 258, figs 138b, b', pl. 90, fig. 2; Buitendijk, 1939: 254, fig. 22, pl. 10, figs 2, 4; Griffin, 1966b: 287 (key); Griffin & Tranter, 1974: 176; 1986: 279; Dai & Yang, 1991: 158, fig. 80A(3), pl. 19(4); Yang & Ko, 2000: 14, fig. 1; Ko & Lee, 2015: 44.

Material examined

One male (pcl 14.9 mm), Seongsan-eup, Seogwipo-si, Jeju-do, Korea, 33°27'33.95"N, 126°56'8.45"E, 9 Aug. 2017; 18 males (pcl 14.4–24.1mm), 13 females (pcl 13.8–19.4 mm), Seongsan-eup, Seogwipo-si, Jeju-do, Korea, 33°27'33.95"N, 126°56'8.45"E, 4 Jul. 2019; 5 males (pcl 14.2–22.8 mm), 3 females (pcl 19.1–21.8 mm), Yerae-dong, Seogwipo-si, Jeju-do, Korea, 33°14'25.68"N, 126°23'48.4"E, 4 Jul. 2019.

Diagnosis

Carapace subquadrate, dorsal surface tuberculate, covered with numerous hooked setae. Hepatic region strongly depressed. Pseudorostrum with dorsal surface tuberculate, covered with numerous hooked setae, vertically deflexed, divided into four lobes. Anterolateral margin with eight to ten spines. Posterior margin with two small spines medially. Orbit opened below. Basal antennal article extremely broad, smooth. Cheliped smooth, short. Ambulatory legs with numerous hooked setae.



Fig. 71. *Micippa platipes* Rüppell, 1830. Male (pcl 16.3 mm), dorsal view.

Type locality

The Red Sea.

Habitat

Intertidal rocky shore, weedy pebbles.

Distribution

This species is widely distributed in the Indo-Pacific region from the eastern coast of Africa to Tonga (Fig. 72).

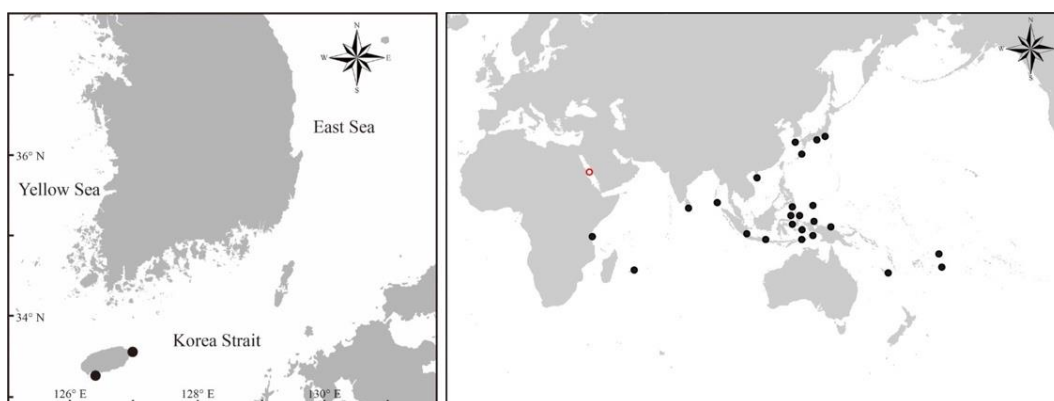


Fig. 72. Distribution of *Micippa platipes* Rüppell, 1830. Open circle=type locality.

Remark

Micippa platipes Rüppell, 1830 has an extremely wide range of distribution, and very large variations have been reported. *Micippa platipes* was found on Jejudo Island in Korean waters, and the area is close to the northern limit of distribution of the species. The species is camouflaged with numerous seaweeds and hydroids, bryozoans, and sponges on the carapace and ambulatory legs.



Fig. 73. Antennae, orbit, and buccal cavity, ventral view. A, *Micippa philyra* (Herbst, 1803) (pcl 20.5 mm); B, *Micippa platipes* Rüppell, 1830 (pcl 16.3 mm).

Micippa platipes is very similar to *M. philyra* (Herbst, 1803). *Micippa platipes* can be distinguished from *M. philyra* based on the following characteristics (Fig. 73): (1) basal antennal article is smooth (granulated in *M. philyra*), (2) carapace has anterolateral border with eight to ten spines (six spines in *M. philyra*), and (3) orbit open below (closed in *M. philyra*).

37. *Micippa thalia* (Herbst, 1803) (Fig. 75) 누덕웃게

Cancer thalia Herbst, 1803: 50, pl. 58, fig. 3.

Pisa (Paramecippe) thalia De Haan, 1833–1849 (1837): pl. 23, fig. 3; 1839: 98.

Micippa thalia—Adams & White, 1848: 15; A. Milne-Edwards, 1872: 238, pl. 11, figs 1, 1a, b; Sakai, 1934: 298; 1935: 67; 1936: 104, pl. 28, fig. 2; 1938: 313, fig. 44, pl. 32, fig. 3; 1965: 90, pl. 42, fig. 3; 1976: 256, fig. 137b, pl. 90, fig. 1; Kim, 1970: 25, pl. 5, fig. 3; 1973: 550, 669, fig. 259, pl. 55, fig. 208; Griffin, 1974: 21; Griffin & Tranter, 1974: 177; Kim & Chang, 1985: 49; Griffin & Tranter, 1986: 279; Dai & Yang, 1991: 158, fig. 80B(1–3), pl. 19(5); Ko & Lee, 2015: 45, pl. 36.

Material examined

MABIK CR00012194, 1 female (pcl 22.7 mm), Nam-gu, Busan-si, Korea, 35°5'58.23"N, 129°7'23.54"E, 12 Sep. 2009; MABIK CR00241024, 1 male (pcl 31.3 mm), Yeongdo-gu, Busan-si, Korea, 21 Sep. 2009, coll. by gill net; MABIK CR00012200, 1 female (pcl 27.9 mm), Nam-gu, Busan-si, Korea, 35°5'50.65"N, 129°7'29.57"E, 13 Oct. 2009, coll. by gill net; MABIK CR00010858, 1 male (pcl 33.1 mm), Saha-gu, Busan-si, Korea, 35°2'29.36"N, 128°59'3.86"E, 11 Aug. 2011, coll. by gill net; 1 male (pcl 23.8 mm), Yeongdo-gu, Busan-si, Korea, 35°3'46.2"N, 129°5'25.9"E, 26 Jun. 2019, coll. by SCUBA diving at 15 m depth.

Diagnosis

Carapace subquadrate, dorsal surface tuberculate, covered with numerous hooked setae. Gastric region with two strong spines on midline. Hepatic region strongly depressed. Cardiac region with two spines transversely. Branchial region with one strong dorsal spine.

Pseudorostrum with dorsal surface tuberculate covered with numerous hooked setae, vertically deflexed, tips curved outwards. Basal antennal article extremely broad, tuberculate. Anterolateral margin with five spines. Cheliped smooth, short. Ambulatory legs with numerous setae.

Type locality

The East Indies.

Habitat

Sandy muddy bottom, 2 to 100 m deep.

Distribution

The species is widely distributed in the Indo-Pacific region from the eastern coast of Africa to the eastern coast of Australia (Fig. 74).

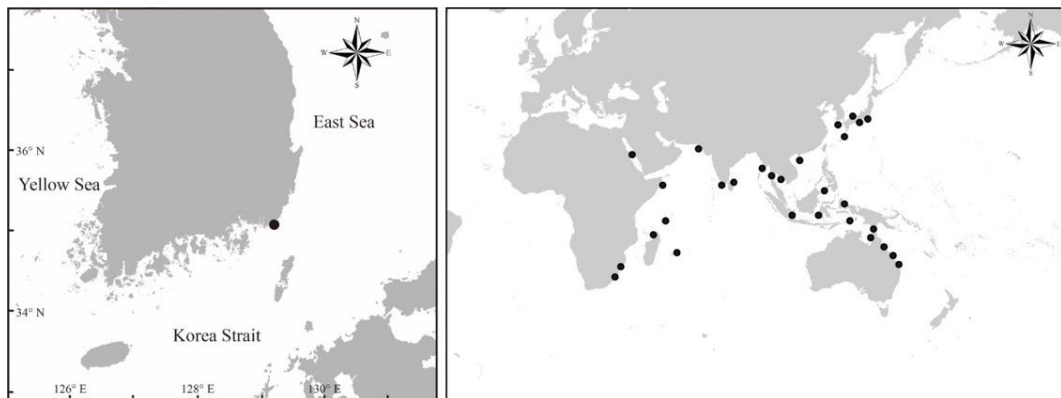


Fig. 74. Distribution of *Micippa thalia* (Herbst, 1803).



Fig. 75. *Micippa thalia* (Herbst, 1803). Male (pcl 23.8 mm), dorsal view.

Remark

In the Korean fauna, in the genus *Micippa* Leach, 1817, *M. thalia* (Herbst, 1803) is similar to *M. cristata* (Linnaeus, 1758). They share a pseudorostrum that is divided into two large lobes. However, *M. thalia* can be distinguished from *M. cristata* based on the following characteristics: (1) orbit open below, (2) pseudorostrum with lateral margin unarmed.

38. *Paramaya spinigera* (De Haan, 1837) (Fig. 77) 털다리게

Maja (Maja) spinigera De Haan, 1837: 93.

Maja (Paramaya) spinigera—De Haan, 1837: pl. 24, fig. 4.

Maja spinigera—Ortmann, 1893: 51; Sakai, 1934: 297; 1936: 98, pl. 25, fig. 3; 1938: 397, pl. 30, fig. 1; 1965: 84, pl. 38; 1976: 237, pl. 83; Serène, 1968: 57; Kim, 1973: 542, pl. 109, fig. 202; Takeda, 1975: 127; 1982: 128; Miyake, 1983: 43, pl. 14 fig. 4; Kim & Chang, 1985: 49; Dai et al., 1986: 136, pl. 18(3); Dai & Yang, 1991: 151, pl. 18(3); Yamaguchi & Baba, 1993: 359, Fig. 116; Ng et al., 2008: 117 (list); Ko & Lee, 2015: 39, pls. 28, 29; Ng & Richer de Forges, 2015: 155, figs 6G, 21A–D, 23A–C, 37A, 40A, 42A, 45I, 50A, 52H, 54A, 56A.

Material examined

One male (pcl 76.5 mm), Beophwan-dong, Seogwipo-si, Jeju-do, Korea, 8 Aug. 1970.

Diagnosis

Carapace ovate; dorsal surface with numerous granules or tubercles, regions distinct. Midline of carapace with five spines consisting of three gastric, one cardiac, one intestinal. Branchial region with two strong spines. Pseudorostrum 0.28 times as long as pcl, divergent distally. Supraorbital cave narrow transversely. Antorbital spine prominent, sharp. Intercalated spine prominent, shorter than antorbital spine, separated from antorbital spine and postorbital spine. Postorbital spine strong. Hepatic spine long, slightly shorter than postorbital spine. Branchial margin with four long spines, with numerous spinules.

Posterior carapace margin with two prominent median spines. Basal antennal article longer than broad, granulated, with two spines distally. Epistome rectangular, longer than broad. Cheliped long, slender, smooth; palm elongated. Ambulatory legs long, slender, covered with long setae; with merus having long dorsodistal spine. In male, G1 gently curved.

Type locality

Japan.

Habitat

Muddy and shell bottom, 15 to 50 m deep.

Distribution

Japan, Taiwan, and Korea (Fig. 76).

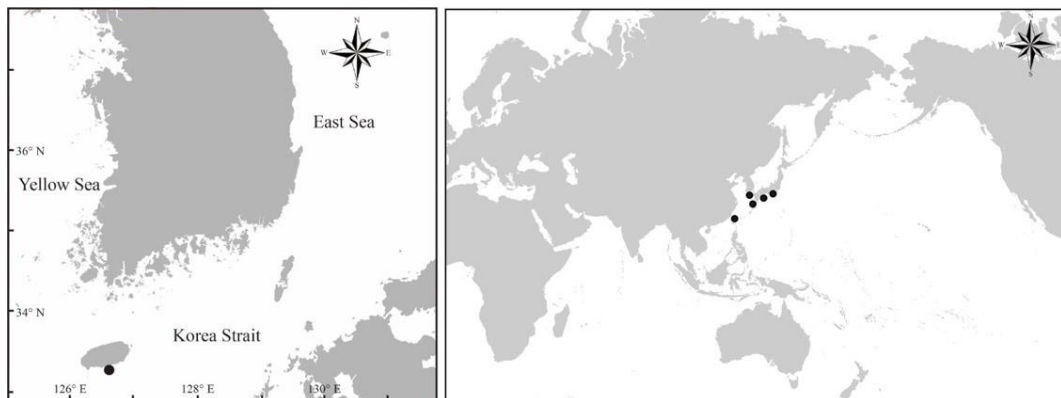


Fig. 76. Distribution of *Paramaya spinigera* (De Haan, 1837).



Fig. 77. *Paramaya spinigera* (De Haan, 1837). Male (pcl 76.5 mm), dorsal view.

Remark

Paramaya spinigera (De Haan, 1837) is rare in Korean waters, all have been found on Jejudo Island. In Korea, *P. spinigera* is the only species of the genus *Paramaya* De Haan, 1837, and the species can be distinguished from other majid crabs based on the following characteristics: (1) carapace has long spines, (2) epistome is elongated, (3) merus of ambulatory legs have distinct spines on the dorsodistal margin, and (4) the pseudorostrum is relatively short.

39. *Prismatopus longispinus* (De Haan, 1839) (Fig. 79) 몽특가시뿔게

Maja (*Chorinus*) *longispina* De Haan, 1833–1849 (1839): 94, pl. G.

Paramithrax coppingeri Haswell, 1882: 750.

Paramithrax (*Chlorinoides*) *longispinus* var. *bituberculata* Miers, 1884: 522.

Chlorinoides longispinus—Miers, 1886: 53; Ortmann, 1893: 53; Serène, 1969: 286, figs 3, 13–15, pl. 3, figs A, B; Kim, 1973: 544, 667, fig. 255, pl. 110, fig. 204a, b; Griffin, 1976: 186; Sakai, 1976: 249, pl. 88, fig. 3; Takeda, 1977: 77; Miyake, 1983: 26; Kim & Chang, 1985: 49.

Acanthophrys longispinus var. *spinossissima* Bouvier, 1906: 488.

Paramithrax (*Chlorinoides*) *longispinus* var. *bispinus* Laurie, 1906: 383.

Acanthophrys longispinus—Balss, 1924: 29; Sakai, 1938: 308, pl. 31, fig. 2; 1965: 87, pl. 40, fig. 1; Kim, 1970: 25.

Thacanophrys longispinus—Griffin & Tranter, 1986: 258.

Prismatopus longispinus—Ng et al., 2008: 118 (list); Ko & Lee, 2015: 40, pl. 30.

Material examined

One female (pcl 22.1 mm), Seogwi-dong, Seogwipo-si, Jeju-do, Korea, 33°13'37.71"N, 126°34'6.07"E, 23 Jul. 2018, coll. by SCUBA diving at 55 m depth; 1 male (pcl 17.4 mm), Seogwi-dong, Seogwipo-si, Jeju-do, Korea, 33°13'36.36"N, 126°34'3.58"E, 27 Jul. 2019, coll. by SCUBA diving at 50 m depth.

Diagnosis

Carapace pyriform; dorsal surface covered with hooked setae. Anterior and posterior gastric regions each with one long, knobbed spine. Cardiac region with two long, knobbed spines side by side with their fused proximally. Intestinal region with one long knobbed spine. Branchial region with two long, knobbed spines. Pseudorostrum 0.4 times as long as pcl, with numerous hooked setae, curved outward, knobbed distally. Supraorbital eave with two preorbital spines. Antorbital spine prominent, slender. Intercalated spine prominent, as long as half of postorbital spine. Postorbital spine bilobed. Hepatic region with two distinct tubercles. Posterior carapace margin with one knobbed median spine. Ambulatory legs with merus having long, knobbed spine distally.

Type locality

Japan.

Habitat

Rocky bottoms or pebbles, 10 to 150 m deep.

Distribution

This species is widely distributed in the Indo-Pacific region from the eastern coast of Africa to the east of Australia (Fig. 78).

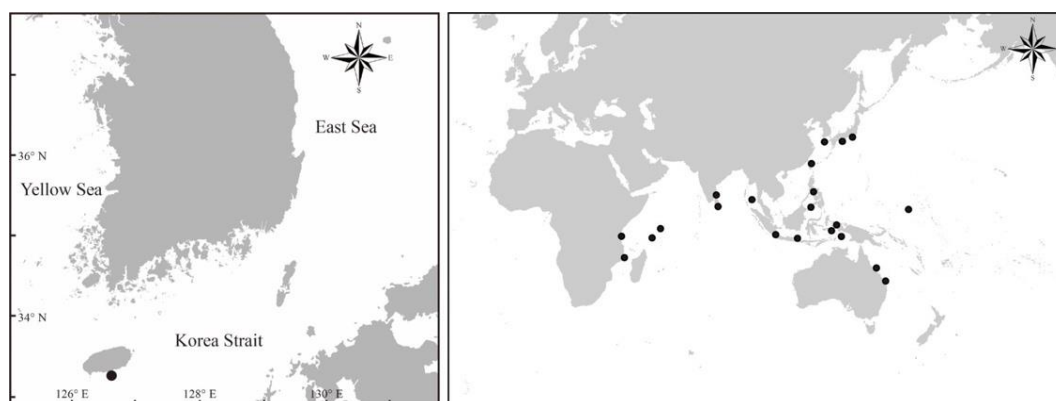


Fig. 78. Distribution of *Pristimolus longispinus* (De Haan, 1839).



Fig. 79. *Pristopus longispinus* (De Haan, 1839). Male (pcl 17.4 mm), dorsal view.

Remark

Prismatopus longispinus (De Haan, 1839) has a very wide range of distribution and there have been many reports of variations in spine formation (De Haan, 1839; Haswell, 1882; Miers, 1884; Laurie, 1906; Bouvier, 1906; Griffin, 1976; Griffin & Tranter, 1986). A follow-up study on the regional distribution and variation in the species is required. Among the known species of *Prismatopus* Ward, 1933, *P. longispinus* can be distinguished easily from congeners based on the following characteristics: (1) the branchial region has one spine, (2) the cardiac region has a pair of spines, and (3) ambulatory legs with merus have one long, knobbed spine on the distal margin.

40. *Pseudomicippe nipponica* (Sakai, 1938) (Fig. 81) 제주어리누덕옷게

Pseudomicippe tenuipes—Balss, 1924: 35, pl. 1, fig. 6; Sakai, 1934: 298; 1935: 67; 1936: 84, pl. 20, fig. 1. [Not *Pseudomicippe tenuipes* A. Milne-Edwards, 1865]

Zewa nipponica Sakai, 1938: 244, fig. 22a–d, pl. 25, fig. 1; 1954: 74; 1965: 71, pl. 31, fig. 3; 1976: 188, figs 99, 100a.

Pseudomicippe nipponica—Griffin & Tranter, 1986: 234, fig. 87b; Lee & Ko, 2013: 132, figs 3, 4; Ko & Lee, 2015: 41, pl. 31.

Material examined

MADBK 172307_001, 1 male (pcl 17.1 mm), Yeosu-si, Jeollanam-do, Korea, 13 Jul. 1984; NIBRIV0000023578, 1 male (pcl 15.3 mm), Tongyeong-si, Gyeongsangnam-do, Korea, 19 Jun. 2001; NIBRIV0000261131, 1 female, Seogwipo-si, Jeju-do, Korea, 33°27'344"N, 126°56'090"E, 24 Jul. 2010; MABIK CR00243356, 1 female (pcl 19.0 mm), Sangye-dong, Seogwipo-si, Jeju-do, Korea, 33°14'23.5"N, 126°23'49.1"E, 28 Jul. 2015; 1 male, Bomok-dong, Seogwipo-si, Jeju-do, Korea, 31 Jan. 2016.

Diagnosis

Carapace pyriform; dorsal surface with tubercles having hooked setae; regions distinct. Gastric region convex, with four tubercles on midline. Cardiac region with four tubercles forming quadrangle. Intestinal region with three tubercles forming inverted triangle. Branchial region with sixteen to eighteen tubercles on dorsal surface. Pseudorostrum with numerous hooked setae, strongly deflexed, slightly curved outward. Supraorbital eave with

one prominent antorbital spine. Postorbital spine present, with one or two accessory spinules on posterior margin. Hepatic margin with three blunt spines. Chelipeds slender, short; movable finger with cutting edge serrated. Ambulatory legs with several rows of long setae, with hooked setae on outer margin.

Type locality

Shimoda, Japan.

Habitat

Rocky bottom with algae, intertidal.

Distribution

Japan, and Korea (Fig. 80).

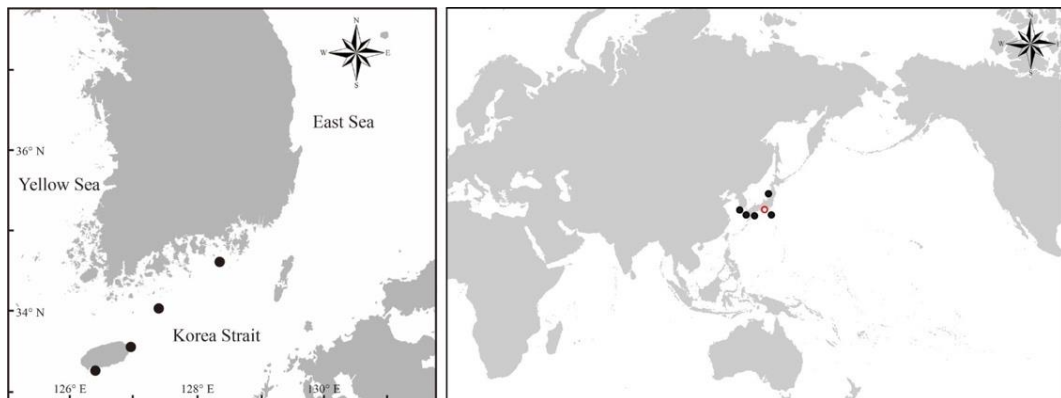


Fig. 80. Distribution of *Pseudomicippe nipponica* (Sakai, 1938). Open circle=type locality.

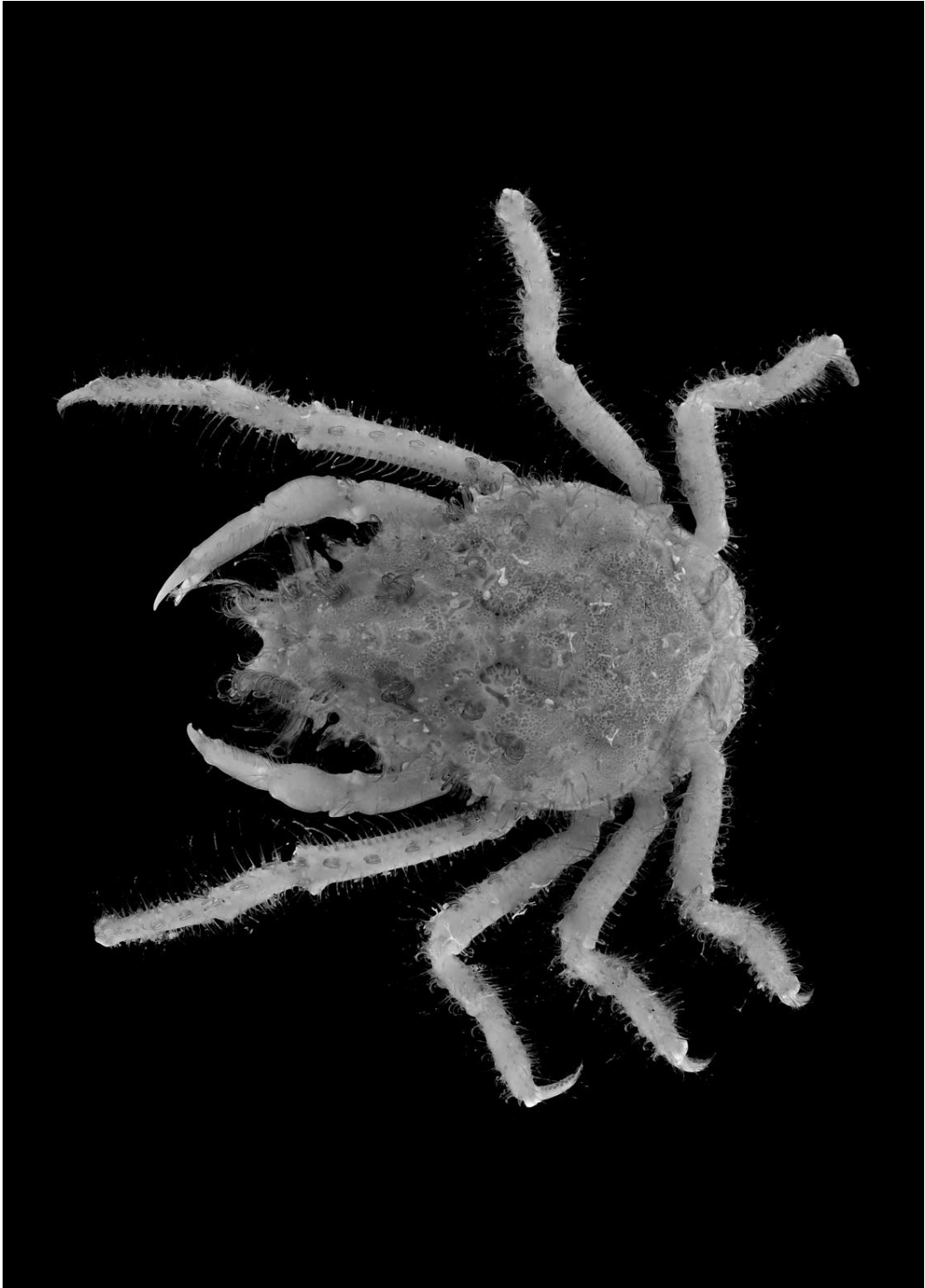


Fig. 81. *Pseudomicippe nipponica* (Sakai, 1938). Male (pcl 19.0 mm) (MABIK CR00243356), dorsal view.

Remark

Two species of the genus *Pseudomicippe* Heller, 1861 are known in Korean waters: *P. nipponica* (Sakai, 1938) and *P. okamotoi* (Sakai, 1938). *Pseudomicippe nipponica* is readily distinguished from *P. okamotoi* by a strongly deflexed pseudorostrum and a movable finger of cheliped serrated. The illustration in Sakai (1938) shows that the posterior carapace margin has two tubercles, but the examined female specimen had only one tubercle on the posterior carapace margin.

41. *Pseudomicippe okamotoi* (Sakai, 1938) (Fig. 82) 어린누덕웃게

Zewa okamotoi Sakai, 1938: 246, fig. 23a–c, pl. 36, fig. 1; 1976: 189, fig. 100b; Kim, 1970: 24, pl. 5, fig. 1; 1973: 527, 664, fig. 246, pl. 103, fig. 192a, b; Kim & Chang, 1985: 45. *Pseudomicippe okamotoi*—Griffin & Tranter, 1986: 226 (key); Ko & Lee, 2015: 41, pl. 31.

Material examined

One female (pcl 22.3 mm), 4 males (pcl 19.6–24.9 mm), Hamo-ri, Daejeong-eup, Seogwipo-si, Jeju-do, Korea, 16 Aug. 1996.

