이학박사학위논문

Taxonomic Study of the Thoracican Barnacles (Crustacea: Thecostraca: Thoracica) in Korean Waters

-Diversity, Host specificity, Distribution-

한국해역 따개비류 (갑각아문: 초갑아강: 완흉상목)의 분류학적 연구

-다양성, 숙주 특이성, 분포연구-

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서울대학교 대학원

생명과학부

김현경

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-Diversity, Host specificity, Distribution-

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Abstract

Thoracican barnacles (Crustacea: Theocostraca: Cirripeda) inhabit almost all marine environments and are the only organism that have sessile habits in their life cycle among crustaceans. The densities of barnacles affect the abundance and ecology of other species. Because barnacles are one of the representative biofouling organisms and cause economic losses due to their worldwide dispersal in ballast water and rapid attachment to the bottoms of ships, studies on the distribution status and ecological characteristics of these species are necessary. However, only fragmentary research has been carried out on Korean barnacles after Kim's (1998) morphological taxonomic studies. In the present study, geographical distribution, abundance, diversity, and classification of Korean thoracican barnacles were investigated. The specimens were collected from the intertidal and subtidal zones between 2016 and 2018 in Korea. A total of 22 species of 15 genera under seven families were identified and classified, of which one coral-associated barnacle species is described as a new species, and another one species is recorded for the first time from Korean waters. To compare the molecular characteristics and investigate the distribution of taxa, a combined phylogenetic analysis was conducted.

In Chapter 1, the biogeography of intertidal and shallow water barnacles in different marine ecosystems of Korea was investigated. Firstly, the species composition in relation to marine ecosystems were confirmed using multivariate analysis. Secondly, environmental factors (sea surface temperature, chlorophyll *a* concentration and salinity) influencing on variation in species abundance among different marine ecosystems were obtained from Giovanni database, NASA, USA. In addition, the current status of the distribution of introduced barnacles was recorded. This study revealed that, the biogeography of intertidal and shallow water barnacles in Korea is strongly influenced by oceanographic currents, sea water temperature, and salinity differences among the marine ecosystems. The morphological diagnoses and species information were also provided based on the original decriptions. In molecular analysis results, 22 studied barnacle species formed their own clade with high support values and confirmed the efficiency of 12S rDNA and COI markers for identifying species as well as discovering cryptic diversity/phenotypic plasticity in Korean barnacles.

In Chapter 2, biodiversity and host specificity of coral-associated barnacles in Korea were examined. Only three coral-associated barnacles *Cantellius arcuatus*, *Cantellius* sp., and *Pyrgomina oulastreae* were each found on three different corals. Based on molecular analysis of two mitochondrial markers, (12S rDNA and COI), *C. arcuatus* matched those collected in Japan, Taiwan, Malaysia, and Papua New Guinea, suggesting that this species has a wide geographical distribution and the host specificity of coral-associated barnacles varies with host availability. Also, *Cantellius* sp. was identified as an unknown species. In addition, the morphological diagnoses and information on four species, including one previously described congeneric species, *C. euspinulosum*, were provided. Results of this study further revealed that, coral-associated barnacles in marginal communities had considerably lower diversity than their subtropical and tropical counterparts and exhibited higher host specificity than those in subtropical and tropical reef systems.

In chapter 3, the taxonomic revision of the genus *Tetraclitella* as the group related to lunnule-like hollows in the shells was conducted. Specimens of various size from Korea, Taiwan and China were examined to describe how hollows form. The molecular analysis based on two mitochondrial DNA (12S rDNA and COI) and one nuclear gene (ITS1) was applied to verify an accuracy of morphological classification and to investigate the distribution of the species. In addition, a taxonomic review was conducted based on their original description and the key of genus was updated. As a result of this study, *T. chinensis* was re-described to include the morphological variation in shell forms (hollowed and multicostate), and the two nominal species were formally synonymized, with *T. multicostata* being reduced to a junior synonym of *T. chinensis*.

Key words: Thoracican barnacle, Biogeography, Biodiversity, Coral-associated barnacle, Host specificity, Taxonomy, Molecular phylogeny

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General Introduction

Barnacles belonging to subphylum Crustacea are one of the largest crustacean group of sessile organisms and are important components in marine ecosystems. They are divided into three main superorders, Acrothoracica, Rhizocephala, Thoracica, based on their habitats, such as borers, burrowers, and endoparasitic dwellers. Of these, Thoracica is free-living barnacles that consist of stalked Pedunculata and unstalked Sessilia and distribute from the intertidal to deep sea. Thoracican barnacles are successful in marine ecosystems as they exist in all marine habitats. Additionally, they are ecologically important members of the marine community in that they are suspension feeders and role as consumers and preys in the marine food web (Begum *et al*., 2004; Chan *et al*., 2009). Some of the most conspicuous and well-known ship fouling species such as *Amphibalanus amphitrite*, *Amphibalanus improvisus*, *Balanus glandula*, and *Megabalanus coccopoma* have resulted in major disturbances of native ecosystems as well as economic losses, and introduced species are today considered a major contributor to global environmental change and a threat to biodiversity (Wrange *et al*., 2016). Despite their ecological and economical importance, taxonomic confusion caused by the extensive variation in morphology and diverse environmental conditions may lead to misidentification of species and difficult to understand of their ecology and biology (Chan *et al*., 2007b).