Diagnosis

Carapace pyriform; dorsal surface with tubercles having hooked setae; regions distinct. Gastric region with five tubercles on midline. Cardiac region with four tubercles forming quadrangle. Intestinal region with three tubercles forming inverted triangle. Branchial region with sixteen to eighteen tubercles on dorsal surface. Pseudorostrum rather slender, with numerous hooked setae, slightly deflexed, slightly curved outward. Supraorbital eave with one prominent antorbital spine. Postorbital spine present, with one accessory spinule on posterior margin. Hepatic margin with two or three blunt spines. Chelipeds stout, short; movable finger with cutting edge having one tooth on middle. Ambulatory legs with several rows of long setae, with hooked setae on outer margin.

Type locality

Gobo, Kii Peninsula, Japan.

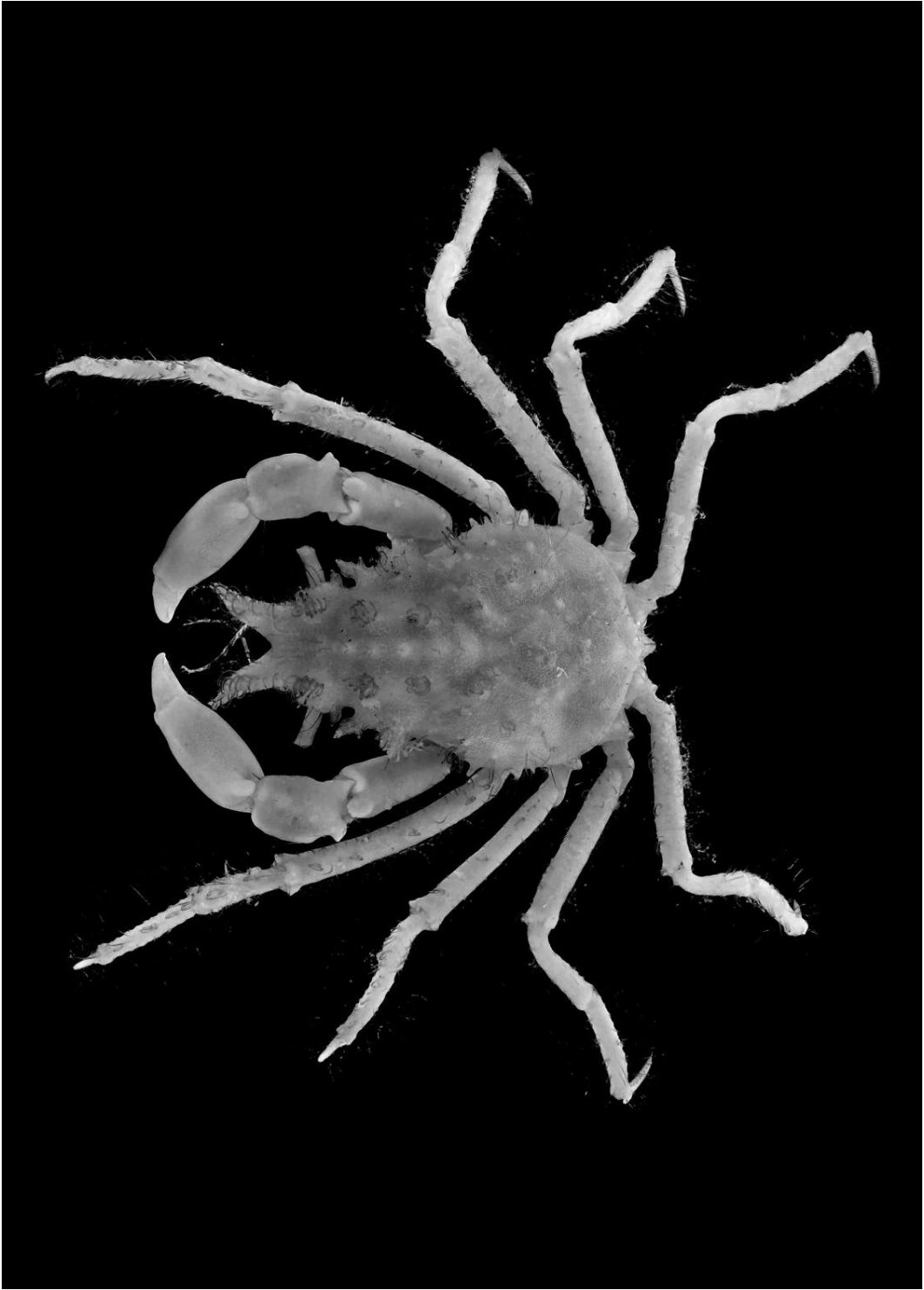


Fig. 82. *Pseudomicippe okamotoi* (Sakai, 1938). Male (pcl 20.0 mm), dorsal view.

Habitat

Rocky, weedy bottom with algae or hydroids.

Distribution

Japan, and Korea (Fig. 83).

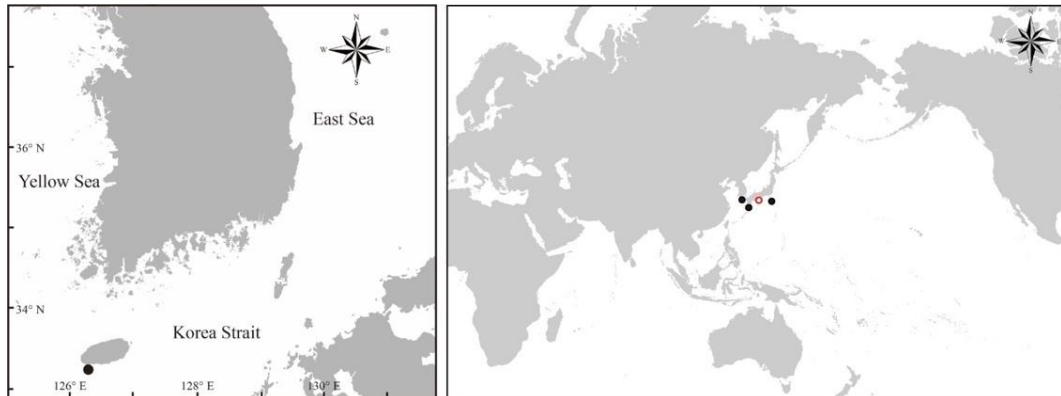


Fig. 83. Distribution of *Pseudomicippe okamotoi* (Sakai, 1938). Open circle=type locality.

Remark

The examined specimens are consistent with the original description of Sakai (1938).

Female, however, had no teeth on the movable finger of the cheliped.

* 42. *Sakaija japonica* (Rathbun, 1932) (Figs 85, 86) 애기물맞이게

Maja sp.—Sakai, 1932: 50, pl. 2, fig. 5, text-fig. 5.

Maja japonica Rathbun, 1932: 33; Sakai, 1965: 83, pl. 37 fig. 1; 1976: 238, pl. 82 fig. 1, text-fig. 126a, b; Serène, 1968: 57; Takeda & Miyake, 1969: 512, pl. 17 figs A, B, pl. 18 fig. B; Miyake, 1983: 44; Dai et al., 1986: 135, pl. 18(1), text-fig. 76; Griffin & Tranter, 1986: 216; Dai & Yang, 1991: 150, pl. 18(1), text-fig. 76; Ng et al., 2001: 12; Takeda, 2001: 235; Ng et al., 2008: 117 (list); Yang et al., 2008: 780.

Maja japonica Yokoya, 1933: 157, text-fig. 56.

Maja nipponensis Sakai, 1934: 297, text-fig. 11; 1938: 299, pl. 38, fig. 1, text-fig. 41.

Maja sakaii—Miyake, 1983: 44, pl. 15 fig. 5. [Not *Maja sakaii* Takeda & Miyake, 1969]

Sakaija japonica—Ng & De Forges, 2015: 169, figs 28A–C, 31A–C, 33A–G, 37K, 40J, 42F, 46G, 51A, B, 52J, 54J, 56H; Ng et al., 2017: 57; Lee et al., 2020: 216, figs 1, 2.

Material examined

MABIK CR00247261, 1 male (cl 25.3 mm, pcl 21.6 mm, cw 17.4 mm), Seogwipo-si, Jeju-do, Korea, 29 Apr. 2018; MABIK CR00247262, 1 male (cl 26.7 mm, pcl 23.8 mm, cw 19.7 mm), Seogwipo-si, Jeju-do, Korea, 15 May 2018; MABIK CR00247264, 1 female (cl 23.8 mm, pcl 20.2 mm, cw 16.4 mm), east of Jeju-do, Korea, 2 May 2019. coll. by otter trawl; MABIK CR00247263, 1 female (cl 18.1 mm, pcl 16.2 mm, cw 14.2 mm), east of Jeju-do, Korea, 6 May 2019. coll. by otter trawl.

Diagnosis

Carapace pyriform; dorsal surface with numerous small rounded granules. Midline of carapace with four spines or tubercles: two gastric, one cardiac, one intestinal. Supraorbital

eave narrow transversely, posterior part slightly wider than anterior part. Antorbital spine prominent, sharp. Intercalated spine prominent, as long as antorbital spine, separated from antorbital and postorbital spines. Postorbital spine largest. Hepatic spine short. Branchial margin with two short spines. Branchial region swollen, rounded, with one small spine. Posterior carapace margin with two small median spines. Pseudorostral spines 0.12–0.18 times as long as pcl, divergent distally. Basal antennal article granulated, with two spines distally. Third maxilliped with ischium granulated. Ambulatory legs with merus relatively short, stouter. In male, G1 prominently curved, with long setae on distal part, tapering distally.

Type locality

Seno Umi, Japan.

Habitat

50 to 540 m deep.

Distribution

Japan, Taiwan, East China Sea, South China Sea, and Korea (Fig. 84).

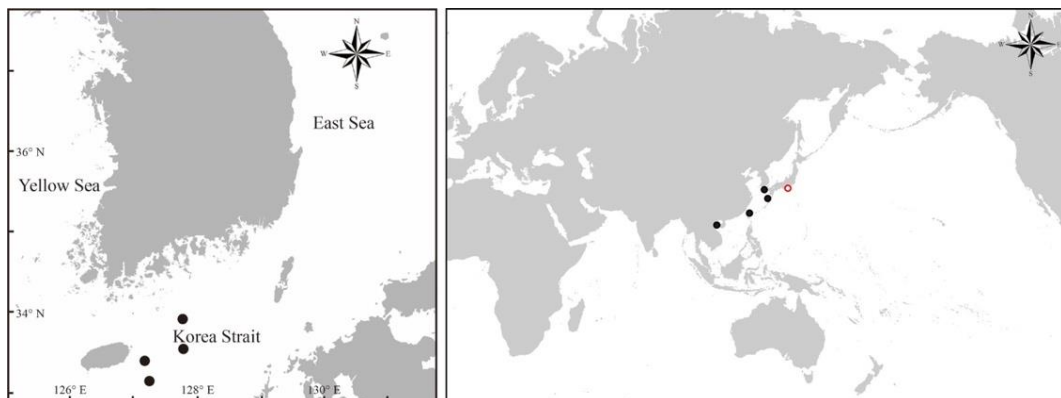


Fig. 84. Distribution of *Sakaija japonica* (Rathbun, 1932). Open circle=type locality.



Fig. 85. *Sakaija japonica* (Rathbun, 1932). Male (cl 25.3 mm, pcl 21.6 mm, cw 17.4 mm) (MABIK CR00247261), dorsal view. Modified from Lee et al. (2020).



Fig. 86. *Sakaija japonica* (Rathbun, 1932). Male (cl 25.3 mm, pcl 21.6 mm, cw 17.4 mm) (MABIK CR00247261). A, Antennae, antennules, epistomes and buccal cavity, ventral view; B, left first gonopod, ventral view; C, tip of left first gonopod, ventral view. Scale bars: B = 1 mm, C = 0.5 mm. Modified from Lee et al. (2020).

Remark

Ng & Richer de Forges (2015) revised the genus *Maja* Lamarck, 1801 and established seven genera. Among these, *Sakaija* Ng & Richer de Forges, 2015 is characterized as follows: (1) the G1 is curved and has distal margins lined with numerous long setae, (2) the carapace is pyriform, (3) the pseudorostral spine is relatively short and (4) the suborbital margin is confluent with the margin of the postorbital tooth (Ng & Richer de Forges, 2015). Six species are known from the Indo-West Pacific: *S. japonica*, *S. sakaii* (Takeda & Miyake, 1969), *S. serenei* Ng & Richer de Forges, 2015, *S. santo* Ng & Richer de Forges, 2015, *S. africana* (Griffin & Tranter, 1986) and *S. longispinosa* Ng & Richer de Forges, 2015.

The examined specimens, collected from around Jeju Island, agree well with the diagnosis of *S. japonica* of Ng & Richer de Forges (2015). Some of the examined specimens showed that the spines on the carapace were more prominent. In addition, the

cheliped of the female is clearly more slender than that of the male. Among the known species of *Sakaija*, *S. japonica* is morphologically closest to *S. sakaii*. The differences between the two species are described under *S. sakaii*.

* 43. *Sakaija sakaii* (Takeda & Miyake, 1969) (Fig. 87) 날씬이애기물맞이게

Maja japonica—Sakai, 1934: 297, text-figs 10; 1936: 99, pl. 25, fig. 2, text-fig. 45; 1938:

299, pl. 30, fig. 2; Takeda, 1982: 128. [Not *Maja japonica* Rathbun, 1932]

Maja sakaii Takeda & Miyake, 1969: 512, pl. 17, fig. C; Serène & Lohavanijaya, 1973: 50

(key); Sakai, 1976: 237, fig. 125a, b, pl. 85 fig. 2; Huang, 1989: 339; 1994: 583; Takeda,

1993: 43; Yang et al., 2008: 780; Ng et al., 2008: 117 (list).

Sakaija sakaii—Ng & Recher De Forges, 2015: 169, figs 28D–G, 33H–J, 46H.

Material examined

One female (cl 16.2 mm, pcl 14.3 mm, cw 10.6 mm), Seogwipo-si, Jeju-do, Korea, 32°52'5.42"N, 127°12'1"E, 29 Apr. 2018, coll. by otter trawl.

Diagnosis

Carapace pyriform; dorsal surface with numerous small rounded granules. Midline of carapace with four prominent spines or tubercles consisting of two gastric, one cardiac, one intestinal. Pseudorostrum 0.13 times as long as pcl, divergent distally. Supraorbital cave narrow transversely, posterior part distinctly wider than anterior part. Antorbital spine prominent, sharp. Intercalated spine prominent, shorter than antorbital spine, separated from antorbital spine and postorbital spine. Postorbital spine largest. Hepatic spine short. Branchial margin with two spines, posterior one longer. Branchial region with one strong spine. Posterior carapace margin with two small median spines. Basal antennal article longer than broad, granulated, with two spines distally. Third maxilliped with ischium granulated. Ambulatory legs with merus relatively long, slender.



Fig. 87. *Sakaija sakaii* (Takeda & Miyake, 1969). Female (cl 16.2 mm, pcl 14.3 mm, cw 10.6 mm), dorsal view.

Type locality

The East China Sea, 29°55.5'N, 127°22.9'E, 126 m.

Habitat

35 to 126 m deep.

Distribution

The East China Sea, Japan, and Korea (Fig. 88).

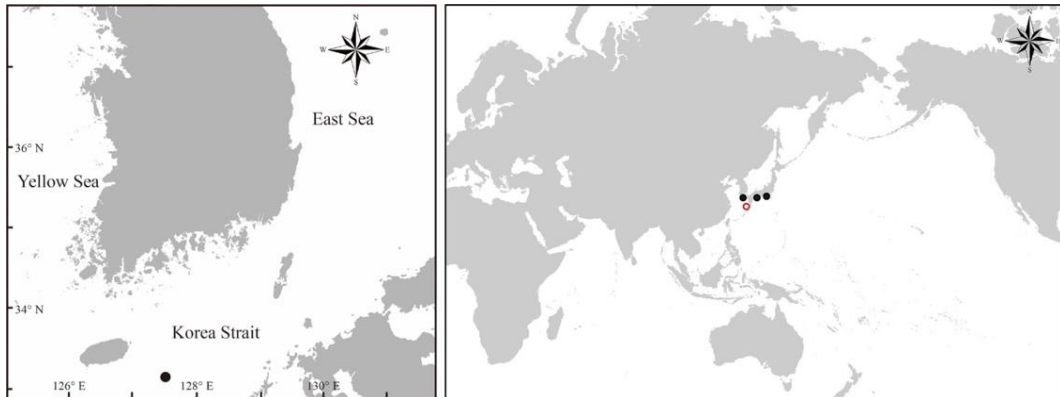


Fig. 88. Distribution of *Sakaija sakaii* (Takeda & Miyake, 1969). Open circle=type locality.

Remark

The single female specimen from Jeju Island is consistent with the diagnosis of Ng & Richer De Forges (2015) but differs based on a single characteristic. Ng & Richer De Forges mentioned that *S. sakaii* has two very low gastric spines. However, the examined specimen had two distinct gastric spines. To date, the reported *S. sakaii* have not exceeded 14 mm in pcl, and the observed specimen was relatively large, 14.34 mm in pcl. Since *S. sakaii* is rarely found, only one aberrant female specimen has been collected, which requires further study.

Sakaija sakaii is morphologically closest to *S. japonica*. However, *S. sakaii* can easily be distinguished from *S. japonica* by the following characteristics: (1) carapace with moderately inflated branchial region (more strongly inflated branchial region in *S. japonica*), (2) the ambulatory legs (particularly the merus) are relatively slender and longer (relatively shorter and stouter in *S. japonica*), and (3) G1 gently curved (more strongly curved in *S. japonica*) (Ng & Richer de Forges, 2015).

* 44. *Schizophroidea simodaensis* Sakai, 1933 (Figs 89–91) 툽니물맞이게

Schizophroidea simodaensis Sakai, 1933: 139, pl. 13 fig. 1; 1938: 304; 1965: 89, pl. 41 fig. 3; 1976: 245, pl. 89 fig. 1; Ng & Boyko, 2017: 208, fig. 8, 9, 16C; Ng & Ahyong, 2018: 387 (key); Lee et al., 2020: 218, figs 3, 4.

Schizophroidea manazuruana Sakai, 1933: 140, fig. 1; 1938: 305; 1965: 89, pl. 41, fig. 4; 1976: 245, pl. 89, fig. 2.

? *Schizophroidea manazuruana*—Buitendijk, 1939: 251.

Material examined

NIBRIV0000104516, 1 male (cl 22.5 mm, pcl 18.7 mm, cw 13.3 mm), Ulleung-eup, Ulleung-gun, Gyeongsangbuk-do, Korea, 37°32'55.96"N, 130°54'54.89"E, 21 May 2008. coll. by SCUBA diving at depth 20m; MABIK CR00247266, 1 female (cl 18.4 mm, pcl 13.7 mm, cw 9.6 mm), Bomok-dong, Seogwipo-si, Jeju-do, Korea, 33°13'47.49"N, 126°35'48.39"E, 31 Jan. 2016. coll. by SCUBA diving at depth 27m; MABIK CR00247265, 1 female (cl 21.2 mm, pcl 17.1 mm, cw 11.6 mm), Bomok-dong, Seogwipo-si, Jeju-do, Korea, 33°13'46.53"N, 126°35'46.26"E, 14 Jan. 2020. coll. by SCUBA diving at depth 17m.

Diagnosis

Carapace pyriform; protogastric region smooth. Supraorbital eave narrow transversely. Antorbital spine prominent, triangular. Intercalated spine prominent, as long as antorbital spine, separated from antorbital spine and postorbital spine. Postorbital spine largest. Hepatic spine broad, triangular. Branchial margin with four spines, posterior one smaller. Intestinal region with one tubercle. Posterior carapace margin with two median spines. Pseudorostral spines 0.31 times as long as pcl, divergent distally. Basal antennal article with inner distal spine as long as outer. Cheliped with carpus of male slightly granulated, with carpus of female smooth. In male, G1 gently curved, tapering distally.



Fig. 89. *Schizophroidea simodaensis* Sakai, 1933. Male (cl 22.5 mm, pcl 18.7 mm, cw 13.3 mm) (NIBRIV0000104516), dorsal view. Modified from Lee et al. (2020).



Fig. 90. *Schizophroida simodaensis* Sakai, 1933. Female (cl 21.2 mm, pcl 17.1 mm, cw 11.6 mm) (MABIK CR00247265), orsal view. Modified from Lee et al. (2020).

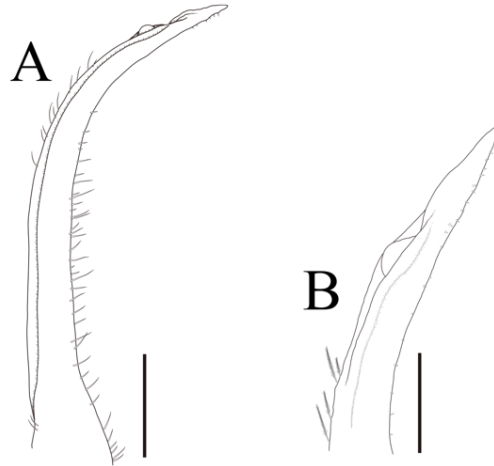


Fig. 91. *Schizophroida simodaensis* Sakai, 1933. Male (cl 22.5 mm, pcl 18.7 mm, cw 13.3 mm) (NIBRIV0000104516). A, Left first gonopod, ventral view; B, tip of left first gonopod, ventral view. Scale bars: A = 1 mm, B = 0.5 mm. Modified from Lee et al. (2020).

Type locality

Shimoda, Japan.

Habitat

Rocky bottoms or weedy pebbles.

Distribution

Japan, (?) Philippines, and Korea (Fig. 92).

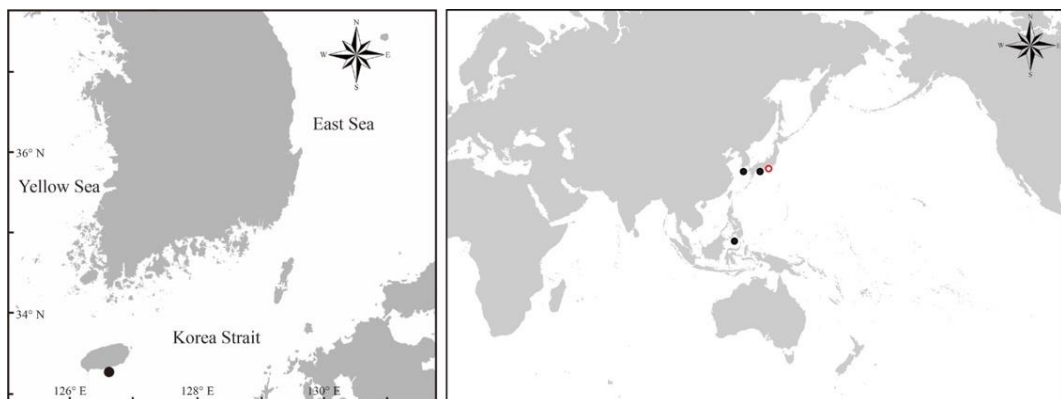


Fig. 92. Distribution of *Schizophroida simodaensis* Sakai, 1933. Open circle=type locality.

Remark

Article 13.3 of the current zoological code (ICZN, 1999) requires that any genus-group name established after 1930 must have a type species assigned to it for the name to be available. *Schizophroida* was established by Sakai (1933) for one known species, *Schizophrys hilensis* Rathbun, 1906, and two new species, *Schizophroida simodaensis* Sakai, 1933, and *Schizophroida manazuruana* Sakai, 1933, both from Japan. While most workers attribute the genus to Sakai (1933) (e.g., Griffin & Tranter, 1986; Ng et al., 2008; Ng & Boyko, 2017; Ng & Ahyong, 2018), this is incorrect. The first authors to make the name *Schizophroida* available are Griffin & Tranter (1986: 238), who diagnosed the genus and identified *Schizophrys hilensis* Rathbun, 1906, as the type species. As such, the genus must be cited as *Schizophroida* Griffin & Tranter, 1986.

Griffin & Tranter (1986) recognized all three species but Ng & Boyko (2017) in describing a new species from Easter Island, noted that the distinguishing characteristics were not reliable for the Japanese species and synonymized *S. manazuruana* under *S. simodaensis*. Ng & Boyko (2017) commented that the diagnostic characteristics of *S. simodaensis* are: (1) carapace with five tubercles behind the postorbital spine, (2) the gastric region is smooth, (3) the supraorbital eave is transversely narrow and (4) the ambulatory merus is relatively longer and more slender in males (see also the revision of the genus by Ng & Ahyong, 2018).

Our observations agree well with the characteristics of *Schizophroida simodaensis* as defined by Ng & Boyko (2017) and Ng & Ahyong (2018). The descriptions and figures of Japanese male specimens by Sakai (1933, 1938, 1976) indicate the presence of a small tubercle on the gastric region but Ng & Boyko (2017) mentioned that this condition is rare. The present specimens from Jejudo Island and Ulleungdo Island have no tubercle on the gastric region.

Buitendijk (1939) recorded an immature female specimen from the sea of Celebes, Philippines, and identified it as *Schizophroida manazuruana*. Buitendijk (1939) gave a brief description of the examined specimen and mentioned that there were five spines on the branchial margin, which is one of the characteristics of *S. simodaensis*. The specimen examined by Buitendijk (1939), however, was very small (cl 5 mm) and it was collected far from the known distribution of the species, and thus this record is suspect. It will need to be re-examined (see Ng & Ahyong, 2018).

Family Oregoniidae Garth, 1958 긴집게발게과

Subfamily Oregoniinae Garth, 1958

Genus *Chionoecetes* Krøyer, 1838 대게속

45. *Chionoecetes japonicus* Rathbun, 1932 (Fig. 94) 홍게

Chionoecetes japonicus Rathbun, 1932: 32; Sakai, 1938: 274; 1963: 12, 16; 1976: 187, pl. 65; 1978: 5; Kamita, 1963: 26, fig. 2; Miyake, 1983: 32, pl. 11, fig. 2; The Korean Society of Systematic Zoology, 1997: 218; Kim & Kim, 2001: 48, figs 39–41; Ko & Lee, 2015: 47, pl. 37.

Chionoecetes angulatus bathyalis Derjugin & Kobjakowa, 1935: 145, fig. 1.

Material examined

MABIK CR00241025, 2 females (pcl 62.5 mm, 62.7 mm), 1 male (pcl 88.2 mm), Uljin-gun, Gyeongsangbuk-do, Korea, 24 May 2009, coll. by otter trawl; MABIK CR00244259, 1 male (pcl 76.2 mm), Gangneung-si, Gangwon-do, Korea, 37°46'20.64"N, 128°57'6.06"E, 22 Aug. 2017, coll. by otter trawl; 1 female, Goseong-gun, Gangwon-do, Korea, 38°10'44.04"N, 128°49'38.58"E, 8 Apr. 2018, coll. by otter trawl at 1,000 m depth; 1 female, Suyeong-gu, Busan, Korea, 36°35'21.55"N, 129°53'12.72"E, 5 Apr. 2019, coll. by otter trawl at 455 m depth.

Diagnosis

Carapace subcircular, slightly broader than long, regions well defined; dorsal surface depressed, covered with ununiformed tubercles. Gastric region slightly convex, with low tubercles. Hepatic region slightly convex. Branchial region convex, with low tubercles. Carapace with slope of posterior part steep. Pseudorostrum very short, broad. Supraorbital eave developed. Intercalated spine very small. Postorbital spine well developed, broad,

triangular. Eyestalk short, cornea large. Hepatic margin with two small broad tubercles. Anterolateral branchial margin with small spines. Posterolateral branchial margin with small tubercles. Cheliped shorter than first to third ambulatory legs; merus with row of spines on inner and outer margins; carpus with spines on outer margin; palm robust, with rows of tubercles on inner and outer margins; fingers smooth, slightly longer than palm, cutting edges with row of tubercles. Ambulatory legs very long, slender, flattened; merus with rows of small tubercles on inner and outer margins; outer margins of carpus with rows of small tubercles on first to third ambulatory legs.

Type locality

off Sawazaki, Sado-gashima, Japan.

Habitat

450 to 2,300 m deep.

Distribution

Japan, and Korea (Fig. 93).

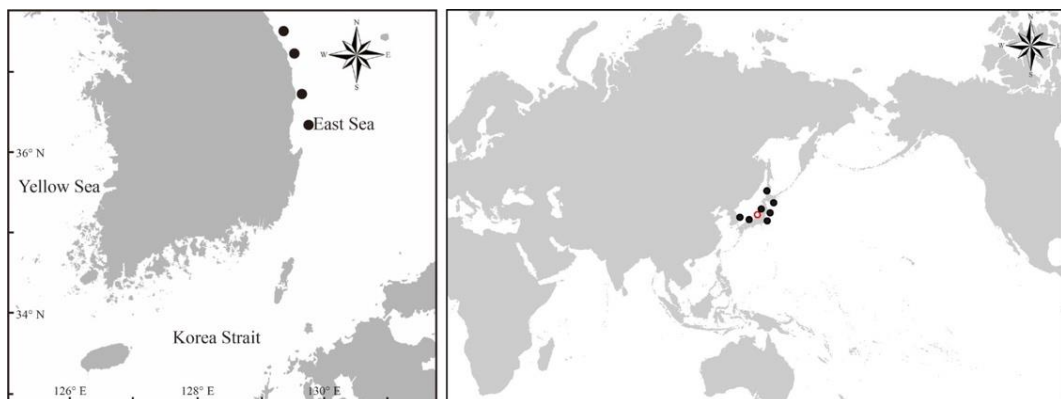


Fig. 93. Distribution of *Chionoecetes japonicus* Rathbun, 1932. Open circle=type locality.

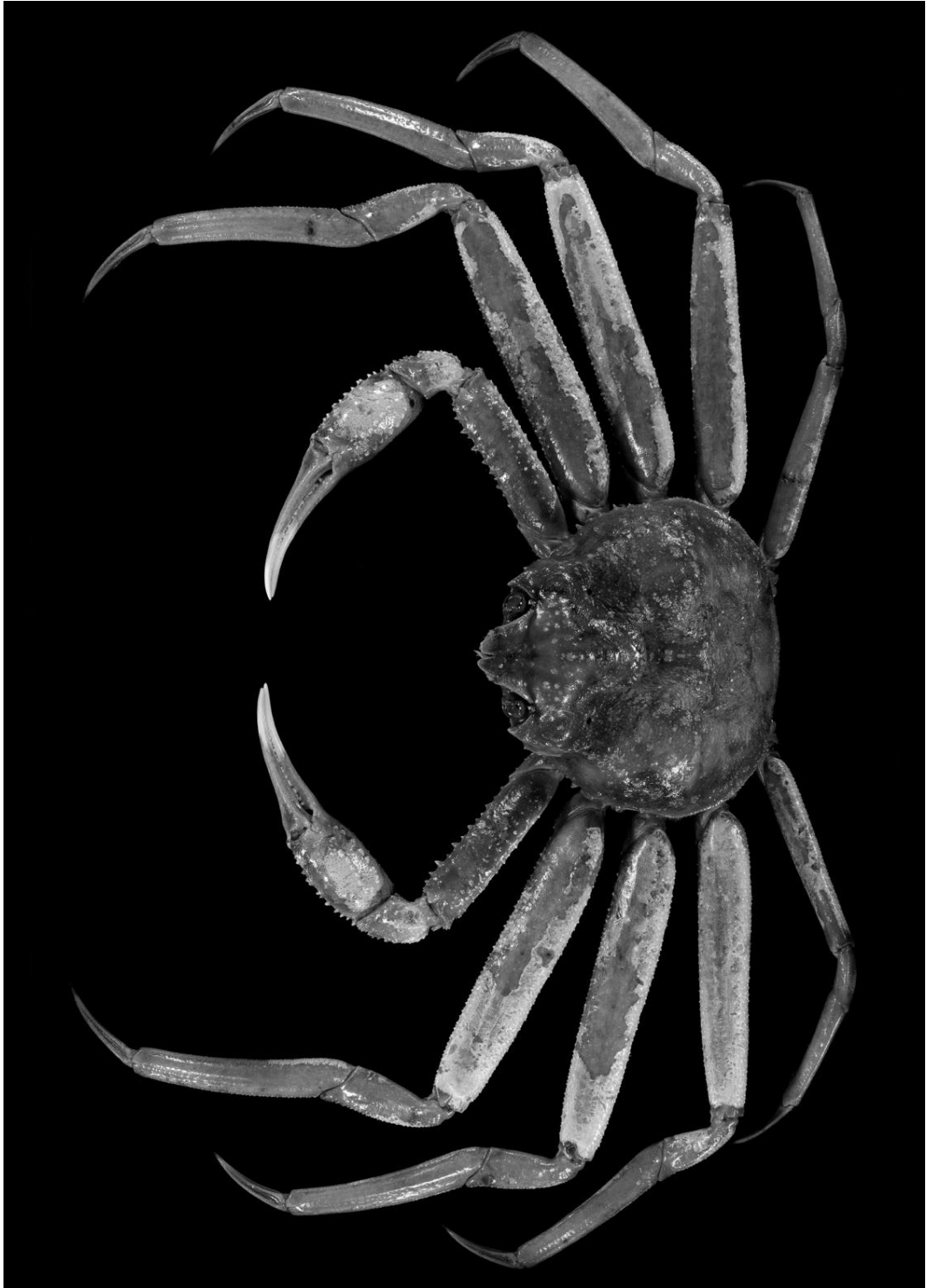


Fig. 94. *Chionoecetes japonicus* Rathbun, 1932. Male (pcl 88.2 mm) (MABIK CR00241025), dorsal view.

Remark

Two species of the genus *Chionoecetes* Krøyer, 1838 have been reported in Korean waters: *C. japonica* Rathbun, 1932, and *C. opilio* (O. Fabricius, 1788). The differences between the two species are described under *C. opilio*.

Chionoecetes japonica inhabits relatively great depths, and the observed specimens were collected at depths of 455 m and 1,000 m.

46. *Chionoecetes opilio* (O. Fabricius, 1788) (Fig. 96) 대게

Cancer opilio O. Fabricius, 1788: 182.

Chionoecetes opilio—Krøyer, 1838: 249; Rathbun, 1893: 74, pl. 4, figs 5–7; 1925: 233, pls. 84, 85; Yokoya, 1933: 165; Sakai, 1934: 295; 1936: 93, pl. 23; 1976: 185, pl. 64; Kamita, 1941: 68, fig. 30; Garth, 1958: 150, pl. 1, fig. 5, pl. 14; Kim, 1970: 24; 1973: 525, 663, fig. 245, pl. 52, fig. 191; Miyake, 1983: 31, pl. 11, fig. 1; Kim & Kim, 2001: 46, figs 37, 38; Ko & Lee, 2015: 48, pl. 38.

Chionoecetes behringianus Stimpson, 1857: 84; 1907: 8.

Chionoecetes opilio elongatus Rathbun, 1924: 3; Sakai, 1938: 275, pl. 28; Takeda, 1973b: 39.

Material examined

One male (pcl 61.7 mm), Gangneung-si, Gangwon-do, Korea, 37°44'29.1"N, 129°2'49.68"E, 10 Apr. 2018, coll. by otter trawl at 300 m depth; 1 female (pcl 69.1 mm), Pohang-si, Gyeongsangbuk-do, Korea, 36°12'32.82"N, 129°45'53.88"E, 14 Apr. 2018, coll. by otter trawl at 128 m depth; 1 female (pcl 52.5 mm), 2 males (pcl 25.31 mm, 26.5 mm), Goseong-gun, Gangwon-do, Korea, 38°16'21.82"N, 128°33'22.56"E, 27 Mar. 2019, coll. by gill net.

Diagnosis

Carapace subcircular, slightly broader than long, regions well defined; dorsal surface depressed, covered with ununiformed tubercles. Gastric region slightly convex, with low tubercles. Hepatic region slightly convex. Branchial region slightly convex, with low tubercles. Carapace with slope of posterior part gentle. Pseudorostrum very short, broad.

Supraorbital cave developed. Intercalated spine very small. Postorbital spine well developed, broad, triangular. Eyestalk short, cornea large. Hepatic margin with four small broad tubercles. Anterolateral branchial margin with small, acute spines. Posterolateral branchial margin with small tubercles. Cheliped shorter than first to third ambulatory legs; merus with row of spines on inner and outer margins; carpus with spines on outer margin; palm robust, with rows of tubercles on inner and outer margins; fingers smooth, longer than palm, cutting edges with row of tubercles. Ambulatory legs very long, slender, flattened; inner margin of merus with rows of small tubercles on first to third ambulatory legs.

Type locality

Greenland.

Habitat

Muddy or sandy bottoms, 200 to 350 m deep.

Distribution

West of Greenland, Arctic Alaska, East coast of Siberia, Bering Sea, Sea of Okhotsk, Kamchatka, Sakhalin, Japan, and Korea (Fig. 95).

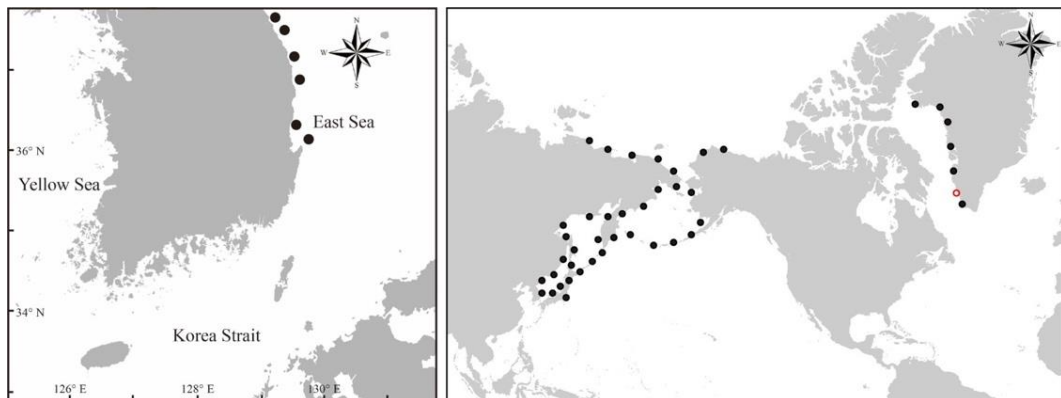


Fig. 95. Distribution of *Chionoecetes opilio* (O. Fabricius, 1788). Open circle=type locality.

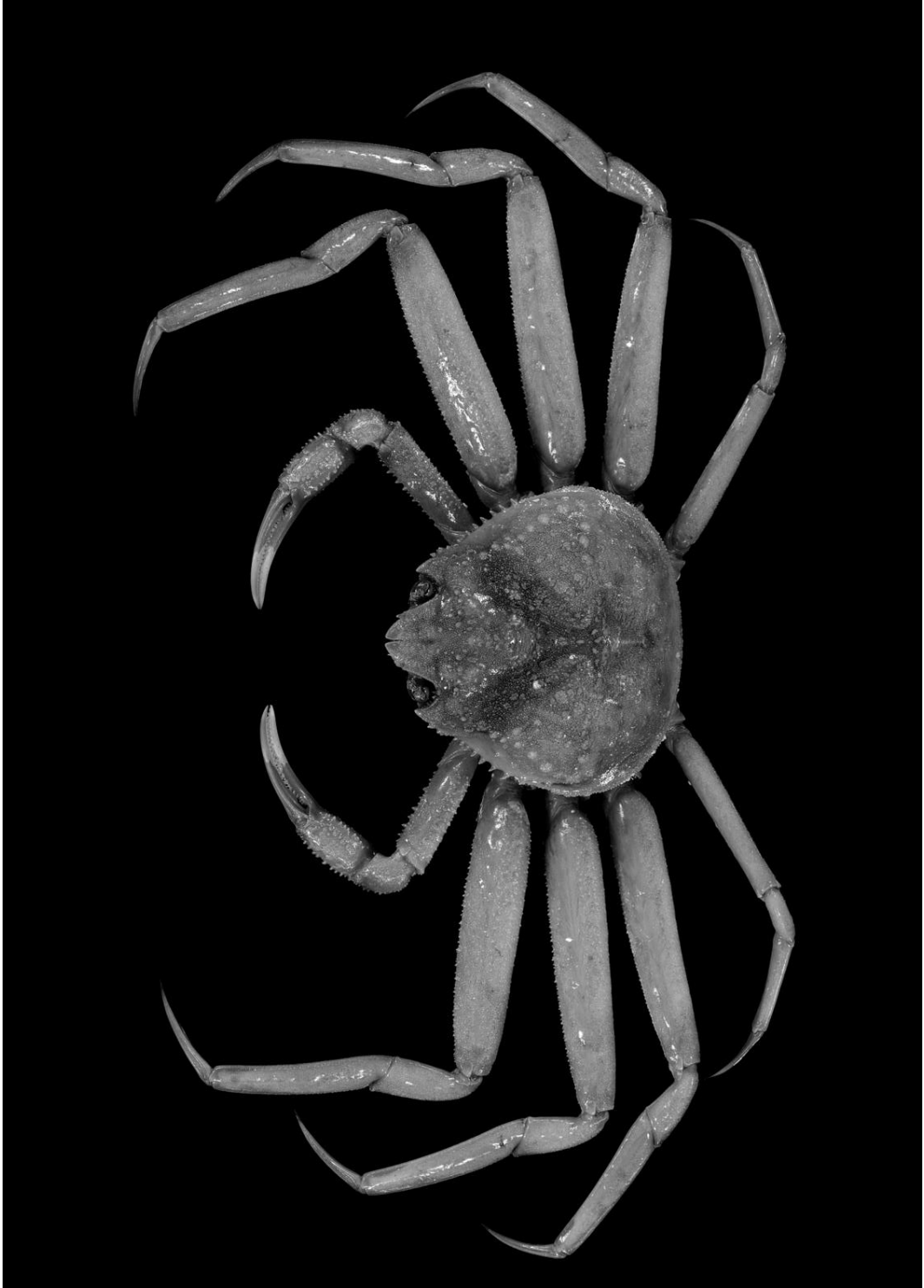


Fig. 96. *Chionoecetes opilio* (O. Fabricius, 1788). Male (pcl 61.7 mm), dorsal view.

Remark

Two species of the genus *Chionoecetes* Krøyer, 1838 are known in Korean waters: *C. japonica* Rathbun, 1932, and *C. opilio* (O. Fabricius, 1788). The two species are very important fishery resources in Korea. *Chionoecetes opilio* is similar to *C. japonica*. *Chionoecetes opilio* can be distinguished from *C. japonica* based on the following characteristics: (1) the slope of the posterior part of the carapace in *C. opilio* is gentle, but in *C. japonica*, the slope is steep, (2) live color is light brown, and dark red in *C. japonica*, 3) *C. opilio* usually inhabit depths between 200 to 300 m, but *C. japonica* inhabits depths near 2,000 m. These two species are recognized as valid species, but natural hybridization is reported (Kim et al., 2012).

Genus *Hyas* Leach, 1814 두꺼비게속

47. *Hyas alutaceus* Brandt, 1851 마이올린두꺼비게

Hyas coarctatus var. *alutacea* Brandt, 1851: 79.

Hyas coarctatus alutacea—Rathbun, 1925: 258, pls. 96, 97; Sakai, 1934: 295; 1938: 276, pl. 37, fig. 1; Kamita, 1941; 72, figs 32, 33; Serène, 1968: 51; Kim, 1970: 24; 1973: 524, fig. 244.

Type locality

Bear Island, near Shantar Island, Okhotsk Sea, Russia.

Habitat

Muddy, sandy or gravelly bottoms, subtidal 30 to 300 m deep.

Distribution

Arctic Ocean, from the Sea of Okhotsk to Alaska, East of Canada, Greenland, Japan, East China Sea, and Korea (Fig. 97).

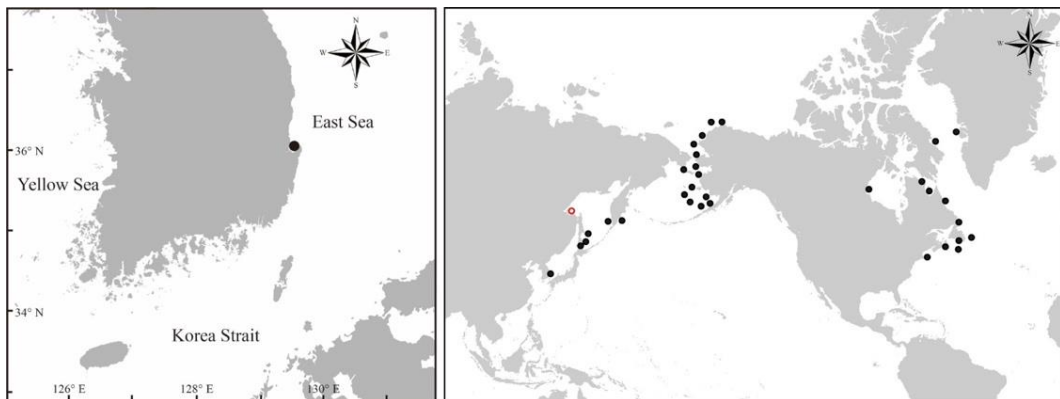


Fig. 97. Distribution of *Hyas alutaceus* Brandt, 1851. Open circle=type locality.

Remark

In Korean waters, Kamita (1941) reported the collection of *Hyas alutaceus* Brandt, 1851 on Pohang, and Kim (1970; 1973) cited it. *Hyas alutaceus* has not been collected in Korean waters since 1935. The author has not yet observed the species. Two species of *Hyas* Leach, 1814 are known in Korean waters: *H. alutaceus* and *H. coarctatus* Leach, 1815. For a detailed discussion of the two species, see remark for *H. coarctatus*.

48. *Hyas coarctatus* Leach, 1815 (Figs 98–99) 두꺼비게

Hyas coarctatus Leach, 1815: 329; Rathbun, 1925: 258, pl. 94, 95; Sakai, 1935: 94, pl. 22, fig. 3; Kamita, 1941, p. 71, fig. 31; Kim, 1973, p. 523, pl. 51, fig. 189; Kim & Kim, 2001: 50, figs 42–44; Ko & Lee, 2015: 49, pls. 39, 40.

Material examined

NIBRIV0000104505, 1 female (pcl 41.1 mm), Yangyang-gun, Gangwon-do, Korea, 21 May 2008, coll. by gill net; NIBRIV0000176805, 1 female (pcl 57.4 mm), Yangyang-gun, Gangwon-do, Korea, 23 May 2010, coll. by gill net; NIBRIV0000176806, 1 male (pcl 53.1 mm), Yangyang-gun, Gangwon-do, Korea, 23 May 2010, coll. by gill net; NIBRIV0000176807, 1 female (pcl 55.2 mm), Yangyang-gun, Gangwon-do, Korea, 23 May 2010, coll. by gill net; NIBRIV0000176804, 1 female (pcl 64.8 mm), Yangyang-gun, Gangwon-do, Korea, 25 May 2010, coll. by gill net; MABIK CR00241030, 2 females (pcl 42.5, 52.1 mm), 3 males (pcl 49.3–80.5 mm), Goseong-gun, Gangwon-do, Korea, 5 Apr. 2011, coll. by otter trawl; MABIK CR00013113, 1 female (pcl 50.0 mm), Samcheok-si, Gangwon-do, Korea, 37°21'30.6"N, 129°23'55.2"E, 19 May 2012, coll. by otter trawl; MABIK CR00013119, 1 female (pcl 45.9 mm), Gangneung-si, Gangwon-do, Korea, 37°40'54"N, 129°5'38.4"E, 19 May 2012, coll. by otter trawl; MABIK CR00013145, 1 female (pcl 44.7 mm), Sokcho-si, Gangwon-do, Korea, 38°9'49.8"N, 128°41'10.8"E, 19 May 2012, coll. by otter trawl; MABIK CR00013128, 1 female (pcl 34.7 mm), Sokcho-si, Gangwon-do, Korea, 38°9'49.6"N, 128°41'10.8"E, 20 May 2012, coll. by otter trawl; NIBRIV0000291302, 1 female (pcl 42.2 mm), Uljin-gun, Gyeongsangbuk-do, Korea, 37°17'N, 129°29'12"E, 29 May 2012, coll. by gill net; MABIK CR00022138, 1 male (pcl

55.2 mm), Sokcho-si, Gangwon-do, Korea, 38°8'87"N, 128°42'30"E, 23 Aug. 2012, coll. by otter trawl; NIBRIV0000753565, 1 male (pcl 43.6 mm), Yangyang-gun, Gangwon-do, Korea, 16 Feb. 2016, coll. by gill net; NIBRIV0000753566, 1 female (pcl 40.5 mm), Yangyang-gun, Gangwon-do, Korea, 16 Feb. 2016, coll. by gill net.

Diagnosis

Carapace pyriform, 1.4 times as long as broad. Gastric region convex, with several tubercles mesially. Cardiac region slightly convex, with one vestigial tubercle. Branchial region swollen, with row of tubercles near margin. Pseudorostrum short, broad, tapered distally, each lobe subcontiguous, covered with hooked setae. Supraorbital eave developed, oblique. Postorbital spine and hepatic spine fused, wing like, expanded laterally. Eyestalk short. Cheliped stout, slightly shorter than first ambulatory leg, with small tubercles on outer margin of merus. Ambulatory legs slender, long, cylindrical; dactylus covered with tomentum. Abdomen of male with six segments and telson, sixth segment broader than fifth segment.

Type locality

Firth of Forth, Plymouth Sound, and Salcombe, United Kingdom.

Habitat

Muddy, sandy, or gravelly bottoms.

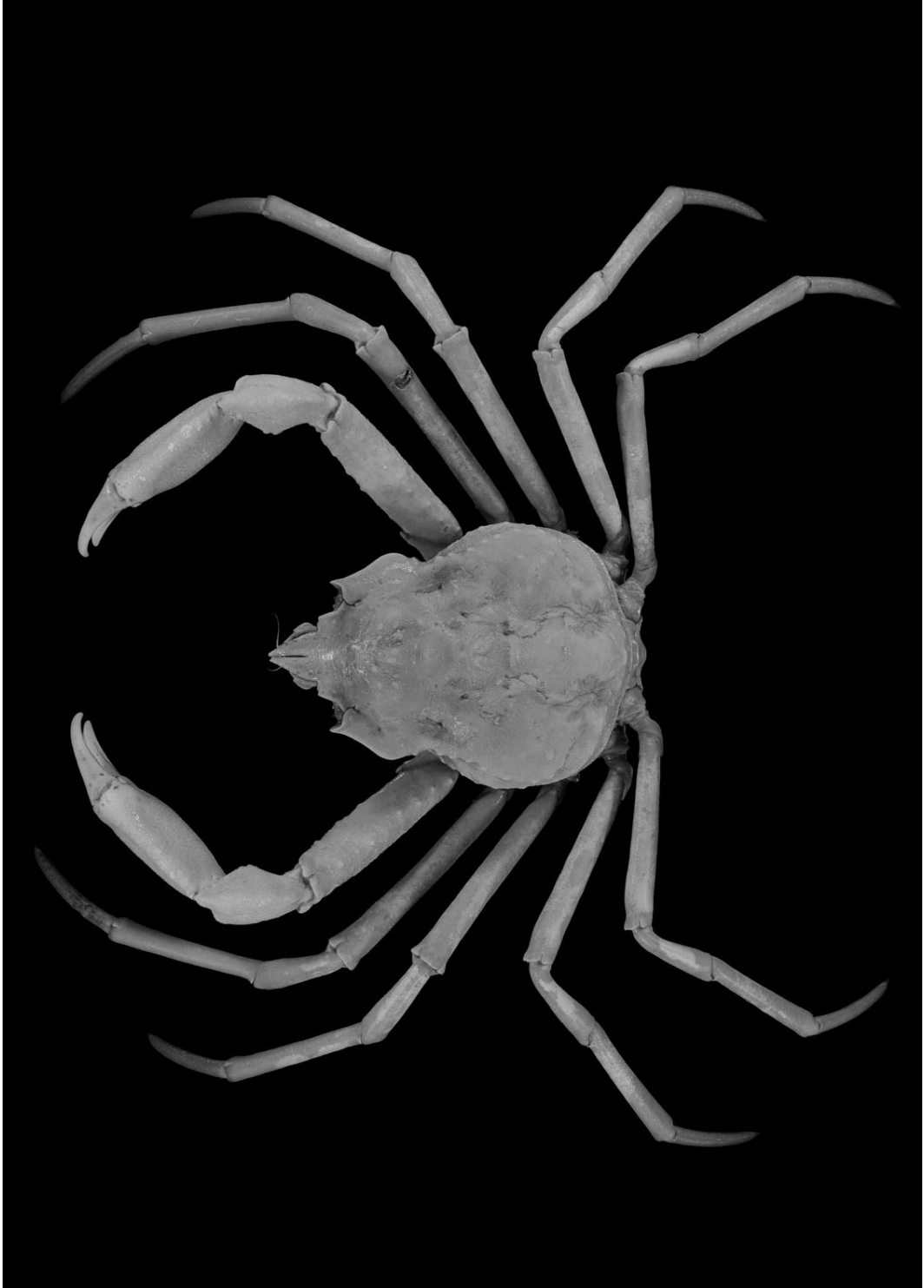


Fig. 98. *Hyas coarctatus* Leach, 1815. Male (pcl 80.4 mm) (MABIK CR00241030), dorsal view.



Fig. 99. *Hyas coarctatus* Leach, 1815. Female (pcl 52.6 mm) (MABIK CR00241030), dorsal view.

Distribution

From the Sea of Okhotsk to the coast of Alaska, Japan, Greenland, North Sea, United Kingdom, Ireland, and Korea (Fig. 100).

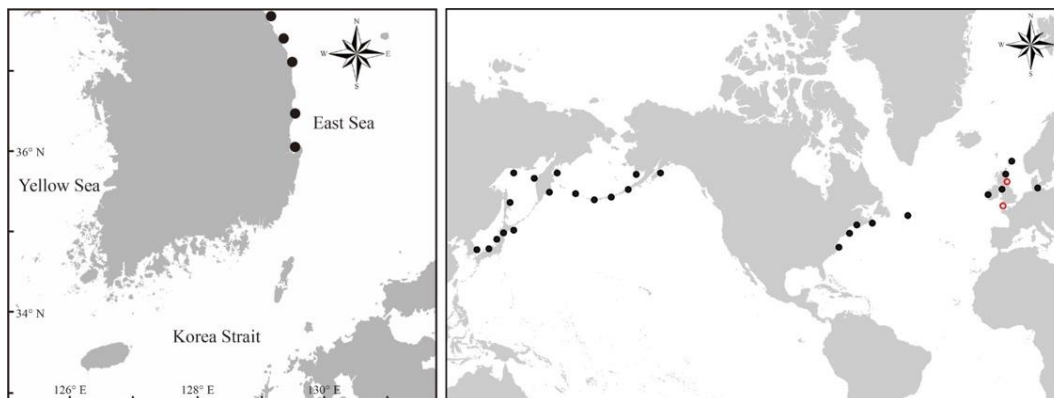


Fig. 100. Distribution of *Hyas coarctatus* Leach, 1815. Open circle=type locality.

Remark

Hyas coarctatus Leach, 1815 and *H. alutaceus* Brandt, 1851 have very wide ranges of habitats around the Arctic Ocean. *Hyas coarctatus* was described as a new species by Leach (1815), and *H. alutaceus* was first reported by Brandt (1851) as a variation of *H. coarctatus*. Later, Rathbun (1925) described *H. alutaceus* as a subspecies of *H. coarctatus*. Rathbun (1925) observed numerous specimens around the Northwest Atlantic, Alaska, and the Bering Sea, and reviewed species of *Hyas* reported in the Americas. She presented the main differences between the two species as a proportion of rostrum length (she measured the length of the rostrum from the tip of the rostrum to the angle which it forms with the orbit) and cl, and further explored differences in the width of the hepatic region. According to Rathbun (1932), the ratio of rostrum length to cl ranges from 4.5 : 1 to 6.4 : 1 in *H. coarctatus* and 7 : 1 to 9.3 : 1 in *H. alutaceus*, and the width of the front one-third of the carapace containing the hepatic region is wider in *H. alutaceus* than in *H. coarctatus*.

Two species of the genus *Hyas* Leach, 1814 are known in Korean waters: *H. coarctatus* Rathbun (1925) and *H. alutaceus* Brandt, 1851. Kamita (1941) reported *H. coarctatus* and *H. alutaceus* in Wonsan and Pohang, respectively. He highlighted the differences between the two species as follows: (1) in *H. coarctatus*, the rostrum is relatively long (in *H. alutaceus*, shorter and narrower), (2) in *H. coarctatus*, the width of the hepatic and branchial regions are normal (in *H. alutaceus*, the hepatic region is narrow and the branchial region is swollen), and (3) in *H. coarctatus*, the ambulatory legs are covered with setae (in *H. alutaceus*, naked).

According to observations of 18 specimens in the Korean *Hyas* deposited in MABIK and NIBR, 6 individuals had a carapace at least 6.4 times longer than the length of the rostrum. In all the specimens examined, however, the widths of the hepatic and branchial regions appeared normal, and the setation of the legs was mixed. In the illustrations of *H. alutaceus* of Kamita (1941, text-fig. 32, 33), which is the only specimen that has been reported in Korean waters, the hepatic region is relatively narrow, although it has a relatively short rostrum and a swollen branchial region. This feature differs somewhat from the illustration of *H. alutaceus* in Rathbun (1932, pl. 96). *Hyas coarctatus* and *H. alutaceus* seem to have to be identified based on comprehensive consideration of various characteristics, and further studies in various regions would be required to determine whether *H. alutaceus* exists in Korean waters.

Genus *Oregonia* Dana, 1851 긴집게발게속

49. *Oregonia gracilis* Dana, 1851 (Fig. 101) 긴집게발게

Oregonia gracilis Dana, 1851: 270; 1852: 106; 1855: pl. 3, fig. 2a–c; Rathbun, 1925: 71, figs 19, 20, pls. 24, 25; Yokoya, 1928: 765; 1933: 141; Shen, 1932: 45, figs 23–25, pl. 2, fig. 1; 1937: 168; Sakai, 1936: 82, fig. 32; 1938: 231, pl. 34, fig. 1; 1976: 183, pl. 63, fig. 1; Kamita, 1941: 63; Garth, 1958: 136, pl. 1, fig. 2, pl. 10, pl. 11, fig. 1; Takeda & Miyake, 1969: 503; Kim, 1970: 24; 1973: 521, 662, figs 241, 242, pls. 101, 102, fig. 188; Miyake, 1983: 30, pl. 10, fig. 5; Kim & Chang, 1985: 45; Dai & Yang, 1991: 125, fig. 63, pl. 13(8); Ko & Lee, 2015: 50, fig. 3E, F, pl. 41.

Oregonia hirta Dana, 1851: 270; 1852: 107; 1855: pl. 3, fig. 3a, b.

Oregonia longimana Bate, 1865: 663.

Material examined

MABIK CR00010774, 1 male (pcl 39.2 mm), 34°41'51"N, 123°15'52.8"E, 5 Aug. 2011, coll. by otter trawl at 100 m depth; MABIK CR00011682, 1 female (pcl 29.1 mm), 34°11'36.6"N, 125°17'24"E, 10 Nov. 2011, coll. by otter trawl at 100 m depth; 1 female (pcl 22.3 mm), 34°18'39"N, 124°46'37.8"E, 11 Nov. 2011, coll. by otter trawl at 100 m depth; 2 females (pcl 36.6 mm, 38.4 mm), 2 male (pcl 32.1 mm, 40.2 mm), Suyeong-gu, Busan, Korea, 35°9'13.29"N, 129°7'40.45"E, 11 Apr. 2019, coll. by otter trawl at 100 m depth.

Diagnosis

Carapace elongated pyriform, region well defined; dorsal surface covered with ununiformed tubercles, with hooked setae. Gastric region convex, with dozen large tubercles. Cardiac region slightly convex, with several small tubercles. Branchial region with numerous tubercles. Pseudorostrum very slender and long, appressed, slightly outward distally, 0.33 times as long as pcl, covered with hooked setae. Supraorbital eave thick, oblique. Postorbital spine well developed, long, sharp distally, projecting obliquely. Hepatic margin inflated laterally, with two to three small tubercles. Eystalk long, slender. In male, cheliped longer than ambulatory legs, with small tubercles and short hooked setae; palm slightly shorter than merus, with small tubercles on dorsal surface. In female, cheliped short, covered with setae. Ambulatory legs long, slender, unarmed, cylindrical; dactylus covered with tomentum. Abdomen of male with six segments and telson, sixth somite broader than fifth somite. In male, G1 strongly curved, stout proximally and slender distally.

Type locality

Puget Sound, Washington, U.S.A.

Habitat

Muddy or mud sandy bottoms, subtidal to 370 m deep.

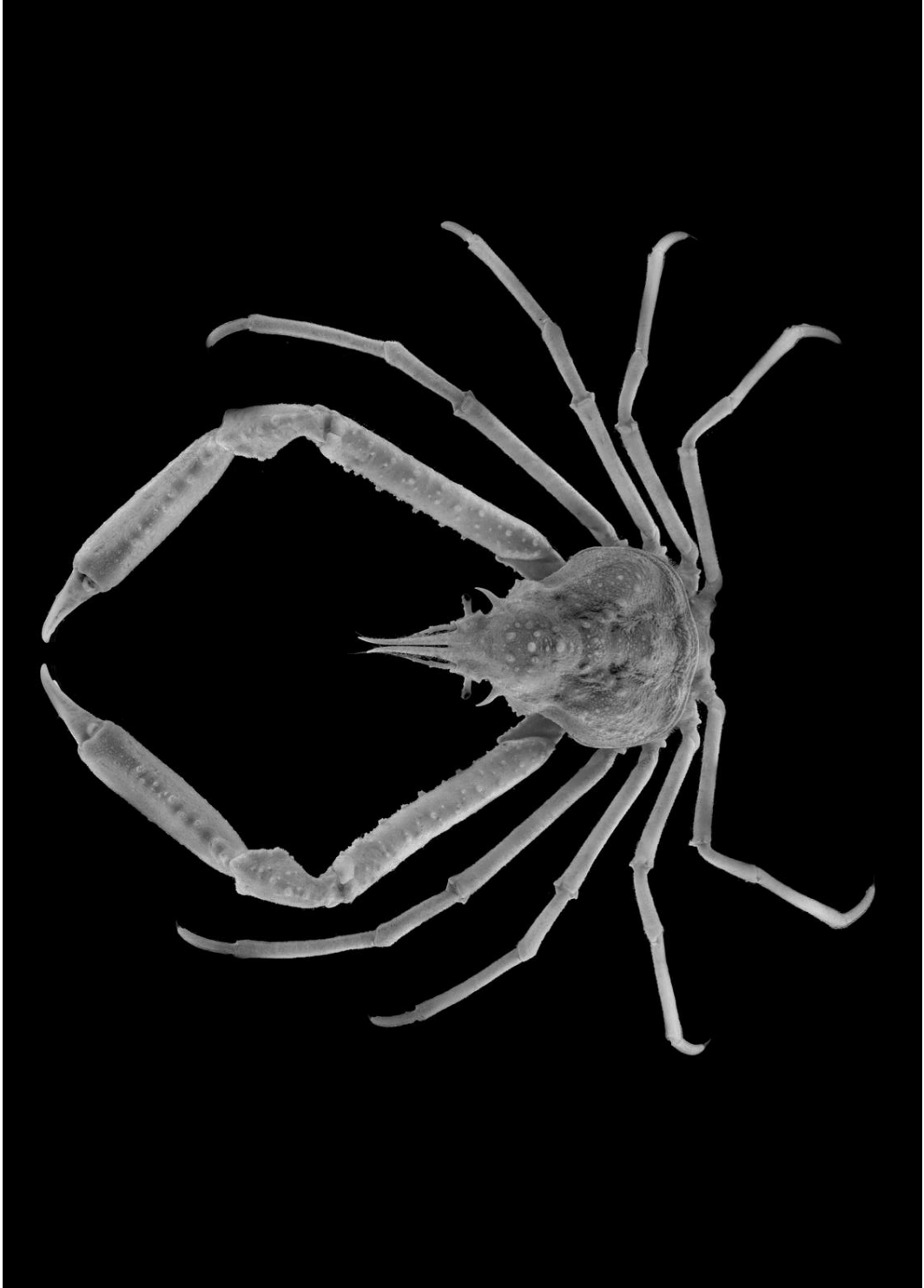


Fig. 101. *Oregonia gracilis* Dana, 1851. Male (pcl 39.2 mm) (MABIK CR00010774), dorsal view.

Distribution

From the Behring Sea to California, Japan, China (Yellow Sea and East China Sea), and Korea (Fig. 102).

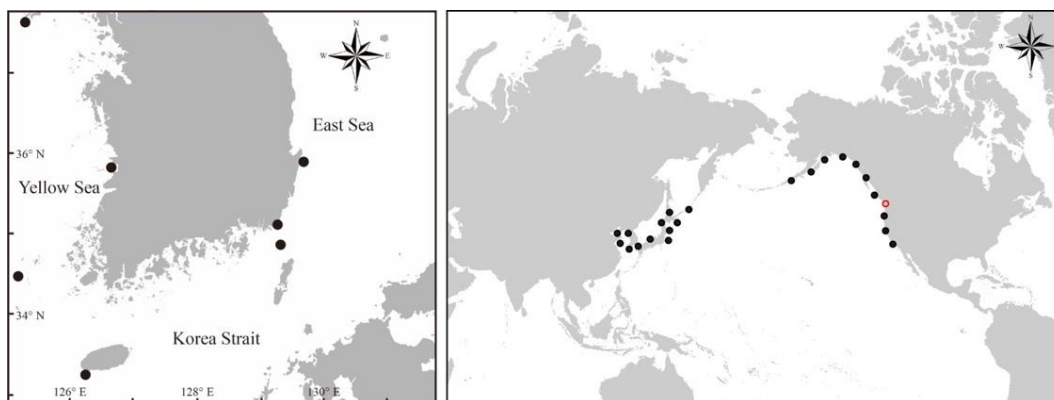


Fig. 102. Distribution of *Oregonia gracilis* Dana, 1851. Open circle=type locality.

Remark

The genus *Oregonia* Dana 1851 can be distinguished from other oregoniids based on the following characteristics: (1) carapace longer than broad, (2) abdomen with the sixth segment of male broader than the fifth segment, (3) pseudorostrum very slender and long. The genus *Oregonia* consists of two species: *O. gracilis* Dana, 1851, *O. bifurca* Rathbun, 1902. Among them, *O. gracilis* is the only species of the genus *Oregonia* in Korea. *Oregonia gracilis* is found in all waters in Korea.

Subfamily Pleistacanthinae Števíć, 2005

Genus *Pleistacantha* Miers, 1879 삼천가시게속

* **50. *Pleistacantha oryx* Ortmann, 1893 (Fig. 103)** 사슴삼천가시게

Pleistacantha oryx Ortmann, 1893: 39; Serène & Lohavanijaya, 1973: 43, pl. 7A; Sakai, 1976: 172, pl. 55 (part); Guinot & Richer de Forges, 1986: 126, fig. 15A–C, 16A, C, Ea, 18A–D, pl. 7, fig. A–D; Griffin & Tranter, 1986: 51 (part); Davie & Short, 1989: 179 (part); Dai & Yang, 1991: 123, pl. 13(5).

Material examined

One male (cl 24.1 mm, pcl 17.9 mm, cw 14.3 mm), Seogwipo-si, Jeju-do, Korea, 33°31'51.56"N, 127°32'53.14"E, 6 May 2019, coll. by otter trawl.

Diagnosis

Carapace pyriform, pcl 1.2 times as long as broad, with numerous small and large spines, regions distinct. Gastric region convex, with four prominent protogastric spines transversely, one prominent mesogastric spine medially. Cardiac region convex, with two large spines transversely. Intestinal region with two spines. Branchial region with two large spines on dorsal surface: anterior one largest. Pseudorostrum slender, 0.35 times as long as pcl, slightly upward, with three spines on ventral surface, with one to two spines on lateral margin. Supraorbital margin with three to four spines increasing in size posteriorly. Hepatic margin with two strong spines: posterior one larger. Interantennular spine bifurcated in distal quarter. Cheliped slender, with several rows of spine; fingers 0.69 times as long as palm. Ambulatory legs extremely long and slender, with spines except for dactylus. Abdomen with six segments and telson. In male, G1 slightly curved, acute distally.



Fig. 103. *Pleistacantha oryx* Ortmann, 1893. Male (pcl 17.9 mm), dorsal view.

Type locality

Sagami Bay, Japan.

Habitat

Muddy, sand muddy, or broken shell bottoms, 50 to 720 m deep.

Distribution

Japan, East China Sea, South China Sea, China (Guangdong), Philippines, Indonesia, and Korea (Fig. 104).

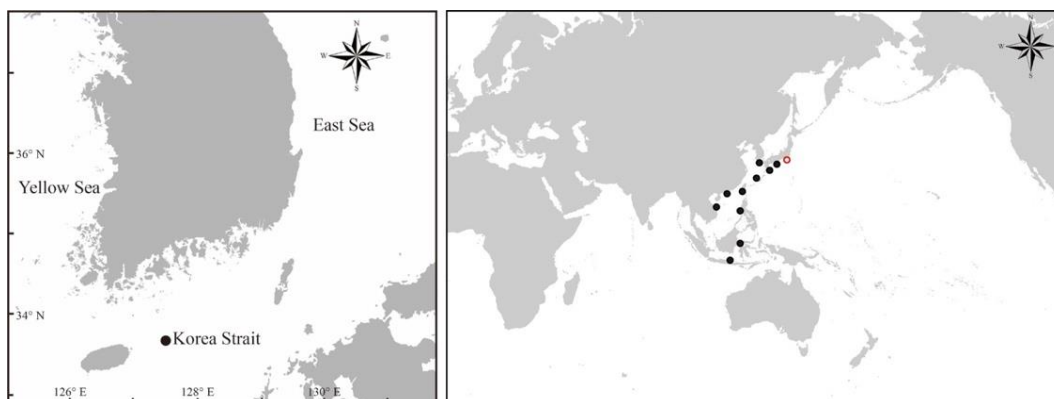


Fig. 104. Distribution of *Pleistacantha oryx* Ortmann, 1893. Open circle=type locality.

Remark

Ahyong & Lee (2006) mentioned that *Pleistacantha oryx* is closely related to *P. maxima* Ahyong & Lee, 2006. The two species share the following characteristics: (1) long pseudorostrum (exceed half pcl), (2) interantennular spine bifurcated in the distal quarter, and (3) the fourth ambulatory leg with merus shorter than pcl. Ahyong & Lee (2006) suggested that *P. oryx* can be distinguished from *P. maxima* based on the following characteristics: (1) pcl not exceeding 32 mm (in *P. maxima*, pcl reaching at least 71 mm),

(2) the gastric and branchial spines shorter than the anterior hepatic spine (in *P. maxima*, those spines as long as or longer than the anterior hepatic spine), (3) in lateral view, the dorsal margin of the pseudorostrum is convex (concave in *P. maxima*), (4) the finger is about 0.7 times as long as the dorsal palm length (0.5 to 0.6 times as long as the dorsal palm length in *P. maxima*), (5) the G1 tip acute and the basal margin of the subdistal papilla convex (in *P. maxima*, the G1 of tip blunt and the basal margin of subdistal papilla straight). The characteristics of the examined specimen are consistent with the features of *P. oryx* excluding the pseudorostrum, which is 0.34 times as long as pcl, although the branchial region is swollen into a bopyrid infection.

51. *Pleistacantha sanctijohannis* Miers, 1879 (Fig. 106) 삼천가시게

Pleistacantha sancti-johannis Miers, 1879: 24, pl. 1, fig. 1; Ortmann, 1893: 39; Sakai, 1934: 293; 1936: 78, pl. 15, fig. 1; 1938: 233, pl. 23, fig. 1; 1965: 70, pl. 30, fig. 3; Serène & Lohavanijaya, 1973: 44, fig. 67–72, pl. 7B.

Pleistacantha sanctijohannis—Kim & Park, 1972: 61, fig. 6A–C, pl. 1, fig. 5; Kim, 1973: 513, 661, fig. 235A–D, pl. 100, fig. 183; 1977: 208; Griffin, 1976: 209; Sakai, 1976: 172, pl. 53, fig. 2; Guinot & Richer de Forges, 1982: 1105; Kim & Kim, 1982: 154; Miyake, 1983: 26, pl. 9, fig. 5; Kim & Chang, 1985: 45; Guinot & Richer de Forges, 1986: 125; Griffin & Tranter, 1986: 52; Ko & Lee, 2015: 32.

Material examined

MABIK CR00011305, 1 female (cl 14.9 mm), Korea, 33°10'27.6"N, 126°22'40.2"E, 16 Nov. 2011, coll. by otter trawl; MABIK CR00013525, 1 male (cl 15.8 mm), Korea, 33°11'18.6"N, 126°32'58.2"E, 1 Apr. 2012, coll. by otter trawl; MABIK CR00216790, 1 female (cl 15.0 mm), Gyeongsangnam-do, Korea, 34°10'30"N, 128°22'37"E, 27 Aug. 2013, coll. by otter trawl; 1 female (cl 9.8 mm), Seogwipo-si, Jeju-do, Korea, 33°11'43.8"N, 127°1'38.9"E, 1 May 2019, coll. by otter trawl; 1 male (cl 14.4 mm), Seogwipo-si, Jeju-do, Korea, 33°22'21.55"N, 127°1'53.27"E, 1 May 2019, coll. by otter trawl.

Diagnosis

Carapace pyriform, pel slightly longer than broad, with numerous small and large spines, regions distinct. Gastric region with three large protogastric spines transversely, one large mesogastric spine medially. Hepatic region with two large spines. Cardiac region with two

large spines transversely. Intestinal region with two spines. Branchial region with two large spines on dorsal surface. Pseudorostrum slender, long, strongly upward, appressed in proximal half to three-quarters, divergent distally. Supraorbital margin with row of small spines. Branchial margin with three large spines. Cheliped robust, with several rows of spine. Ambulatory legs extremely long and slender, with small spines except for dactylus. Abdomen with six segments and telson.

Type locality

Off the coast of Mie Prefecture, Japan.

Habitat

Muddy, sand muddy, or broken shell bottoms, 30 to 540 m deep.

Distribution

Japan, East China Sea, South China Sea, Philippines, Indonesia, and Korea (Fig. 105).

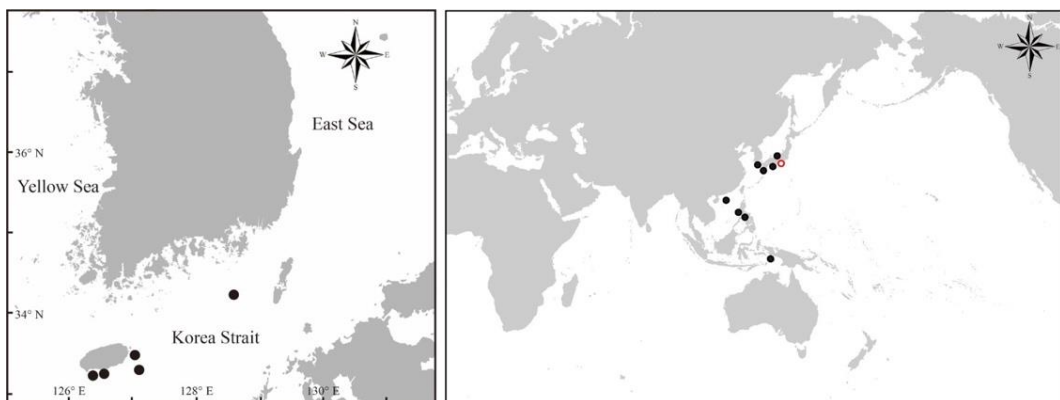


Fig. 105. Distribution of *Pleistacantha sanctijohannis* Miers, 1879. Open circle=type locality.



Fig. 106. *Pleistacantha sanctijohannis* Miers, 1879. Male (pcl 15.8 mm) (MABIK CR00013525), dorsal view.

Remark

Ahyong et al. (2005) mentioned that male *Pleistacantha sanctijohannis* Miers, 1879 has distinct inflated cheliped propodus, and this is one of the main characteristics of the species. However, one of the observed male specimens (pcl 14.4 mm) had no inflated propodus of chela.

Molecular analysis

Molecular analysis based on the mitochondrial *COXI* gene sequence was performed. A total of 658 bp of mitochondrial *COXI* was obtained from 246 specimens of majoid species, and 38 clades were divided as a result of a phylogenetic analysis (Fig. 107). Pairwise distances of the 38 majoid crabs are listed in Table 3. Each clade represented a low P-distance value, which implies that they are the same species. In most cases, molecular analysis of the morphologically identified taxon confirmed that it was divided into distinctly independent clades. For the species that cause confusion morphologically, the analysis was performed in reverse taxonomy. *Pugettia quadridens sensu lato* was found to be divided into four clades as a result of molecular analysis (Fig. 107). Furthermore, *COXI* genetic distance showed that while the interspecies divergences between *Pugettia ferox* and *P. incisa* were very close, the NJ tree formed an independent group for each (Fig. 107).

Table 3. Pairwise genetic distance (K2P distance) of *COXI* sequences for 38 majoid crabs.

Species	Individuals	P-distance range (%)
1. <i>Huenia heraldica</i>	1	-
2. <i>Menaethius monoceros</i>	5	0–1.06
3. <i>Pugettia ferox</i>	49	0–0.76
4. <i>Pugettia incisa</i>	6	0.15–0.84
5. <i>Pugettia intermedia</i>	28	0–0.46
6. <i>Pugettia marissinica</i>	1	-
7. <i>Pugettia nipponensis</i>	2	0
8. <i>Pugettia quadridens</i>	25	0–0.61
9. <i>Pugettia vulgaris</i>	16	0.15–1.82
10. <i>Xenocarcinus conicus</i>	2	1.06
11. <i>Hyastenus elongatus</i>	11	0–0.8
12. <i>Hyastenus pleione</i>	1	-
13. <i>Naxioides robillardi</i>	3	0
14. <i>Scyra compressipes</i>	14	0–0.91
15. <i>Paratymolus pubescens</i>	1	-
16. <i>Achaeus japonicus</i>	5	0.15–0.46
17. <i>Achaeus lacertosus</i>	2	0.3
18. <i>Achaeus spinosus</i>	2	0
19. <i>Achaeus tuberculatus</i>	4	0–0.46
20. <i>Cyrtomaia platypes</i>	1	-
21. <i>Platymaia wyvillethomsoni</i>	4	0.15–0.46
22. <i>Pyromaia tuberculata</i>	4	0
23. <i>Entomonyx spinosus</i>	3	0.15–0.30
24. <i>Leptomithrax bifidus</i>	3	0–0.30
25. <i>Leptomithrax edwardsii</i>	6	0–0.15
26. <i>Micippa platipes</i>	3	0.15–0.30
27. <i>Micippa thalia</i>	3	0
28. <i>Primatopus longispinus</i>	1	-
29. <i>Pseudomicippe nipponica</i>	2	0.99
30. <i>Sakaija japonica</i>	6	0–1.37
31. <i>Sakaija sakaii</i>	1	-
32. <i>Schizophroida simodaensis</i>	3	0–0.15
33. <i>Chionoecetes japonicus</i>	2	0
34. <i>Chionoecetes opilio</i>	3	0
35. <i>Hyas coarctatus</i>	14	0.15–1.82
36. <i>Oregonia gracilis</i>	3	0–0.30
37. <i>Pleistacantha oryx</i>	1	-
38. <i>Pleistacantha sanctijohannis</i>	5	0–0.61

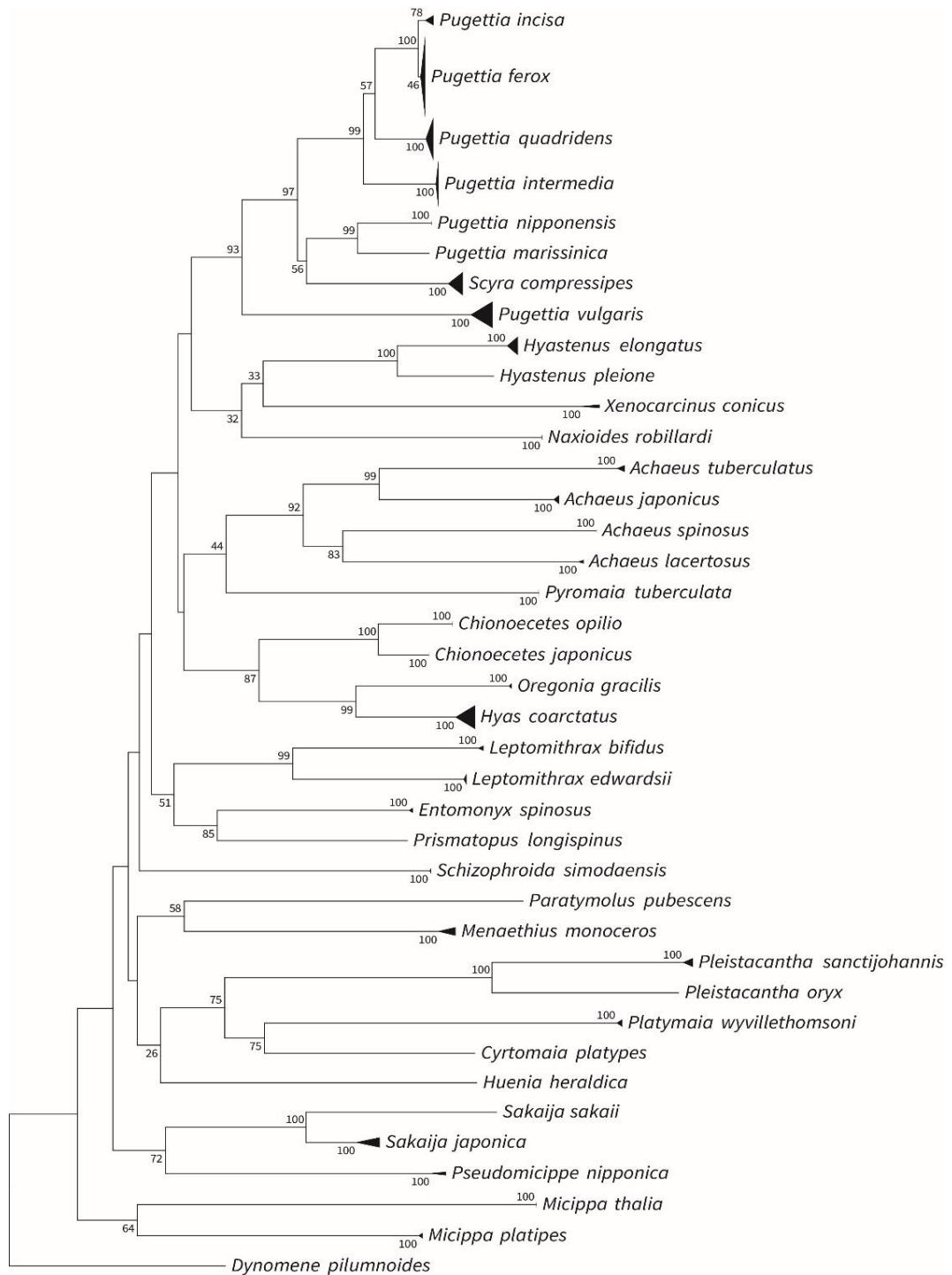


Fig. 107. Neighbor-joining (NJ) tree of *COXI* sequences for 38 majoid crabs and *Dynomene pilumnoides* as out-group.

1.4. Discussion

One objective of this study was to survey the diversity of majoid crabs in Korean waters. In addition to a literature survey, 331 majoid crab specimens from Korean waters were examined. As a result, the number of majoid crab species identified in Korean waters has expanded from 42 species of 25 genera to 51 species of 29 genera. Among these, nine species of six genera were recorded for the first time in Korean waters. Korean majoid crab diversity is relatively low in comparison with that in neighboring countries: Japan has 161 species of 72 genera (Sakai, 2005), China has 132 species of 51 genera (Liu, 2008), and Taiwan has 70 species of 44 genera (Ng et al., 2017); however, the diversity in Korean waters is noteworthy considering the geographical challenges such as marine areas and latitude. In addition, it has been confirmed that all families except the Mithracidae (which occur in the Americas) are represented, indicating high diversity at higher taxonomic levels. It appears that the Korean marine environment is influenced by the warm (the Kuroshio Current) and cold (the North Korean coastal current) currents, and species from various marine habitats have been discovered, including boreal species (Oregoniinae) and temperate species.

The highest species diversity occurs around Jejudo Island where 33 species of 20 genera were either collected in this study or previously recorded. Twenty species were found only in this location and all previously unrecorded species identified in this study were found off the coast of Jejudo Island.

The species composition in areas away from the land (15 km or more) was different from that near the shore. Most of the diversity surveys conducted to date have been SCUBA

diving, intertidal zone, and fishing port surveys close to the shore, and majoid crabs occurring in offshore waters have mainly been collected by commercial fishing vessels. Given that species with no commercial value are usually abandoned at sea by fishing vessels, only a very small number of majoid crab specimens have been obtained from deeper waters to date. However, in this study, a large number of offshore species were collected from waters 15 km or more from the shore by the trawler of a research vessel. This offshore survey included species rarely found in Korean waters (*Pugettia incisa*, *Achaeus tuberculatus*, *Entomonyx spinosus*, *Leptomithrax bifidus*, and *L. edwardsii*) and species not previously reported in this geographical location (*Pugettia marissinica*, *P. nipponensis*, *Naxioides robillardi*, *Cyrtomaia platypes*, *Sakaija japonica*, *S. sakaii*, *Pleistacantha oryx*, and *P. sanctijohannis*). This suggests that, rather than these species being rare, there are many regions that have not yet been surveyed in deeper Korean waters, and the occurrence and composition of species in these areas remain unknown. The proportion of species collected in these offshore areas accounted for over 25% of Korean majoid crab diversity. Therefore, if a diversity of habitats is studied using various survey methods, it is expected that the number of recorded majoid crab species inhabiting Korean waters will be further increased.

The molecular taxonomic analysis in this study confirmed the majoid crabs inhabiting the Korean waters and revised the various identification errors. In most cases, molecular analysis of the morphologically identified taxon confirmed that it was divided into distinctly independent clades. For species, that cause confusion in morphologically, the analysis was performed in reverse taxonomy. *Pugettia quadridens sensu lato* has been reported in five species in Korean waters (*P. ferox*, *P. intermedia*, *P. pellucens*, *P. quadridens*, and *P. vulgaris*). These species are confusing in morphologically, and many

misidentifications have been reported. (see taxonomic accounts, this Chapter). Thus, *Pugettia quadridens sensu lato* performed a molecular analysis first and then a morphological analysis was performed, considering the individuals belonging to each clade to be the same species. The results showed that *P. ferox*, *P. intermedia*, *P. quadridens*, and *P. vulgaris* inhabit Korean waters. In immature or smaller individuals, a number of cases have been found where the morphological characteristics between species appear to be mixed or do not appear well. Molecular identification may be useful for identifying these individuals. The species that was not confirmed in this study is *P. pullucens*, and it is necessary to conduct additional research to ascertain the existence of the species in Korean waters (see remark of *P. pellucens*). The main features of *Pugettia quadridens sensu lato* excluding *P. pellucens* are shown in Table 4.

Table 4. Main characteristics of *Pugettia quadridens sensu lato*.

<i>P. ferox</i>	<i>P. intermedia</i>	<i>P. quadridens</i>	<i>P. vulgaris</i>
Protogastric tubercles separated equally from mesogastric tubercle than from metagastric tubercle	Protogastric tubercles more separated from mesogastric tubercle than from metagastric tubercle	Gastric region with tubercles often vestigial	Gastric region unarmed
Ambulatory legs often smooth	Ambulatory legs with club-shaped setae sparsely	Ambulatory legs often smooth	Ambulatory legs often smooth
Cardiac and intestinal regions separated	Cardiac and intestinal regions separated	Cardiac and intestinal regions almost fused	Cardiac and intestinal regions separated
In male, G1 with mesial lobe shorter than dorsal lobe	In male, G1 with mesial lobe as long as dorsal lobe	In male, G1 with mesial lobe shorter than dorsal lobe	In male, G1 with mesial lobe as long as dorsal lobe
In female, gonopore comma-shaped	In female, gonopore elongated transversely	In female, gonopore comma-shaped	In female, gonopore comma-shaped

COXI genetic distance showed that the interspecies divergences between *Pugettia ferox* and *P. incisa* were very close, but the NJ tree (Fig. 107) formed an independent group. Upon observation of the morphological characteristics, the postocular and hepatic spines were fully fused in *P. incisa*, whereas *P. ferox* tended to be partially fused. In the genus *Pugettia*, *P. incisa* is thought to have originated recently from *P. ferox*.

In *Hyas*, there are not many reports on *H. alutaceus*, and the illustrations and descriptions by Kamita (1941) in Korean waters are somewhat different from those reported by Rathbun (1925), thus requiring further study (see remark of *H. coarctatus*, this Chapter). *COXI* genetic distances were analyzed from individuals in the genus *Hyas* representing various variations collected in Korean waters. *COXI* genetic distance was analyzed using individuals in *H. coarctatus*, which represent various morphological variations collected in Korean waters. The results showed a low P-distance value (0.15–1.82 %), indicating that the species has a wide range of morphological variations (see remark of *H. coarctatus*, this Chapter).

Chapter 2.

Phylogenetic relationship in majoid crabs based on complete mitochondrial genome

2.1. Introduction

It has been generally accepted that the superfamily Majoidea is monophyletic (reviewed in Ng et al., 2008; but see Brösing et al., 2007). However, there has been constant controversy over internal classifications (Hultgren & Stachowicz, 2008; Tsang et al., 2014; Davie et al., 2015b). The phylogenetic patterns within majoid crabs have changed considerably over time (Ng et al., 2008; Davie et al., 2015b). Based on the classification organized on American fauna by Garth (1958), taxonomists have recognized eight families: Epialtidae MacLeay, 1838, Inachidae MacLeay, 1838, Inachoididae Dana, 1851, Majidae Samouelle, 1819, Mithracidae MacLeay, 1838, Oregoniidae Garth, 1958, Pisidae Dana, 1851, and Tychidae Dana, 1851 (Garth, 1958; Hendrickx, 1995, 1999; Guinot & Richer de Forges, 1997; Boschi, 2000; Martin & Davis, 2001). However, this classification has been confined to the American fauna, and there has been continuous taxonomic confusion, such as the definition of each family due to the lack of comprehensive revision of numerous species in the Indo-West Pacific (Ng et al., 2008; Davie et al., 2015b). As it became difficult to deduce phylogeny only by morphological analysis, attempts were made to study the phylogenetic patterns through partial genes of mitochondria and nucleic acids (Sotelo et al., 2009; Tsang et al., 2014; Windsor & Felder, 2014). Efforts have been made to shed light on the phylogeny of majoid crabs, including the introduction of a larval study to address the differences between the morphological and molecular phylogeny that arise from this (Hultgren & Stachowicz, 2008; Hultgren et al., 2009; Marco-Herrero et al., 2013). As a result, six families of majoid crabs (Epialtidae, Inachidae, Inachoididae, Majidae, Mithracidae, and Oregoniidae) are now recognized (Davie et al., 2015a, b), but some questions remain unanswered.

In recent years, the use of complete mitochondrial DNA sequence for phylogeny tracking has been attempted in various taxa (Cunha et al., 2009; Allcock et al., 2011; Shi et al., 2015; Basso et al., 2017; Bai et al., 2018; Palero et al., 2019). Mitochondria possess their own DNA and have evolved together, this occurred from the time eukaryotes were transformed to modern species through intracellular symbiosis by bacteria. Various studies (e.g., nucleotide sequence, amino acid sequence, and gene arrangement) are possible with the complete mitochondrial DNA sequencing, and have the advantage of being easy to handle because of the small size (within 20 kb) of the entire sequence. As a benefit of this phylogenetic analysis, complete mitochondrial genome sequencing was performed in many brachyurans (Ji et al., 2014; Shi et al., 2015; Basso et al., 2017; Bai et al., 2018; Wang et al., 2020; Zhang et al., 2020). However, in majoid crabs, only 4 species belonging to 3 families have been reported complete mitochondrial sequence (as of March 2020).

This chapter aims: (1) to report the complete mitochondrial sequence, including all families of the currently unknown majoid crabs, and (2) to verify the existing phylogenetic hypotheses for the superfamily Majoidea, by using the mitochondrial genome.

2.2. Materials and methods

Sampling and mtDNA extraction

In this mitochondrial genome study, a total of 10 species of majoid crabs were sequenced, selecting two or more species from each family, where possible. The specimens used in this study were collected in Korea from 2018 to 2019. The same sampling method was used as described in Materials and Methods, Chapter 1. The specimens were identified based on their morphological characteristics and tissue for analysis was extracted from their appendages. To obtain high-purity mitochondrial DNA (mtDNA), mitochondria were extracted from these tissues using the Qproteome Mitochondria Isolation Kit (Qiagen, Hilden, Germany), and mtDNA was obtained from the extracted mitochondria using the QiaAmp DNA Micro Kit (Qiagen, Hilden, Germany). In addition, the concentration of mtDNA extracted using REPLI-g Mitochondrial DNA (Qiagen, Hilden, Germany) and Exo-Resistant Random primer (Thermo Fisher, Waltham, USA) was amplified to increase the concentration.

Sequencing, assembly, annotation, and gene order

Next-Generation Sequencing (NGS) using the Illumina HiSeq 2500 platform (Illumina, San Diego, USA) was performed on the extracted mtDNA to obtain short read sequences which were analyzed and assembled using Geneious ver. 9.1.8. (Biomatter, Auckland, New Zealand). For each species of mtDNA complete sequence, gene annotation by location in the mtDNA sequence was performed using the mitochondrial genome annotation server (Bernt et al., 2013).

Rearrangements of mitochondrial gene order were estimated using CREx (Bernt et al., 2007). To infer possible evolutionary scenarios among gene sequences, comparisons were made in consideration of inversion, transposition, reverse transposition, and tandem duplication random loss (TDRL) events.

Sequence alignment

A total of 16 species (Table 5) belonging to eight families of the complete mitochondrial genomes were used for the phylogenetic analysis of majoid crabs, including 10 species belonging to five families determined through this study, four species belonging to three families registered in the NCBI, and two species belonging to two families of out-groups. The species used were extracted from 13 protein-coding genes (PCGs) and two rRNA nucleotide sequences for each species using the Genious ver. 9.1.8. program. The PCGs were converted to amino acids, and nucleotides and amino acids corresponding to the stop codons of each PCG were removed. The PCGs and two rRNA nucleotide sequences were grouped for each gene and multiple-aligned using MAFFT v7.308 (Katoh & Standley, 2013). Using the RevTrans program (Wernersson & Pedersen, 2003), the corresponding PCG nucleotide multiple alignments were performed based on the amino acid codon frame. The Gblocks v9.01b (Castresana, 2000) program (set to the default options) was used to remove nucleotide and amino acid sequences aligned in ambiguous positions among multiple aligned sequences and to extract only useful information for phylogenetic analysis. Geneious ver. 9.1.8. was used to create a concatenated dataset from the edited nucleotide sequence (13 PCGs + 2 rRNAs) and amino acid sequence (13 PCGs).

Table 5. Complete mitochondrial genomes used in this study for phylogenetic analysis.

Species	Family	Subfamily	Location	Length (bp)	GC content (%)	Accession No.
<i>Menaethius monoceros</i>	Epialtidae	Epialtinae	Korea, Jejudo-Island	15,612	31.2	This study
<i>Pugettia intermedia</i>	Epialtidae	Epialtinae	Korea, Seocheon	15,786	31.9	This study
<i>Hyastenus elongatus</i>	Epialtidae	Pisinae	Korea, Jejudo-Island	15,986	27.2	This study
<i>Scyra compressipes</i>	Epialtidae	Pisinae	Korea, Pohang	16,358	32.8	This study
<i>Achaeus japonicus</i>	Inachidae	Inachinae	Korea, Pohang	15,543	23.8	This study
<i>Achaeus spinosus</i>	Inachidae	Inachinae	Korea, Jejudo-Island	15,775	30.2	This study
<i>Pyromaia tuberculata</i>	Inachoididae	Inachoidinae	Korea, Tongyeong	15,442	24.4	This study
<i>Entomonyx spinosus</i>	Majidae	Majinae	Korea, Jejudo-Island	15,370	31.1	This study
<i>Maja crispata</i>	Majidae	Majinae	Italy, Venice	16,592	29.7	NC_035424
<i>Maja squinado</i>	Majidae	Majinae	North Adriatic Sea	16,598	29.2	NC_035425
<i>Micippa platipes</i>	Majidae	Majinae	Korea, Jejudo-Island	15,386	31.0	This study
<i>Maguimithrax spinosissimus</i>	Mithracidae	-	-	15,817	31.0	NC_025518
<i>Chionoecetes japonicus</i>	Oregoniidae	Oregoniinae	-	15,341	29.6	AB735678
<i>Oregonia gracilis</i>	Oregoniidae	Oregoniinae	Korea, Busan	15,737	33.4	This study
<i>Somanniathelphusa boyangensis</i>	Gecarcinucidae	-	-	17,032	27.6	NC_032044
<i>Huananpotamon lichuanense</i>	Potamidae	Potamiscinae	China, Fujian	15,380	26.8	NC_031406

Phylogenetic analysis

Phylogenetic relationships were estimated using maximum likelihood (ML) analysis and the Bayesian inference (BI) approach. PartitionFinder and PartitionFinderProtein v. 2.1.1 (Lanfear et al., 2012) were used to estimate the best-fit model for inferring the phylogenetic tree. As a result, GTR+I+G and MTART+I+G+F were derived as the best-fit models for ML analysis of nucleotides and amino acids, respectively, and the best-fit model for BI analysis was derived for each nucleotide and PCGs as listed in Table 6. The ML analysis was performed using RAxML v.8.2.9 (Stamatakis, 2014), and the bootstrap was performed 1,000 times. The BI analysis was carried out using MrBayes v.3.2.7a (Huelsenbeck & Ronquist, 2001), and the combined dataset was run for 10 million generations, sampling every 1,000 generations, with the first 25% of trees discarded as burn-in.

Table 6. Substitution models of each gene used for Bayesian inference (BI) in this study.

Gene	Nucleotides	Amino acids
<i>ATP6</i>	GTR+I+G	MTMAM+I+G
<i>ATP8</i>	GTR+I+G	MTMAM+G
<i>COX1</i>	GTR+I+G	MTMAM+I+G
<i>COX2</i>	GTR+I+G	MTMAM+I+G
<i>COX3</i>	GTR+I+G	MTREV+I+G
<i>CYTB</i>	GTR+I+G	MTREV+I+G
<i>NAD1</i>	GTR+I+G	MTREV+I+G
<i>NAD2</i>	GTR+I+G	MTMAM+G
<i>NAD3</i>	GTR+I+G	MTREV+G
<i>NAD4</i>	GTR+I+G	MTMAM+I+G
<i>NAD4L</i>	GTR+G	MTMAM+G
<i>NAD5</i>	GTR+I+G	MTREV+I+G
<i>NAD6</i>	HKY+I+G	MTMAM+G
<i>rrnL</i> (16S rRNA)	GTR+I+G	-
<i>rrnS</i> (12S rRNA)	GTR+I+G	-

2.3. Results

Characteristics of Majoidea mitochondrial genomes

The complete mitochondrial genomes of 10 majoid crab species were determined. All mitogenomes represented a circular form and the length ranged from 15,370 bp (*Entomonyx spinosus*) to 16,358 bp (*Scyra compressipes*). All species contained 13 PCGs, 22 tRNAs, and 2 rRNAs, in keeping with most crustacean mitogenomes (Basso et al., 2017). In most of the 10 species analyzed, the heavy strand contained 14 tRNAs and 9 protein-coding genes (*COX1*, *COX2*, *COX3*, *CYTB*, *NAD2*, *NAD3*, *NAD6*, *ATP6*, and *ATP8*), while the light strand contained the ribosomal genes (*rrnS* and *rrnL*), 8 tRNAs, and 4 protein-coding genes (*NAD1*, *NAD4*, *NAD4L*, *NAD5*). However, *rrnL*, tRNA-P, *NAD4*, and *NAD4L* for *Achaeus japonicus* and tRNA-L1 for *Pyromaia tuberculata* were located in the heavy instead of the light strand. The length of each PCG of 14 majoid crab species analyzed was generally similar. In the PCGs, the start codons were mainly ATG, but in some cases, ATA, ATC, ATT, and GTG codons were also designated. The stop codon was mainly TAA, but in *COX1*, all species except *P. tuberculata* were terminated to T. In *NAD2*, the TAG codon was designated as a stop codon in all species except *Menaethius monoceros* and *P. tuberculata*. The GC content ranged from 23.8% (*A. japonicus*) to 33.4% (*Oregonia gracilis*).

Phylogenetic analyses

For the nucleotide dataset, the phylogenetic tree results were consistent in both the ML and BI analyses. The phylogenetic tree (Fig. 108) showed that the Oregoniidae is monophyletic

and located at the base of the tree. The Inachidae + Inachoididae were placed near the base of the tree, above the Oregoniidae and formed a sister group with the Epialtidae + Mithracidae + Majidae. The Majidae and Epialtidae appeared to be paraphyletic. The Inachoididae was sister to the Inachidae, a relationship strongly supported in both the ML and BI analyses. The Mithracidae appeared as a sister of a branch of the Epialtidae (*Hyastenus elongatus*). In the Majidae, *Micippa platipes* was grouped with the Epialtidae and Mithracidae, rather than with the other members of the Majidae. Within the Epialtidae, the subfamilies Epialtinae (*Menaethius monoceros* and *Pugettia intermedia*) and Pisinae (*Scyra compressipes* and *H. elongatus*) were polyphyletic. In the analysis based on the amino acid sequence of the PCGs, the BI analysis was consistent with the nucleotide-based ML and BI analysis phylogenetic tree results but the ML analysis result (Fig. 109) was different. The Majidae appeared to be polyphyletic and, instead of the Inachidae + Inachoididae, one clade of the Majidae (*Entomonyx spinosus*, *Maja crispate*, and *M. squinado*) was placed near the base of the tree, above the Oregoniidae. However, this result showed a low bootstrap value.

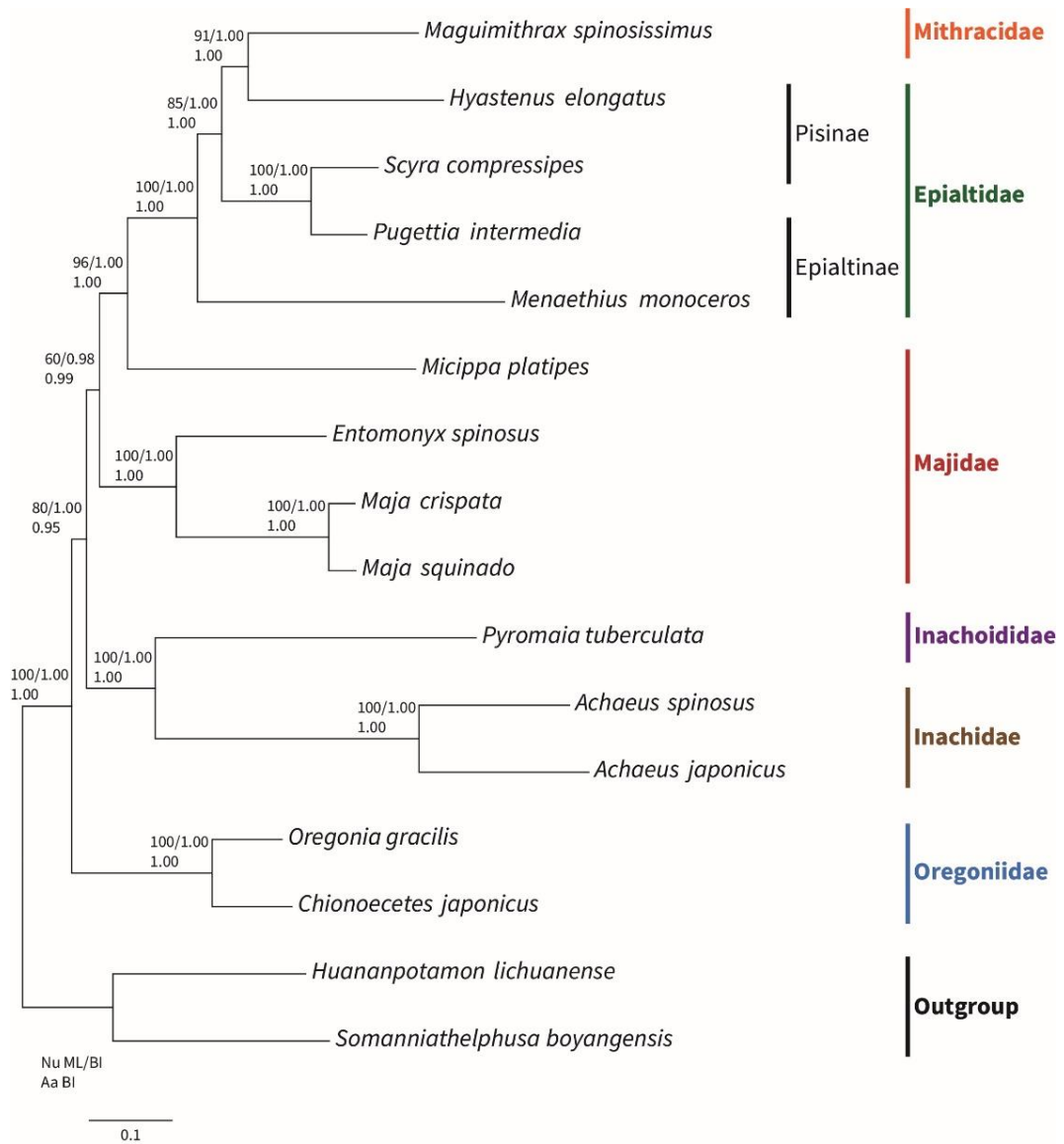


Fig. 108. Phylogenetic tree of the ML and BI analyses based on nucleotides and the BI analysis based on amino acids of 14 mitogenomes in the Majoidea. The values of bootstrap support (ML) and posterior probability (BI) are shown in the nodes.

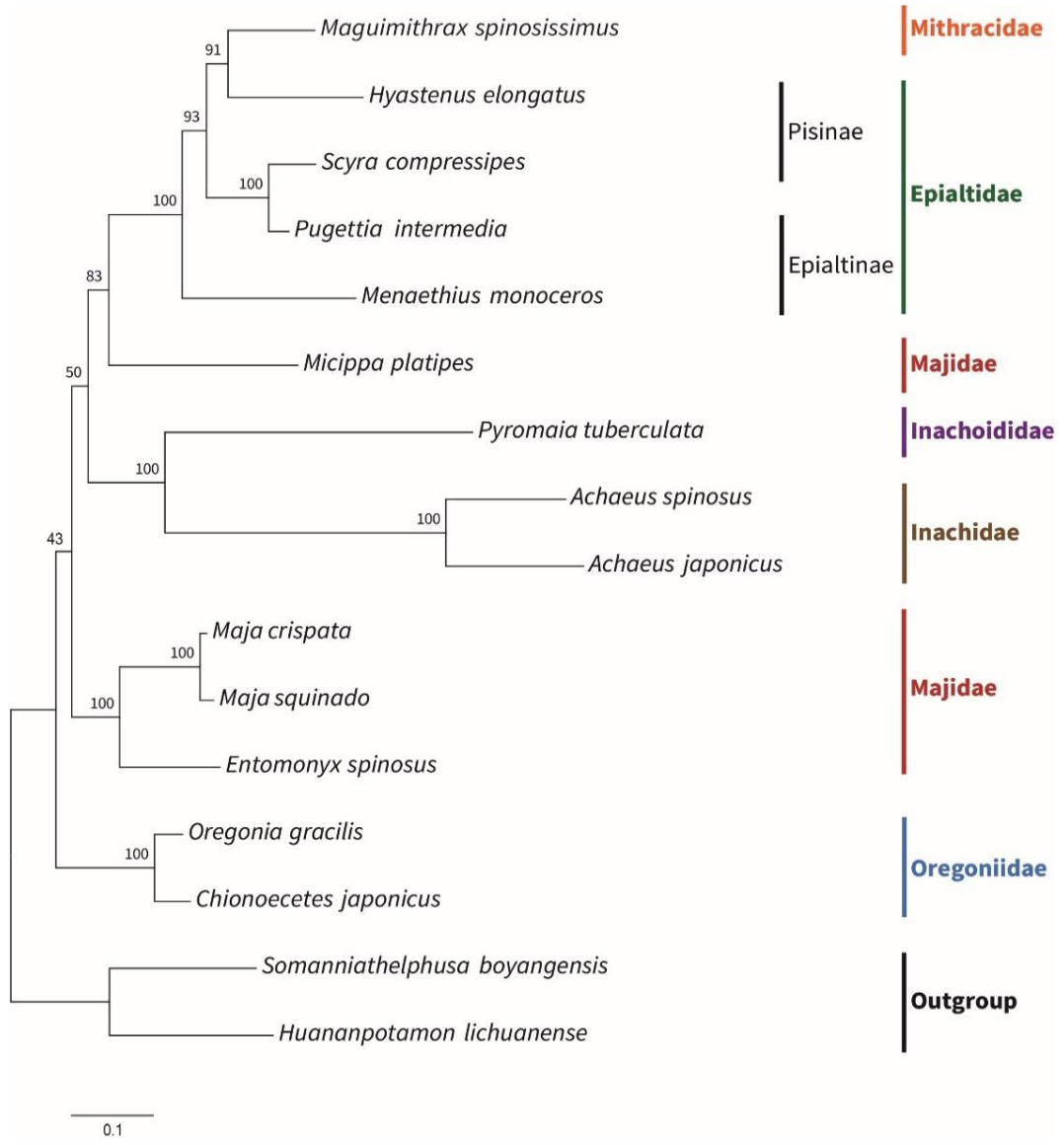


Fig. 109. Phylogenetic tree of the ML analysis based on amino acids of 14 mitogenomes in the Majoidea. The values of bootstrap support (ML) is shown in the nodes.

Mitochondrial gene order

The gene order patterns of 14 species of majoid crabs varied within each family (Figs 110, 111). In the Oregoniidae, located at the base of the Majoidea phylogenetic tree, the two species (*Chionoecetes japonicus* and *Oregonia gracilis*), showed the same gene order patterns. This gene order pattern partially appeared in the Epialtidae (*Hyastenus elongatus* and *Pugettia intermedia*) and Majidae (*Entomonyx spinosus* and *Micippa platipes*), while other species showed rearrangement. The Inachidae, Inachoididae, and *Pugettia intermedia* (one of the Epialtidae species), represented a unique arrangement within known crab genomes.

In the case of the gene order patterns of the inachids, compared with those of the oregoniids, TDRL occurred in the section from *NAD4* to *rrnS* and inversion occurred in the tRNA-I and tRNA-Q section. Comparing *Achaeus japonicus* with *A. spinosus*, there was an inversion between *NAD4* and *rrnL*.

In *Pyromaia tuberculata* (Inachoididae), reverse transposition of tRNA-L1 occurred, and TDRL occurred between tRNA-H and tRNA-Y.

In addition to the known gene order patterns in the Majidae, two types of gene order patterns have been shown to exist in this family, as the newly known *Entomonyx spinosus* and *Micippa platipes* were found to have gene order patterns consistent with the oregoniids. In the genus *Maja*, TDRL occurred between tRNA-H and tRNA-W. The TDRL in this genus appears to be secondary because it is different from that found in the related species *E. spinosus*, and in the oregoniids.

In the Epialtidae, only tRNAs were transferred between species and the order of PCGs was the same. In *Scyra compressipes*, tRNA-A, tRNA-R, and tRNA-N were transposed with each other. In *Menaethius monoceros*, tRNA-I and tRNA-Q were transposed with each

other. *Hyastenus elongatus* and *Pugettia intermedia* conserved the gene order patterns of the oregoniids, and the gene order patterns of *Maguimithrax spinosissimus* (Mithracidae) were closest to those of these species.

● Pattern Bra: *Chionoecetes japonicus*, *Oregonia gracilis*, *Entomonyx spinosus*, *Micippa platipes*, *Pugettia intermedia*, *Hyastenus elongatus*



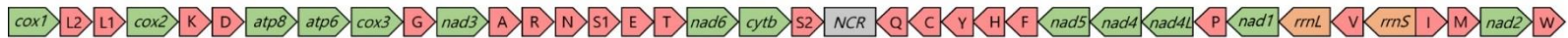
● Pattern Asp: *Achaeus spinosus*



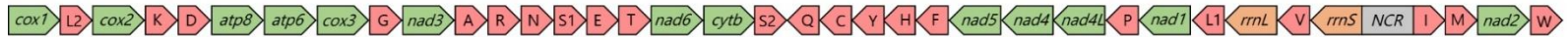
● Pattern Aja: *A. japonicus*



● Pattern Pyr: *Pyromaia tuberculata*



243 ● Pattern Maj: *Maja crispata*, *M. squinado*



● Pattern Men: *Menaethius monoceros*



● Pattern Scy: *Scyra compressipes*



● Pattern Mag: *Maguimithrax spinosissimus*



Fig. 110. The eight gene order patterns for 14 species of majoid crabs. The genes that rearranged their position relative to Pattern Bra are shown with underlined in blue.

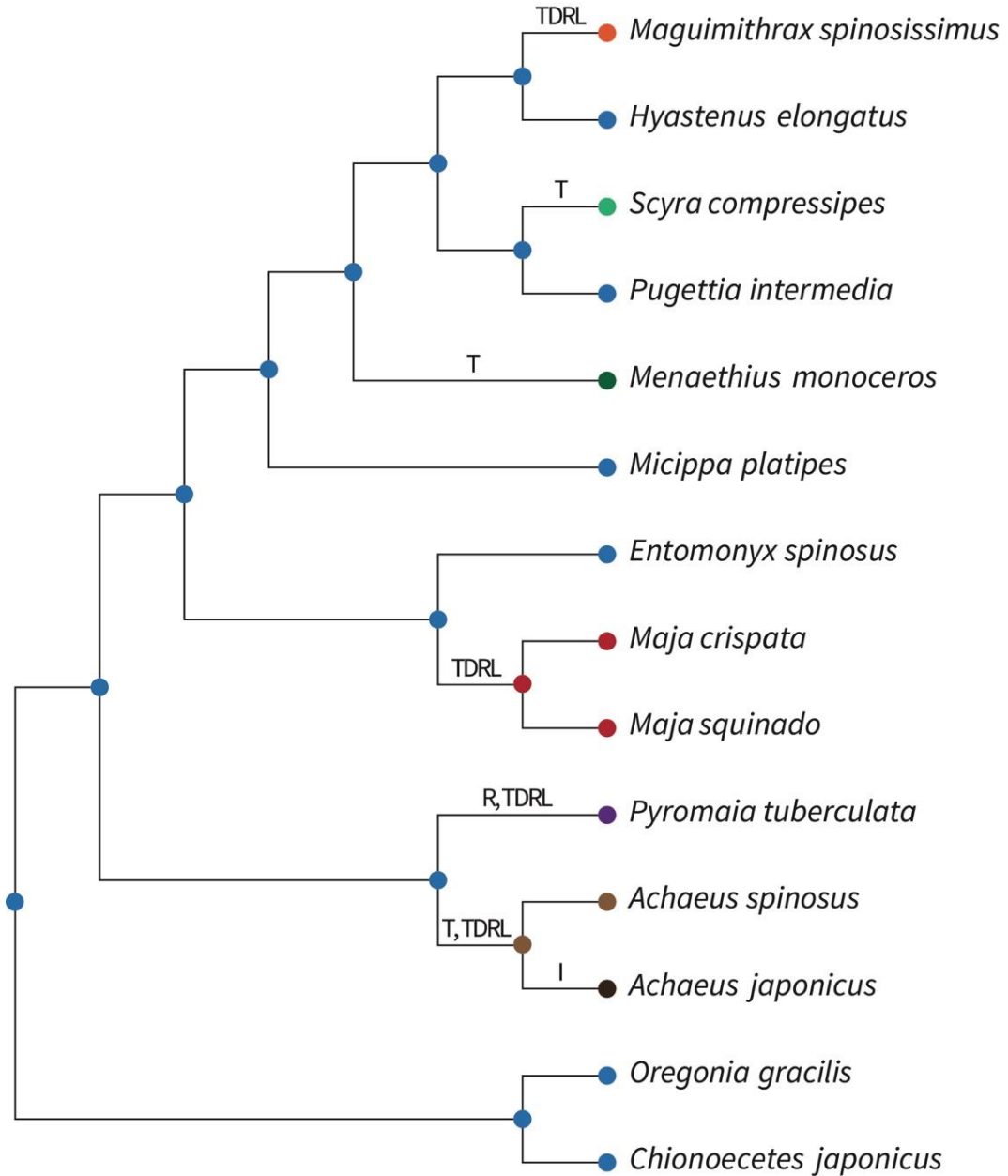


Fig. 111. Possible evolutionary scenario for mitochondrial gene rearrangement within Majoidea estimated using CREx based on their phylogenetic relationships. Rearrangement events inferred by CREx are given above the branches as 'I' for inversion, 'T' for transposition, 'R' for reverse transposition, 'TDRL' for tandem duplication random loss.

2.4. Discussion

The complete mitochondrial genomes of 10 majoid crab species were determined in this study. The result is an expansion of the known mitogenomes from three families and four species into six families and 14 species. The mitogenomes of seven species in the Epialtidae, Inachidae, and Inachoididae are being reported for the first time.

Phylogenetic analyses

To date, molecular phylogenetic studies of majoid crabs have been conducted using only partial DNA sequences (including *COXI*, 16S rRNA, 28S rRNA, and Histone H3) for a limited number of families (Hultgen & Stachowicz, 2008; Hultgen et al., 2009; Marco-Herrero et al., 2013; Tsang et al., 2014; Windsor & Felder, 2014). This study is the first phylogenetic analysis using complete mitochondrial genome of all six families (Epialtidae, Inachidae, Inachoididae, Majidae, Mithracidae, and Oregoniidae) currently recognized as majoid crabs.

In most majoid crab phylogenetic analyses using larva and molecular species, the Oregoniidae appears monophyletic and is known as the most primitive group (Rice, 1983; 1988; Clark & Webber, 1991; Marques & Pohle, 1998; Marques & Pohle, 2003; Hultgen & Stachowicz, 2008; Hultgen et al., 2009; Marco-Herrero et al., 2013). This study corroborated these previous findings because the Oregoniidae was shown to be monophyletic with a strong branch support value (ML 100% BP, BI 1.00 BP) and was located at the base of the phylogenetic tree (Figs 108, 109).

There has been controversy about which family branched off after the Oregoniidae. Hultgen and Stachowicz (2008) mentioned that additional studies were needed to determine which of the Inachidae, Majidae, or Oregoniidae is the most basal family in the phylogenetic tree. In a larva-based phylogenetic study, Marques and Pohle (2003) reported that the Oregoniidae and the Inachidae + Inachoididae formed a clade and, based on fossil records (Breton, 2009), Guinot et al. (2013) mentioned that the Oregoniidae and Inachidae + Inachoididae were more ancient groups. In this study, the phylogenetic tree appeared in two forms (Figs 108, 109). In the ML and BI analyses based on nucleotides and the BI analysis based on amino acids, the Inachidae + Inachoididae were located at the base of the phylogenetic tree, above the Oregoniidae whereas, in the ML analysis based on amino acids, the Majidae, except for *Micippa platipes*, was located at the base, above the Oregoniidae. A possible reason for these different results is bias due to the small number of samples used in this study. The Inachidae + Inachoididae and the Epialtidae + Majidae + Mithracidae formed a sister group (Fig. 108) showing monophyly with strong branch support values (nucleotides: ML 80% BP, BI 1.00 BPP; amino acids: BI 0.95 BP). On the other hand, the Majidae, (excluding *M. platipes*) and the Inachidae + Inachoididae + Epialtidae + Mithracidae + *M. platipes* (Fig. 109) represented a sister group with a weak branch support value (amino acids: ML 43% BP). Therefore, this study indicated that the Inachidae + Inachoididae, along with the Oregoniidae, are located at the base of the tree, according to the results of the nucleotide-based ML and BI analyses and the BI analysis based on amino acids. These findings support the results of previous studies.

The Inachidae and Inachoididae have been recognized as morphologically related families because they share the following features: the absence of orbits and extremely slender basal antennal articles (Clark & Webber, 1991; Ng et al., 2008); however, no

molecular level research has been conducted to verify the relationship between these two families. In this study, although the results were analyzed with a small number of species, *Achaeus* (Inachidae) and *Pyromaia tuberculata* (Inachoididae) were the sister group with a very strong branch support value (nucleotides: ML 100% BP, BI 1.00 BPP; amino acids: ML 100% BP, BI 1.00 BPP), corroborating the results of the morphological analysis that these two families are closest to each other.

There was little association of *Micippa platipes* with other Majidae species. The Majidae was shown to be paraphyletic (Fig. 108), and polyphyletic (Fig. 109), both due to *M. platipes*. Previous studies also show a different placement of *Micippa* according to different alignment or tree construction methods (Hultgen & Stachowicz, 2008; Hultgen et al., 2009). Previously, *Micippa* was classified as a genus of Mithracinae (i.e., Mithracidae), then excluded by Windsor and Felder (2014) and temporarily moved to the Majidae because of its morphological similarity. In order to clearly establish the taxonomic position of *Micippa*, various analyses are needed in more taxa within the Majidae.

In Tsang et al. (2014), the Epialtidae and Majidae were referred to as polyphyletic, but the higher taxonomic level of the species classified as Majidae, at the time, were changed: *Mithraculus coryphe* and *M. forceps* to the Mithracidae, and *Tiarinia* spp. to the Epialtidae. The results of Tsang et al. (2014), when the current classification system (Davie et al., 2015a) is applied, are that the Epialtidae is paraphyletic and the Mithracidae, closest to the Epialtidae. This is consistent with previous larval- and molecular-based analyses (Rice, 1988; Pohle & Marques, 2000; Marques & Pohle, 2003; Hultgen & Stachowicz, 2008) and corroborates the findings of this study that the Epialtidae and Mithracidae (*Maguimithrax spinosissimus*) are closely related.

The Epialtidae are not clearly distinguished at the subfamily level. In previous larval and molecular based analyses, the Epialtinae and Pisinae were shown to be paraphyletic (Hultgen & Stachowicz, 2008; Hultgen et al., 2009). In this study, these two subfamilies appeared polyphyletic, as shown in Fig. 7 of Marco-Herrero et al. (2013). The Epialtidae and Pisidae were recognized as independent families (Gripin & Tranter, 1986; Martin & Davis, 2001), but were reclassified as subfamilies of the Epialtidae by Ng et al., (2008). Griffin and Tranter (1986) distinguished the Epialtinae and Pisinae mainly by orbit and supraorbital cave; however, these features do not provide a clear distinction between these two subfamilies (Ng et al., 2008) and such morphological differences do not appear to be the main features that distinguish the phylogenetic subfamily. Hultgen and Stachowicz (2008) commented on the possibility that species belonging to the Epialtinae and Pisinae shared similar habitats and consequently shared similar forms through convergent evolution. Among the species included in this study, *Hyastenus elongatus* and *Scyra compressipes* (Pisinae) inhabit the subtidal zone, and *Pugettia intermedia* and *Menaethius monoceros* (Epialtidae) live amongst the intertidal algae. These results add credibility to the hypothesis of Hultgen and Stachowicz (2008). As a result of previous studies and the results of this study, it seems that reclassification is needed through further studies of the unexplored genus to solve the polyphyletic phylogenetic problems in these subfamilies.

Mitochondrial gene order

Brachyurans, with 18 gene order patterns reported so far, are known to have a relatively high diversity of gene order patterns in comparison with other arthropods (Basso et al., 2017; Zhang et al., 2020). Among them, the Majoidea appears to have a high diversity of gene order within the family, compared to the previously known gene order of brachyurans.

Previously there were three known gene order patterns in the majoid crabs. Through this study, eight gene order patterns of the Majoidea have been revealed (Fig. 110), four of which (Pattern Asp, Pattern Aja, Pattern Pyr, and Pattern Scy) were not previously known in brachyurans. Generally, gene order patterns are widely conserved at higher taxonomic levels (Boore & Brown, 1998), and differences between the taxa are clear (Babbucci et al., 2014). In the case of the general brachyuran gene order pattern (Pattern Bra), the key characteristic is that tRNA-H is located between tRNA-E and tRNA-F, and this is the plesiomorphic condition for the Brachyura (Basso et al., 2017). In the gene order patterns of the oregoniids located at the base of the phylogenetic tree, Pattern Bra is present and a modified pattern Bra or pattern Bra itself appears in the Majoidea as a whole, indicating that they all stem from a common ancestor. Previous studies have shown that gene order is conserved within family level (Arndt & Smith, 1998; Dowton & Austin, 1999; Bensch & Harlid, 2000; Hickerson & Cunningham, 2000; Bauza-Ribot et al., 2009; Irisarri et al., 2014; Basso et al., 2017; but see Zhang et al., 2020); however, the results of this study indicate that gene order variation has occurred within the family, even within the genus. It has been discovered that high levels of rearrangement, including PCGs, have occurred in *Achaeus* spp. and in *Pyromaia tuberculata*. In the case of the genus *Achaeus*, it appears that inversion occurred in the section from *NAD4* to *rrnL* in Pattern Aja. It is very rare that the arrangement of PCGs in a genus changes (Rawlings et al., 2001; Matsumoto et al., 2009). The inversion in Pattern Aja might be secondary because it differs from that found in its congener, Pattern Asp, and in Pattern Bra. Nevertheless, the sequence of 26 genes from *COXI* to *rrnS* was consistently conserved in both Patterns Asp and Aja, and tRNA-I and tRNA-Q were commonly transposed. This pattern is the only one in the brachyuran gene order patterns, and it is presumed to be a synapomorphy of these two species or the genus *Achaeus*.

Ng et al. (2008) referred to the Inchildae and Inachoididae as closely related families; however, it was difficult to infer the relationship between these two families from a limited number of gene order patterns. Further study using more species from each family is needed to elucidate this relationship. The gene rearrangement that occurred in Pattern Pyr also represents a high level of rearrangement and, given that it includes rearrangement of the *NCR*, it seems unlikely that these changes appeared independently in other taxa. However, based on the results of only one species, it is not yet possible to determine whether Pattern Pyr is a synapomorphy in the Inachoididae or the genus *Pyromaia*.

In Pattern Mag, Pattern Men, and Pattern Scy, only tRNAs were rearranged, without evidence of rearrangement of the PCGs. This represents a low-level rearrangement but Patterns Mag and Scy are the only patterns in brachyurans. In this study, the same gene order patterns as in sesarmids were evident in Pattern Men. This is the first such case in brachyurans; however, previous insect studies have shown that taxa proven to be taxonomically distant can share the same gene order patterns due to low-level gene arrangement (Babbucci et al., 2014; Yang et al., 2016). Basso et al. (2017) noted that sharing a similar gene order pattern is evidence that these taxa originated from a common ancestor but care should be taken in assigning them the status of mitochondrial genomic apomorphies and, if low-level gene arrangements occur between unrelated taxa, these should be understood in a phylogenetic context. For this reason, the characteristic of sharing gene order patterns between *Menaethius monoceros* (section Heterotremata) and sesarmid crabs (section Thoracotremata), which are taxonomically distant from each other, can be said to be genetic convergence rather than synapomorphy.

When looking at the gene order patterns of known crabs, most of them show conservative appearances at the family or superfamily level (Basso et al., 2017).

Nevertheless, some taxa such as Potamidae showed conservative appearances at the genus level (Zhang et al., 2020). Although it is difficult to affirm the gene order patterns of majoid crabs analyzed so far, we have observed that majoid crabs are also partially conservative at the genus level rather than at the family level (Fig. 111). Considering the characteristics of majoid crabs, which have relatively diverse gene order patterns, these characteristics can be used as features to identify taxa.

In previous studies and in the phylogenetic tree analysis in this study, there were taxa with unclear placement (*Micippa*) and taxa with persistent polyphyly (Epialtinae and Pisinae). It is necessary to review the morphology and molecular characteristics of these taxa and, judging from the results of the gene order pattern study, more gene order patterns are expected to be discovered in the future. The gene order patterns that have been identified so far are insufficient to fully understand the history of the evolution of the Majoidea, which appears to have evolved in a complex manner. In order to elucidate the taxonomic position and phylogenetic relationships of the Majoidea, more research is needed using more species.

Conclusion

The findings of this study have increased the diversity of recorded Korean majoid crabs to 51 species out of 29 genera belonging to five families. Of these, six genera and nine species are new records in Korean waters, all collected off the coast of Jeju Island. Many of the species identified in this study were collected from deeper waters, 15 km or more offshore. Additional surveys of the waters around Jeju Island are expected to yield further increases in the number of new majoid crab species.

There has been confusion regarding the identification of *Pugettia quadridens sensu lato* inhabiting Korean waters, as there are five species associated with *P. quadridens* in this geographical location. Through molecular and morphological analyses, this study has corrected the misidentification of *P. quadridens sensu lato* reported in Korea. During this study, specimens of a Korean *P. pellucens* were not confirmed; however, it is not known whether this species actually occurs in Korean waters and there is a need for additional comparisons with specimens collected from the type locality.

Complete mitochondrial genomes were determined for ten species of majoid crabs, and the molecular analyses conducted in this study have expanded the number of known mitogenomes from three families and four species to six families and 14 species. Seven of which were first reported in the Epialtidae, Inachidae, and Inachoididae. Consequently, the complete mitochondrial genomes of all families of the currently recognized majoid crabs have been revealed.

A phylogenetic analysis was performed based on the complete mitochondrial genomes of six families. Oregoniidae was located at the base of the phylogenetic tree, followed by

Inachidae and Inachoididae. The genus *Micippa* of the Majidae needs further study regarding its phylogenetic placement. The Epialtidae appeared to be polyphletic at the subfamily level, and the morphological characteristics that distinguish this subfamily should be redefined. The Mithracidae was found to be closest to the Epialtidae.

The diversity of gene order patterns of majoid crabs was found to be relatively high. Eighteen gene order patterns are known in brachyurans, and eight of these are found only in majoid crabs. The Oregoniidae, known as the most primitive majoid crab family, has the most common gene order pattern in brachyurans. The same or modified gene order patterns appear in generally all majoid crabs, suggesting that they originated from the common ancestor. However, the gene order patterns have been found to differ within the family; therefore, research on a broader range of species is needed to thoroughly investigate their evolutionary relationships.

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국문 초록

물맞이게상과는 게하목 중에서 가장 다양한 종이 포함된 분류군 중 하나로 전세계에 900종이 넘게 보고되어있다. 많은 종 수만큼 형태적으로도 다양하여 그동안 종을 동정하거나 계통을 분석하는데 혼란이 있었다. 본 연구에서는 1) 형태학적 형질과 분자생물학적 형질을 이용하여 한국산 물맞이게상과의 분류학적 연구결과를 제시하고, 2) 미토콘드리아 전체 유전체를 이용하여 물맞이게상과의 계통유연관계를 추론하였다.

1장에서는 문헌 및 표본 조사를 통하여 한국해역에 물맞이게류 5과 29속 51종이 서식하는 것을 확인하였고 이에 대한 종목록, 분류검색표, 기재 및 분포 지도 등을 제시하였다. 본 연구를 통해 제주도에서 새롭게 채집된 6속 8종의 물맞이게류를 한국미기록 종으로 보고 하였다. 이와 함께 제주도 근해에서 채집된 종은 20속 33종으로 우리나라 다른 해역에 비해 물맞이게류의 종 다양성이 가장 높았으며 이 중 제주도에서만 발견된 종은 20종이었다. 육지에서 멀리 떨어진 해역에서는 지금까지 한국에서 보고되지 않은 미기록종과 드물게 서식이 확인된 종들을 확인할 수 있었다.

형태적 유사성으로 오동정이 잦았던 *Pugettia quadridens sensu lato*에 대해 형태 및 *COX1* 분자 형질을 비교 분석하여 재동정을 하였다. 지금까지 한국에서 *P. quadridens*로 알려져 있었던 ‘뿔물맞이게’가 *P. ferox*임을 확인하였고 *P. quadridens* 역시 서식하고 있는 것을 확인하였다. 본 연구에서 *P. pellucens*에 대

한 한국해역의 서식은 확인하지 못하였는데 한국해역에서의 실존 여부에 대한 후속 연구가 필요하다.

2장에서는 물맞이계상과의 계통유연관계를 추론하기 위해 10종의 미토콘드리아 전체 유전체의 염기서열을 분석하여 결정하였다. 이 중 7종은 빨물맞이계과, 거미다리계과, 한뿔두드럭계과에서 처음으로 미토콘드리아 전체 유전체의 염기서열이 결정된 것이다. 계통유연관계는 물맞이계상과의 6개 과를 모두 포함시킨 14종의 미토콘드리아 전체 유전체 염기서열을 이용하여 Maximum likelihood와 Bayesian inference 방법으로 분석하였다. 분석결과 긴집게발계과가 가장 먼저 분기되었고 거미다리계과와 한뿔두드럭계과가 그 다음으로 분기된 것으로 추론할 수 있었다. 물맞이계과에 속하는 누덕웃계속의 분류학적 위치에 대한 논의는 추가적인 연구가 필요할 것으로 보인다. 빨물맞이계과는 아과 수준에서 다계통이었으며, Mithracidae는 빨물맞이계과와 가장 가까웠다.

물맞이계상과에서 미토콘드리아 유전자 배열 순서의 다양성은 계하목에서도 상당히 높은 것으로 나타났다. 지금까지 알려진 계하목에서의 유전자 배열 순서는 18가지 였으나 물맞이계상과 내에서는 8가지가 나타났다. 일반적으로 유전자 배열 순서는 과 수준에서 보존적인 것으로 알려져 있었으나 물맞이계상과에서는 부분적으로 속 수준에서 보존적인 경향이 나타났다.

Appendix

Table 1. Gene content of the mitochondrial genome of *Menaethius monoceros*.

Feature	Position		Codons	
	Start	End	Initiation	Termination
Cytochrome c oxidase subunit 1 (<i>COX1</i>)	1	1,534	ATG	T
tRNA-L2	1,535	1,599		
Cytochrome c oxidase subunit 2 (<i>COX2</i>)	1,605	2,285	ATG	TAA
tRNA-K	2,292	2,357		
tRNA-D	2,359	2,424		
ATP synthase F0 subunit 8 (<i>ATP8</i>)	2,425	2,583	ATC	TAA
ATP synthase F0 subunit 6 (<i>ATP6</i>)	2,577	3,251	ATT	TAA
Cytochrome c oxidase subunit 3 (<i>COX3</i>)	3,261	4,052	ATG	TAA
tRNA-G	4,052	4,116		
NADH dehydrogenase subunit 3 (<i>NAD3</i>)	4,117	4,470	ATT	TAA
tRNA-A	4,469	4,533		
tRNA-R	4,538	4,601		
tRNA-N	4,603	4,667		
tRNA-S1	4,667	4,733		
tRNA-E	4,748	4,815		
tRNA-H	4,815	4,879		
tRNA-F	4,880	4,944		
NADH dehydrogenase subunit 5 (<i>NAD5</i>)	4,939	6,664	ATG	T
NADH dehydrogenase subunit 4 (<i>NAD4</i>)	6,699	8,039	GTG	TAA
NADH dehydrogenase subunit 4L (<i>NAD4L</i>)	8,033	8,329	ATG	TAA
tRNA-T	8,335	8,398		
tRNA-P	8,399	8,462		
NADH dehydrogenase subunit 6 (<i>NAD6</i>)	8,465	8,974	ATC	TAA
Cytochrome b (<i>CYTB</i>)	8,974	10,110	ATG	TAA
tRNA-S2	10,109	10,176		
NADH dehydrogenase subunit 1 (<i>NAD1</i>)	10,202	11,146	ATA	TAA
tRNA-L1	11,235	11,301		
16S rRNA (<i>rrnL</i>)	11,302	12,663		
tRNA-V	12,664	12,736		
12S rRNA (<i>rrnS</i>)	12,737	13,533		
Non coding region (<i>NCR</i>)	13,534	14,040		
tRNA-Q	14,041	14,109		
rRNA-I	14,245	14,309		
tRNA-M	14,318	14,383		
NADH dehydrogenase subunit 2 (<i>NAD2</i>)	14,384	15,388	ATG	TAA
tRNA-W	15,394	15,459		
tRNA-C	15,469	15,530		
tRNA-Y	15,537	15,601		

Table 2. Gene content of the mitochondrial genome of *Pugettia intermedia*.

Feature	Position		Codons	
	Start	End	Initiation	Termination
Cytochrome c oxidase subunit 1 (<i>COX1</i>)	1	1,534	ATG	T
tRNA-L2	1,535	1,602		
Cytochrome c oxidase subunit 2 (<i>COX2</i>)	1,614	2,294	ATG	TAA
tRNA-K	2,303	2,367		
tRNA-D	2,368	2,432		
ATP synthase F0 subunit 8 (<i>ATP8</i>)	2,433	2,591	ATG	TAA
ATP synthase F0 subunit 6 (<i>ATP6</i>)	2,585	3,259	ATT	TAA
Cytochrome c oxidase subunit 3 (<i>COX3</i>)	3,259	4,048	ATG	T
tRNA-G	4,049	4,114		
NADH dehydrogenase subunit 3 (<i>NAD3</i>)	4,115	4,468	ATT	TAA
tRNA-A	4,467	4,531		
tRNA-R	4,533	4,598		
tRNA-N	4,602	4,667		
tRNA-S1	4,668	4,733		
tRNA-E	4,736	4,804		
tRNA-H	4,804	4,868		
tRNA-F	4,869	4,931		
NADH dehydrogenase subunit 5 (<i>NAD5</i>)	4,935	6,659	ATG	TAA
NADH dehydrogenase subunit 4 (<i>NAD4</i>)	6,700	8,049	ATG	TAA
NADH dehydrogenase subunit 4L (<i>NAD4L</i>)	8,043	8,342	ATG	TAA
tRNA-T	8,345	8,406		
tRNA-P	8,407	8,471		
NADH dehydrogenase subunit 6 (<i>NAD6</i>)	8,474	8,980	ATT	TAA
Cytochrome b (<i>CYTB</i>)	8,980	10,116	ATG	TAA
tRNA-S2	10,115	10,181		
NADH dehydrogenase subunit 1 (<i>NAD1</i>)	10,224	11,159	ATG	TAA
tRNA-L1	11,229	11,297		
16S rRNA (<i>rrnL</i>)	11,298	12,652		
tRNA-V	12,653	12,720		
12S rRNA (<i>rrnS</i>)	12,721	13,523		
Non coding region (<i>NCR</i>)	13,524	14,375		
tRNA-I	14,376	14,440		
rRNA-Q	14,438	14,505		
tRNA-M	14,513	14,579		
NADH dehydrogenase subunit 2 (<i>NAD2</i>)	14,580	15,584	ATG	TAG
tRNA-W	15,583	15,651		
tRNA-C	15,644	15,707		
tRNA-Y	15,708	15,774		

Table 3. Gene content of the mitochondrial genome of *Hyastenus elongatus*.

Feature	Position		Codons	
	Start	End	Initiation	Termination
Cytochrome c oxidase subunit 1 (<i>COX1</i>)	1	1,534	ATG	T
tRNA-L2	1,535	1,600		
Cytochrome c oxidase subunit 2 (<i>COX2</i>)	1,622	2,302	ATG	TAA
tRNA-K	2,328	2,397		
tRNA-D	2,398	2,462		
ATP synthase F0 subunit 8 (<i>ATP8</i>)	2,463	2,621	ATG	TAA
ATP synthase F0 subunit 6 (<i>ATP6</i>)	2,615	3,289	ATT	TAA
Cytochrome c oxidase subunit 3 (<i>COX3</i>)	3,289	4,077	ATG	TAA
tRNA-G	4,077	4,141		
NADH dehydrogenase subunit 3 (<i>NAD3</i>)	4,142	4,495	ATT	TAA
tRNA-A	4,498	4,562		
tRNA-R	4,566	4,631		
tRNA-N	4,633	4,696		
tRNA-S1	4,699	4,764		
tRNA-E	4,767	4,833		
tRNA-H	4,849	4,916		
tRNA-F	4,918	4,984		
NADH dehydrogenase subunit 5 (<i>NAD5</i>)	4,988	6,721	ATG	TAA
NADH dehydrogenase subunit 4 (<i>NAD4</i>)	6,731	8,104	ATG	TAA
NADH dehydrogenase subunit 4L (<i>NAD4L</i>)	8,098	8,403	ATT	TAA
tRNA-T	8,472	8,542		
tRNA-P	8,543	8,606		
NADH dehydrogenase subunit 6 (<i>NAD6</i>)	8,615	9,118	ATA	TAA
Cytochrome b (<i>CYTB</i>)	9,118	10,254	ATG	TAG
tRNA-S2	10,253	10,317		
NADH dehydrogenase subunit 1 (<i>NAD1</i>)	10,388	11,326	ATG	TAG
tRNA-L1	11,401	11,467		
16S rRNA (<i>rrnL</i>)	11,468	12,824		
tRNA-V	12,825	12,893		
12S rRNA (<i>rrnS</i>)	12,894	13,721		
Non coding region (<i>NCR</i>)	13,722	14,471		
tRNA-I	14,472	14,538		
rRNA-Q	14,566	14,633		
tRNA-M	14,705	14,772		
NADH dehydrogenase subunit 2 (<i>NAD2</i>)	14,773	15,777	ATT	TAG
tRNA-W	15,776	15,841		
tRNA-C	15,850	15,912		
tRNA-Y	15,917	15,985		

Table 4. Gene content of the mitochondrial genome of *Scyra compressipes*.

Feature	Position		Codons	
	Start	End	Initiation	Termination
Cytochrome c oxidase subunit 1 (<i>COX1</i>)	1	1,534	ATG	T
tRNA-L2	1,535	1,601		
Cytochrome c oxidase subunit 2 (<i>COX2</i>)	1,613	2,293	ATG	TAA
tRNA-K	2,301	2,365		
tRNA-D	2,366	2,433		
ATP synthase F0 subunit 8 (<i>ATP8</i>)	2,434	2,592	ATA	TAA
ATP synthase F0 subunit 6 (<i>ATP6</i>)	2,586	3,260	ATT	TAA
Cytochrome c oxidase subunit 3 (<i>COX3</i>)	3,260	4,049	ATG	T
tRNA-G	4,050	4,116		
NADH dehydrogenase subunit 3 (<i>NAD3</i>)	4,114	4,470	ATA	TAA
tRNA-R	4,541	4,605		
tRNA-N	4,610	4,674		
tRNA-A	4,740	4,802		
tRNA-S1	4,939	5,004		
tRNA-E	5,007	5,074		
tRNA-H	5,074	5,139		
tRNA-F	5,140	5,204		
NADH dehydrogenase subunit 5 (<i>NAD5</i>)	5,208	6,932	ATG	TAA
NADH dehydrogenase subunit 4 (<i>NAD4</i>)	6,973	8,322	ATG	TAA
NADH dehydrogenase subunit 4L (<i>NAD4L</i>)	8,325	8,615	ATG	TAA
tRNA-T	8,618	8,681		
tRNA-P	8,682	8,746		
NADH dehydrogenase subunit 6 (<i>NAD6</i>)	8,749	9,252	ATC	TAA
Cytochrome b (<i>CYTB</i>)	9,252	10,388	ATG	TAA
tRNA-S2	10,387	10,452		
NADH dehydrogenase subunit 1 (<i>NAD1</i>)	10,478	11,410	ATT	TAA
tRNA-L1	11,417	11,525		
16S rRNA (<i>rrnL</i>)	11,598	13,008		
tRNA-V	13,009	13,080		
12S rRNA (<i>rrnS</i>)	13,081	13,894		
Non coding region (<i>NCR</i>)	13,895	14,959		
tRNA-I	14,960	15,023		
rRNA-Q	15,021	15,088		
tRNA-M	15,099	15,164		
NADH dehydrogenase subunit 2 (<i>NAD2</i>)	15,165	16,169	ATG	TAG
tRNA-W	16,168	16,236		
tRNA-C	16,229	16,292		
tRNA-Y	16,293	16,357		

Table 5. Gene content of the mitochondrial genome of *Achaeus japonicus*.

Feature	Position		Codons	
	Start	End	Initiation	Termination
Cytochrome c oxidase subunit 1 (<i>COX1</i>)	1	1,534	ATG	T
tRNA-L2	1,535	1,600		
Cytochrome c oxidase subunit 2 (<i>COX2</i>)	1,602	2,282	ATG	TAA
tRNA-K	2,283	2,439		
tRNA-D	2,416	2,477		
ATP synthase F0 subunit 8 (<i>ATP8</i>)	2,480	2,638	ATT	TAA
ATP synthase F0 subunit 6 (<i>ATP6</i>)	2,632	3,306	ATT	TAA
Cytochrome c oxidase subunit 3 (<i>COX3</i>)	3,306	4,097	ATG	TAA
tRNA-G	4,099	4,164		
NADH dehydrogenase subunit 3 (<i>NAD3</i>)	4,165	4,518	ATT	TAA
tRNA-A	4,518	4,580		
tRNA-R	4,590	4,651		
tRNA-N	4,655	4,718		
tRNA-S1	4,721	4,779		
tRNA-E	4,783	4,850		
tRNA-H	4,853	4,920		
tRNA-F	4,922	4,985		
NADH dehydrogenase subunit 5 (<i>NAD5</i>)	4,985	6,716	GTG	T
tRNA-T	6,732	6,794		
NADH dehydrogenase subunit 6 (<i>NAD6</i>)	6,813	7,322	ATT	TAA
Cytochrome b (<i>CYTB</i>)	7,326	8,462	ATG	TAA
tRNA-S2	8,469	8,535		
NADH dehydrogenase subunit 1 (<i>NAD1</i>)	8,542	9,477	ATG	TAA
tRNA-L1	9,500	9,563		
tRNA-V	9,569	9,635		
12S rRNA (<i>rrnS</i>)	9,636	10,434		
Non coding region (<i>NCR</i>)	10,435	11,005		
16S rRNA (<i>rrnL</i>)	11,006	12,323		
tRNA-P	12,324	12,392		
NADH dehydrogenase subunit 4L (<i>NAD4L</i>)	12,430	12,729	ATG	TAA
NADH dehydrogenase subunit 4 (<i>NAD4</i>)	12,723	14,051	ATG	TAA
rRNA-Q	14,087	14,155		
tRNA-I	14,215	14,281		
tRNA-M	14,287	14,350		
NADH dehydrogenase subunit 2 (<i>NAD2</i>)	14,351	15,358	ATT	TAG
tRNA-W	15,357	15,421		
tRNA-C	15,414	15,476		
tRNA-Y	15,477	15,541		

Table 6. Gene content of the mitochondrial genome of *Achaeus spinosus*.

Feature	Position		Codons	
	Start	End	Initiation	Termination
Cytochrome c oxidase subunit 1 (<i>COX1</i>)	1	1,534	ATG	T
tRNA-L2	1,535	1,601		
Cytochrome c oxidase subunit 2 (<i>COX2</i>)	1,603	2,283	ATG	TAA
tRNA-K	2,287	2,350		
tRNA-D	2,410	2,474		
ATP synthase F0 subunit 8 (<i>ATP8</i>)	2,473	2,631	ATC	TAG
ATP synthase F0 subunit 6 (<i>ATP6</i>)	2,625	3,299	ATT	TAA
Cytochrome c oxidase subunit 3 (<i>COX3</i>)	3,299	4,090	ATG	TAA
tRNA-G	4,090	4,152		
NADH dehydrogenase subunit 3 (<i>NAD3</i>)	4,153	4,503	ATC	TAA
tRNA-A	4,502	4,567		
tRNA-R	4,568	4,629		
tRNA-N	4,633	4,699		
tRNA-S1	4,700	4,758		
tRNA-E	4,759	4,827		
tRNA-H	4,830	4,892		
tRNA-F	4,894	4,959		
NADH dehydrogenase subunit 5 (<i>NAD5</i>)	4,963	6,684	ATA	TAA
tRNA-T	6,713	6,775		
NADH dehydrogenase subunit 6 (<i>NAD6</i>)	6,802	7,311	ATT	TAA
Cytochrome b (<i>CYTB</i>)	7,312	8,454	ATG	TAA
tRNA-S2	8,457	8,521		
NADH dehydrogenase subunit 1 (<i>NAD1</i>)	8,521	9,453	ATG	TAA
tRNA-L1	9,468	9,537		
tRNA-V	9,564	9,633		
12S rRNA (<i>rrnS</i>)	9,634	10,456		
NADH dehydrogenase subunit 4 (<i>NAD4</i>)	10,457	11,782	ATG	TAA
NADH dehydrogenase subunit 4L (<i>NAD4L</i>)	11,776	12,069	ATG	TAA
tRNA-P	12,101	12,167		
16S rRNA (<i>rrnL</i>)	12,168	13,484		
Non coding region (<i>NCR</i>)	13,485	14,332		
rRNA-Q	14,333	14,400		
tRNA-I	14,442	14,506		
tRNA-M	14,508	14,571		
NADH dehydrogenase subunit 2 (<i>NAD2</i>)	14,572	15,579	ATT	TAG
tRNA-W	15,578	15,642		
tRNA-C	15,635	15,695		
tRNA-Y	15,699	15,762		

Table 7. Gene content of the mitochondrial genome of *Pyromaia tuberculata*.

Feature	Position		Codons	
	Start	End	Initiation	Termination
Cytochrome c oxidase subunit 1 (<i>COX1</i>)	1	1,533	ATG	TAA
tRNA-L2	1,547	1,609		
tRNA-L1	1,626	1,688		
Cytochrome c oxidase subunit 2 (<i>COX2</i>)	1,762	2,443	ATG	T
tRNA-K	2,444	2,505		
tRNA-D	2,504	2,568		
ATP synthase F0 subunit 8 (<i>ATP8</i>)	2,570	2,734	ATG	TAA
ATP synthase F0 subunit 6 (<i>ATP6</i>)	2,731	3,402	ATA	TAA
Cytochrome c oxidase subunit 3 (<i>COX3</i>)	3,402	4,191	ATG	T
tRNA-G	4,192	4,253		
NADH dehydrogenase subunit 3 (<i>NAD3</i>)	4,254	4,604	ATG	TAA
tRNA-A	4,607	4,669		
tRNA-R	4,671	4,731		
tRNA-N	4,731	4,794		
tRNA-S1	4,796	4,862		
tRNA-E	4,863	4,927		
tRNA-T	4,937	4,998		
NADH dehydrogenase subunit 6 (<i>NAD6</i>)	5,015	5,518	ATT	TAA
Cytochrome b (<i>CYTb</i>)	5,518	6,654	ATG	TAG
tRNA-S2	6,653	6,715		
Non coding region (<i>NCR</i>)	6,716	7,171		
rRNA-Q	7,172	7,240		
tRNA-C	7,249	7,308		
tRNA-Y	7,323	7,390		
tRNA-H	7,394	7,459		
tRNA-F	7,467	7,532		
NADH dehydrogenase subunit 5 (<i>NAD5</i>)	7,537	9,261	GTG	TAA
NADH dehydrogenase subunit 4 (<i>NAD4</i>)	9,297	10,622	ATG	TAA
NADH dehydrogenase subunit 4L (<i>NAD4L</i>)	10,616	10,909	ATG	TAA
tRNA-P	10,920	10,981		
NADH dehydrogenase subunit 1 (<i>NAD1</i>)	10,988	11,911	ATA	TAA
16S rRNA (<i>rrnL</i>)	11,912	13,266		
tRNA-V	13,267	13,334		
12S rRNA (<i>rrnS</i>)	13,335	14,111		
tRNA-I	14,230	14,297		
tRNA-M	14,300	14,364		
NADH dehydrogenase subunit 2 (<i>NAD2</i>)	14,368	15,378	ATT	TAA
tRNA-W	15,377	15,441		

Table 8. Gene content of the mitochondrial genome of *Entomonyx spinosus*.

Feature	Position		Codons	
	Start	End	Initiation	Termination
Cytochrome c oxidase subunit 1 (<i>COX1</i>)	1	1,534	ATG	T
tRNA-L2	1,535	1,599		
Cytochrome c oxidase subunit 2 (<i>COX2</i>)	1,602	2,289	ATG	T
tRNA-K	2,290	2,355		
tRNA-D	2,356	2,420		
ATP synthase F0 subunit 8 (<i>ATP8</i>)	2,421	2,579	ATG	TAA
ATP synthase F0 subunit 6 (<i>ATP6</i>)	2,573	3,247	ATT	TAA
Cytochrome c oxidase subunit 3 (<i>COX3</i>)	3,247	4,036	ATG	T
tRNA-G	4,037	4,099		
NADH dehydrogenase subunit 3 (<i>NAD3</i>)	4,100	4,453	ATT	TAA
tRNA-A	4,453	4,514		
tRNA-R	4,517	4,579		
tRNA-N	4,580	4,645		
tRNA-S1	4,648	4,716		
tRNA-E	4,717	4,784		
tRNA-H	4,784	4,847		
tRNA-F	4,848	4,912		
NADH dehydrogenase subunit 5 (<i>NAD5</i>)	4,914	6,647	ATG	TAA
NADH dehydrogenase subunit 4 (<i>NAD4</i>)	6,688	8,034	ATG	TAG
NADH dehydrogenase subunit 4L (<i>NAD4L</i>)	8,028	8,327	ATG	TAA
tRNA-T	8,330	8,392		
tRNA-P	8,393	8,454		
NADH dehydrogenase subunit 6 (<i>NAD6</i>)	8,457	8,966	ATT	TAA
Cytochrome b (<i>CYTB</i>)	8,966	10,100	ATG	T
tRNA-S2	10,101	10,166		
NADH dehydrogenase subunit 1 (<i>NAD1</i>)	10,180	11,115	ATA	TAA
tRNA-L1	11,142	11,207		
16S rRNA (<i>rrnL</i>)	11,208	12,499		
tRNA-V	12,500	12,570		
12S rRNA (<i>rrnS</i>)	12,571	13,381		
Non coding region (<i>NCR</i>)	13,382	13,954		
tRNA-I	13,955	14,020		
rRNA-Q	14,021	14,089		
tRNA-M	14,094	14,158		
NADH dehydrogenase subunit 2 (<i>NAD2</i>)	14,159	15,163	ATG	TAG
tRNA-W	15,162	15,232		
tRNA-C	15,239	15,300		
tRNA-Y	15,304	15,369		

Table 9. Gene content of the mitochondrial genome of *Micippa platipes*.

Feature	Position		Codons	
	Start	End	Initiation	Termination
Cytochrome c oxidase subunit 1 (<i>COX1</i>)	1	1,534	ATG	T
tRNA-L2	1,535	1,598		
Cytochrome c oxidase subunit 2 (<i>COX2</i>)	1,603	2,290	ATG	T
tRNA-K	2,291	2,358		
tRNA-D	2,359	2,423		
ATP synthase F0 subunit 8 (<i>ATP8</i>)	2,424	2,582	ATG	TAA
ATP synthase F0 subunit 6 (<i>ATP6</i>)	2,576	3,250	ATT	TAA
Cytochrome c oxidase subunit 3 (<i>COX3</i>)	3,250	4,039	ATG	T
tRNA-G	4,040	4,103		
NADH dehydrogenase subunit 3 (<i>NAD3</i>)	4,104	4,457	ATT	TAA
tRNA-A	4,456	4,520		
tRNA-R	4,522	4,584		
tRNA-N	4,586	4,650		
tRNA-S1	4,648	4,712		
tRNA-E	4,713	4,779		
tRNA-H	4,802	4,866		
tRNA-F	4,867	4,929		
NADH dehydrogenase subunit 5 (<i>NAD5</i>)	4,929	6,656	ATG	TAA
NADH dehydrogenase subunit 4 (<i>NAD4</i>)	6,684	8,030	ATG	TAA
NADH dehydrogenase subunit 4L (<i>NAD4L</i>)	8,024	8,323	ATG	TAA
tRNA-T	8,326	8,389		
tRNA-P	8,390	8,452		
NADH dehydrogenase subunit 6 (<i>NAD6</i>)	8,455	8,958	ATC	TAA
Cytochrome b (<i>CYTB</i>)	8,958	10,092	ATG	T
tRNA-S2	10,093	10,160		
NADH dehydrogenase subunit 1 (<i>NAD1</i>)	10,186	11,142	ATA	TAA
tRNA-L1	11,140	11,206		
16S rRNA (<i>rrnL</i>)	11,207	12,477		
tRNA-V	12,478	12,549		
12S rRNA (<i>rrnS</i>)	12,550	13,361		
Non coding region (<i>NCR</i>)	13,362	13,974		
tRNA-I	13,975	14,039		
rRNA-Q	14,046	14,114		
tRNA-M	14,119	14,184		
NADH dehydrogenase subunit 2 (<i>NAD2</i>)	14,185	15,186	ATG	TAG
tRNA-W	15,185	15,253		
tRNA-C	15,260	15,320		
tRNA-Y	15,321	15,386		

Table 10. Gene content of the mitochondrial genome of *Oregonia gracilis*.

Feature	Position		Codons	
	Start	End	Initiation	Termination
Cytochrome c oxidase subunit 1 (<i>COX1</i>)	1	1,534	ATG	T
tRNA-L2	1,535	1,599		
Cytochrome c oxidase subunit 2 (<i>COX2</i>)	1,610	2,297	ATG	T
tRNA-K	2,298	2,364		
tRNA-D	2,365	2,429		
ATP synthase F0 subunit 8 (<i>ATP8</i>)	2,430	2,588	ATG	TAG
ATP synthase F0 subunit 6 (<i>ATP6</i>)	2,582	3,256	ATT	TAA
Cytochrome c oxidase subunit 3 (<i>COX3</i>)	3,256	4,045	ATG	T
tRNA-G	4,046	4,111		
NADH dehydrogenase subunit 3 (<i>NAD3</i>)	4,112	4,465	ATT	TAA
tRNA-A	4,469	4,531		
tRNA-R	4,532	4,592		
tRNA-N	4,593	4,657		
tRNA-S1	4,662	4,728		
tRNA-E	4,731	4,796		
tRNA-H	4,808	4,871		
tRNA-F	4,879	4,942		
NADH dehydrogenase subunit 5 (<i>NAD5</i>)	4,948	6,675	ATG	TAA
NADH dehydrogenase subunit 4 (<i>NAD4</i>)	6,693	8,045	ATG	TAA
NADH dehydrogenase subunit 4L (<i>NAD4L</i>)	8,039	8,338	ATG	TAA
tRNA-T	8,341	8,405		
tRNA-P	8,406	8,468		
NADH dehydrogenase subunit 6 (<i>NAD6</i>)	8,471	8,977	ATT	TAA
Cytochrome b (<i>CYTB</i>)	8,977	10,113	ATG	TAG
tRNA-S2	10,112	10,178		
NADH dehydrogenase subunit 1 (<i>NAD1</i>)	10,204	11,139	ATA	TAA
tRNA-L1	11,166	11,231		
16S rRNA (<i>rrnL</i>)	11,232	12,542		
tRNA-V	12,543	12,615		
12S rRNA (<i>rrnS</i>)	12,616	13,429		
Non coding region (<i>NCR</i>)	13,430	14,321		
tRNA-I	14,322	14,389		
rRNA-Q	14,378	14,454		
tRNA-M	14,465	14,531		
NADH dehydrogenase subunit 2 (<i>NAD2</i>)	14,532	15,539	ATG	TAG
tRNA-W	15,538	15,605		
tRNA-C	15,611	15,672		
tRNA-Y	15,674	15,737		

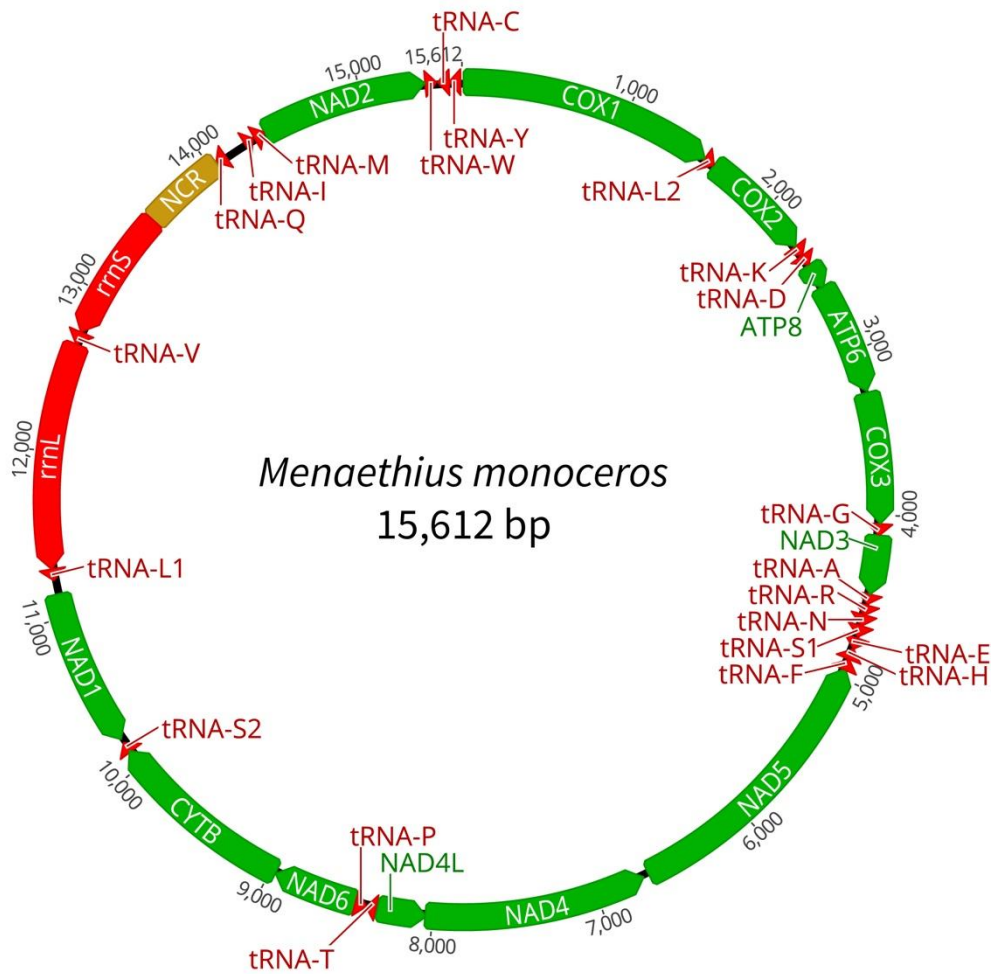


Fig. 1. Complete mitochondrial genome of *Menaethius monoceros* (Latreille, 1825), included 13 protein-coding genes (green), 22 tRNA and two rRNA (red).

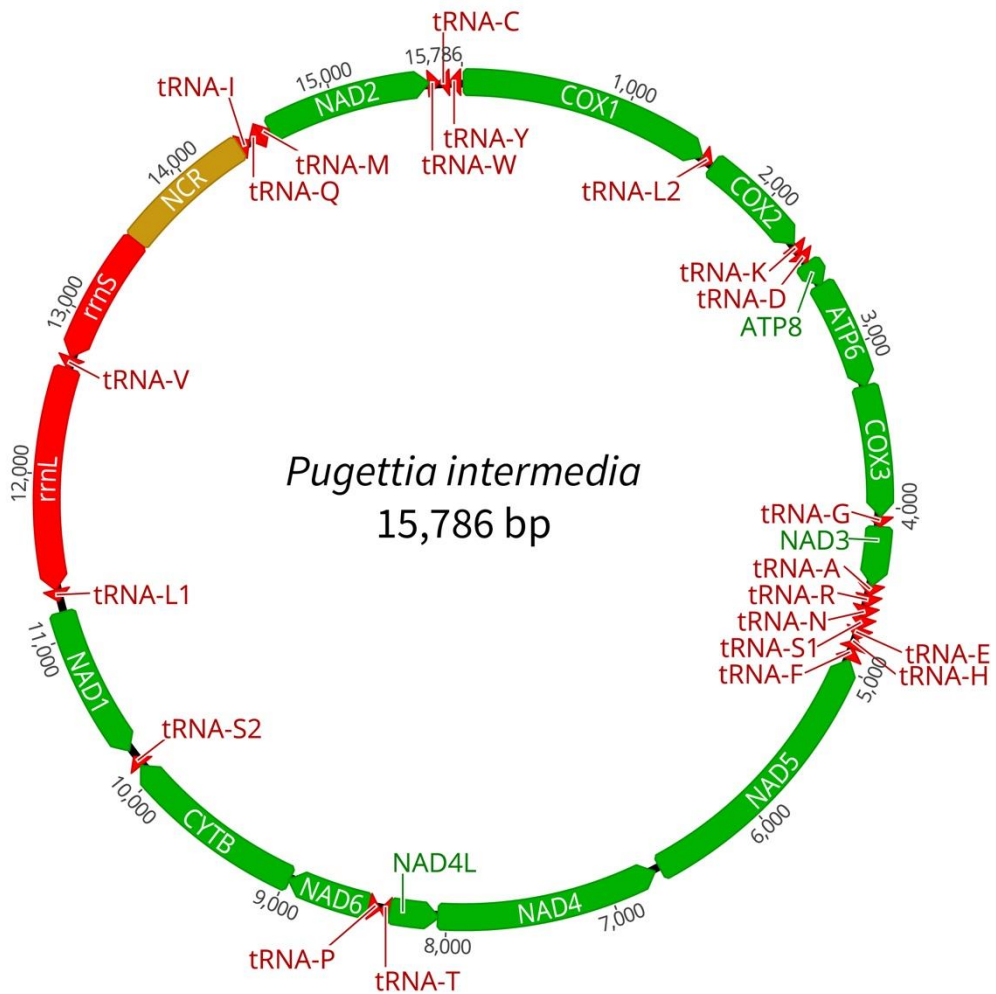


Fig. 2. Complete mitochondrial genome of *Pugettia intermedia* Sakai, 1938, included 13 protein-coding genes (green), 22 tRNA and two rRNA (red).

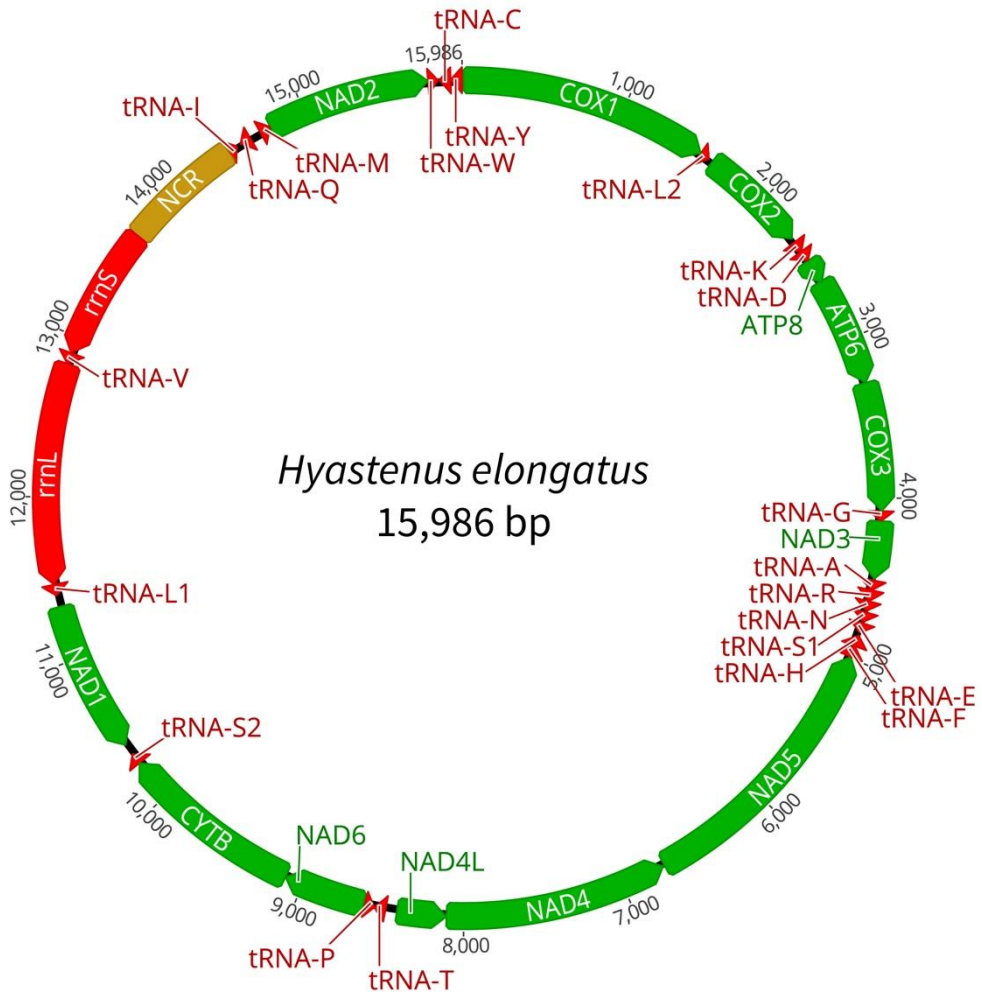


Fig. 3. Complete mitochondrial genome of *Hyastenus elongatus* Ortmann, 1893, included 13 protein-coding genes (green), 22 tRNA and two rRNA (red).

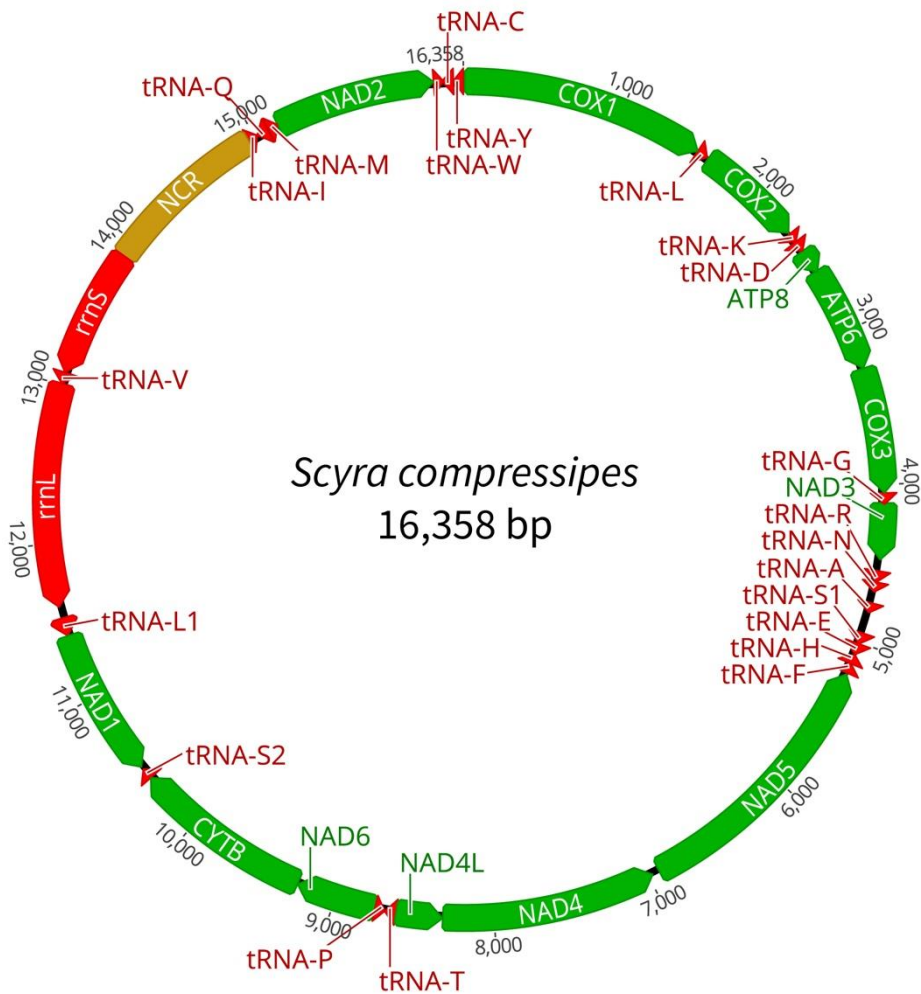


Fig. 4. Complete mitochondrial genome of *Scyra compressipes* Stimpson, 1857, included 13 protein-coding genes (green), 22 tRNA and two rRNA (red).

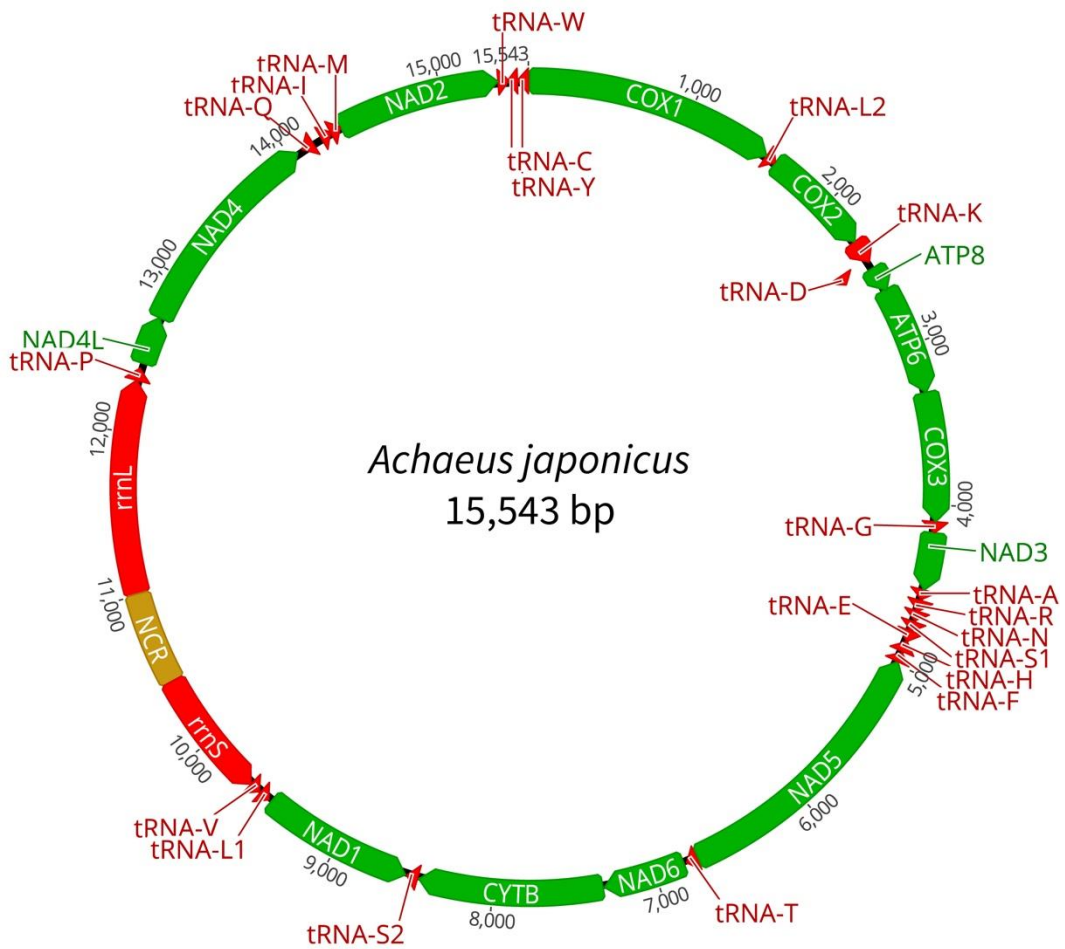


Fig. 5. Complete mitochondrial genome of *Achaeus japonicus* (De Haan, 1839), included 13 protein-coding genes (green), 22 tRNA and two rRNA (red).

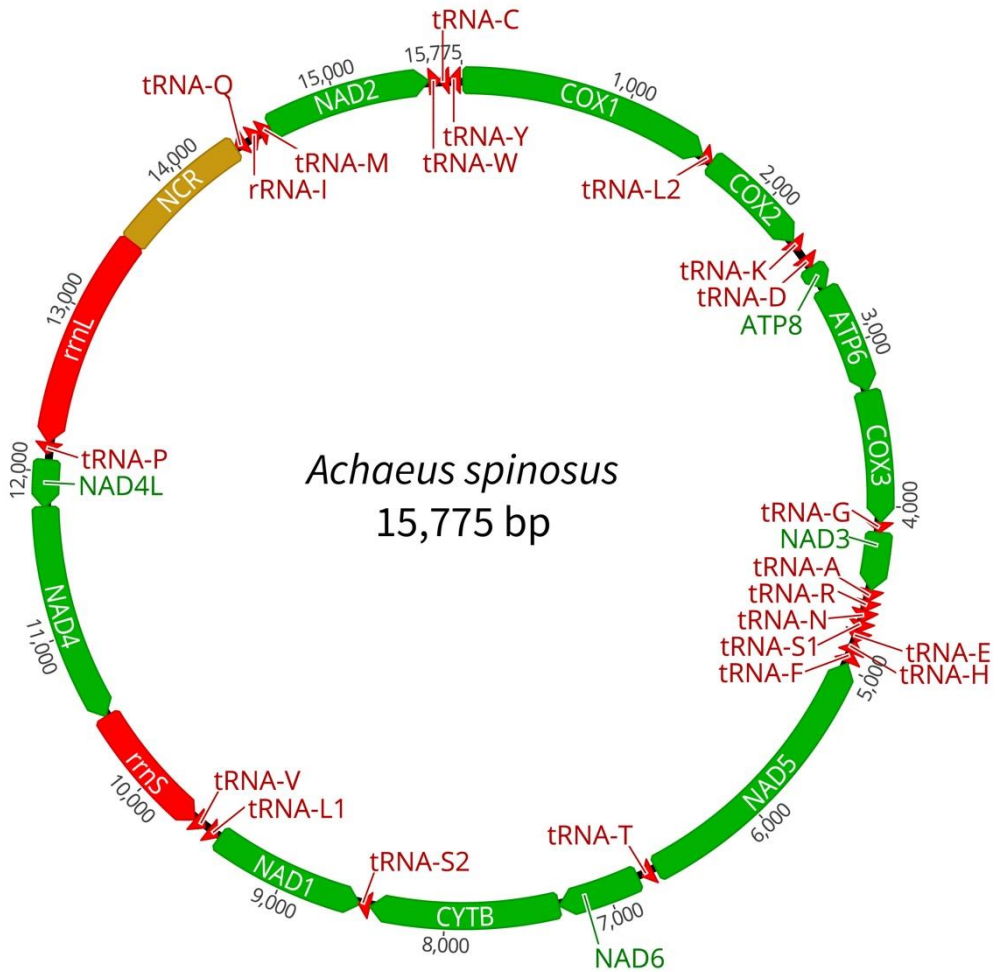


Fig. 6. Complete mitochondrial genome of *Achaeus spinosus* Miers, 1879, included 13 protein-coding genes (green), 22 tRNA and two rRNA (red).

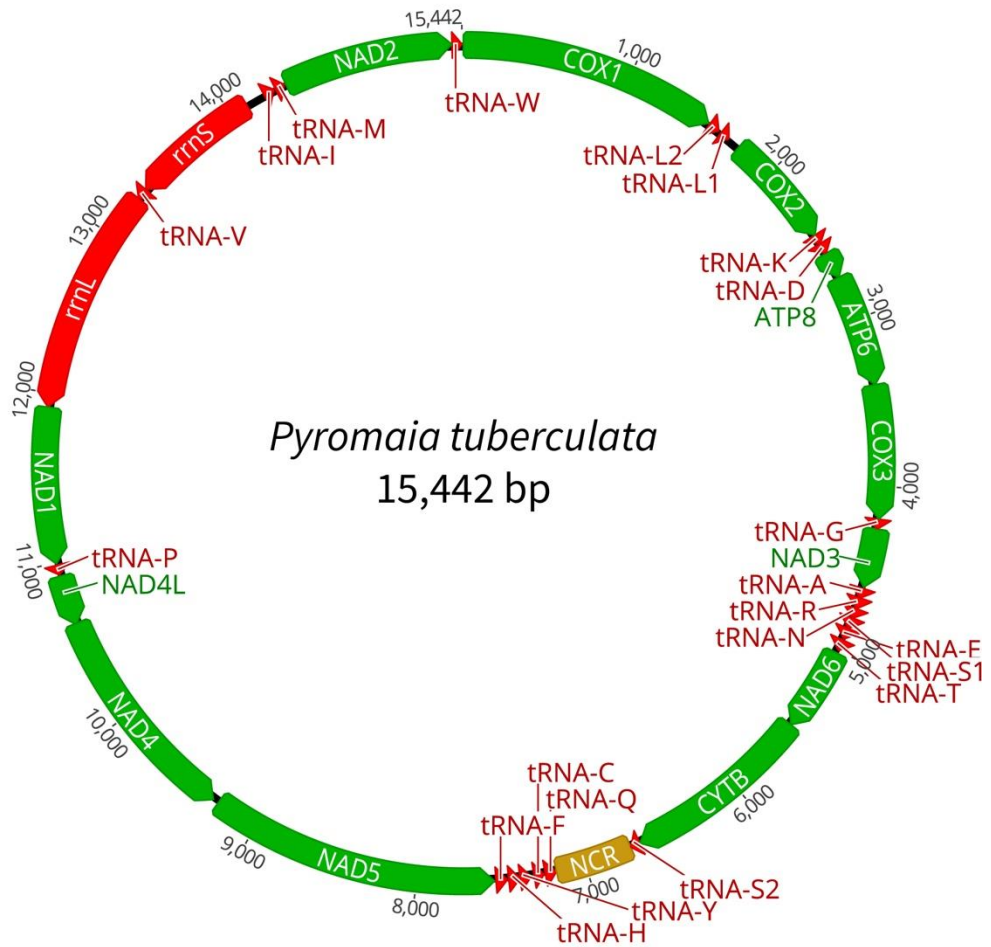


Fig. 7. Complete mitochondrial genome of *Pyromaia tuberculata* (Lockington, 1877), included 13 protein-coding genes (green), 22 tRNA and two rRNA (red).

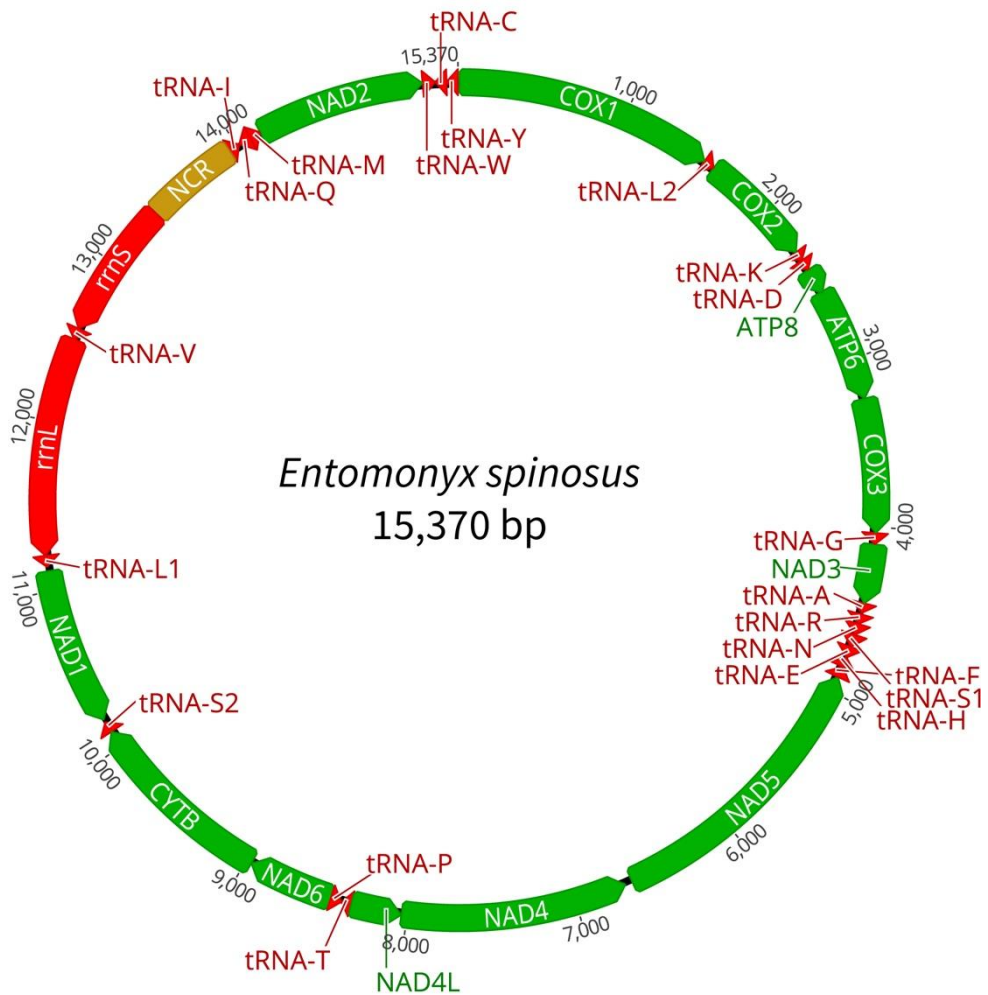


Fig. 8. Complete mitochondrial genome of *Entomonyx spinosus* Miers, 1884, included 13 protein-coding genes (green), 22 tRNA and two rRNA (red).

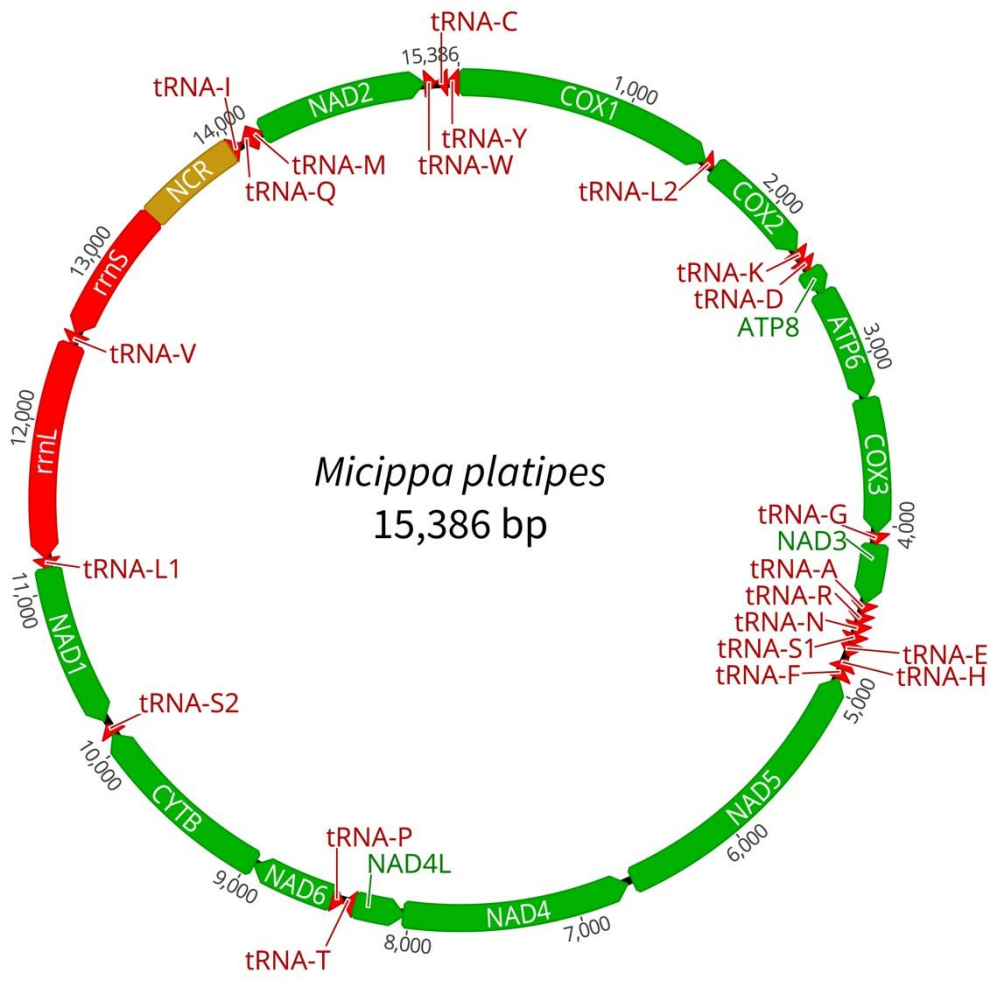


Fig. 9. Complete mitochondrial genome of *Micippa platipes* Rüppell, 1830, included 13 protein-coding genes (green), 22 tRNA and two rRNA (red).

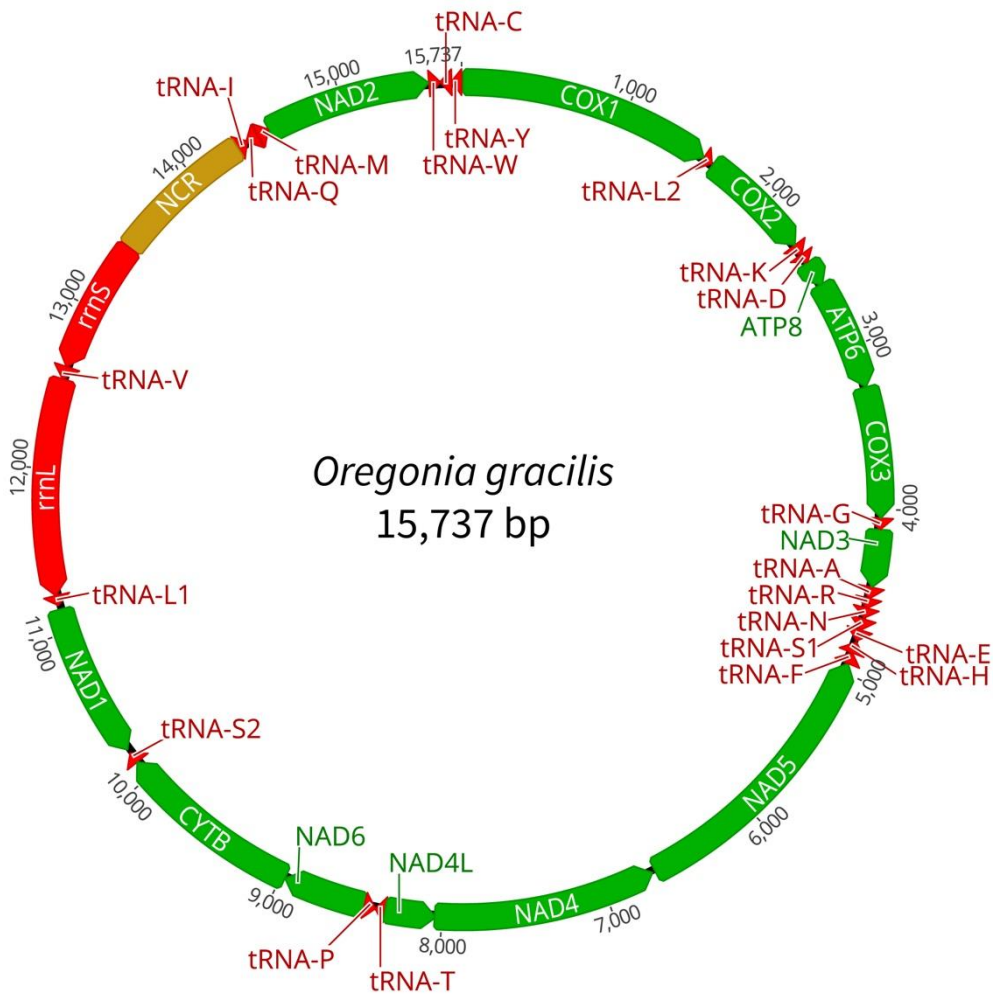


Fig. 10. Complete mitochondrial genome of *Oregonia gracilis* Dana, 1851, included 13 protein-coding genes (green), 22 tRNA and two rRNA (red).