Thoracican barnacles, chosen as model organisms for studying evolution and phylogeny in the 18 century by Darwin, contain over 1,220 species belonging to 18 families throughout oceans around the world (Martin & Jinny, 2007). Most of them are dominant occupiers in intertidal zones, particularly on rocky shores, shallow and deep waters. They have evolved diverse morphological forms, lifestyles and reproductive strategies as an adaptation to these diverse environmental conditions (Chan & Høeg, 2015). The thoracican barnacles are often used as model and representative species to study the biogeography of intertidal species, as they are the major space occupiers and have wide geographical distribution (Southward, 1991; Chan *et al*., 2007a, b; Tasng *et al*., 2008a, b, 2011). Understanding the biogeography and ecology of barnacles enables to recognize the present biodiversity status and predict changes under the effect of global warming (Firth *et al*., 2009; Tittensor *et al*., 2010). Chan *et al*. (2009) reviewed and reported on the distribution of 94 thoracican barnacles in Taiwan, suggesting that their distribution was related to marine currents and climate patterns. Among different marine ecosystems, the rocky intertidal barnacles are strongly affected by both physical and biological factors (*e.g*., thermal stress and competition). Increased seawater temperature also has resulted in range shifts of intertidal barnacles and their abundance.

However, the study the biogeographical distribution of Korean barnacles is nonexistent after Kim (1980). And Kim (1998) only published an illustrated encyclopedia of the Korean barnacles without the geographical distribution of thoracican barnacles in different marine ecosystems of Korea. The baseline biogeographic pattern species is still poorly known. Reports on the biogeography of Korean barnacles in different marine ecosystems and climate zones are necessary to provide a quantitative baseline for biogeographic data.

Also, there have been revisions in classification. Kolbasov (1993) revised the genus *Acasta* Leach, 1817 and established a subfamily Acastinae suggesting for five genera, *Archiacasta, Neoacasta, Euacasta, Acasta*, and *Pectinoacasta*, based on the relationship between sponge hosts and morphological characteristics. Also, the phylogenetic revision of Pitombo

(2003) established a subfamily Amphibalaninae, as a result, Balanidae is classified into four subfamilies (Amphibalaninae, Balaninae, Concavinae, and Megabalaninae) and 17 genera.

The taxonomic studies of barnacles began in the 16th century when stalked barnacles (*Lepas* spp.) attached to floating woods and has been extensively conducted since Darwin (1854). Pilsbry (1907) was the first to record *Capitulum mitella* from Busan, the southern part of Korea. Utinomi (1967, 1970) reported six species from Korea, including *Fistulobalanus kondakovi* [Mokpo], *F. albicostatus* [Mokpo, Busan, Gunsan, Jeju], *Capitulum mitella* [Jeju], *Tetraclitella chinensis*, and *T. darwini* [Jeju]. Kim and Kim (1980) who updated the cirripedes of Korean and reported 18 species, including four new species and one subspecies. Paik *et al*. (1981) further recorded 19 species from the eastern parts of Korea. In 1988, three new records of cirripeds including one stalked barnacle, *Paralepas phyllacanthusi* and two sponge-inhabiting barnacles, *Acasta paraspinifera* and *A. chejudoensis* from Jeju Island were reported by Kim and Kim (1988). Currently, there are 12 families, 30 genera, and 63 species of thoracican barnacles (including sponge and coral barnacles) are recorded so far. These records are based on the previous classification scheme (Kim, 1988). However, the recent classification scheme changed and transferred many taxa to other taxonomic groups (Pitombo, 2004). Thus far, one stalked barnacle and 13species of thoracican barnacles transferred to the different genera among Korean barnacles. Also, most previous species descriptions of Korean barnacles focused on intertidal and shallow-water species, while deep-sea Cirripedia fauna received very scant attention. The number of Korean barnacle species is less than 5% of the worldwide barnacle species. Compared to reported species of neighboring countries such as 198 species from China (Liu & Ren, 2007) and 191 species form Taiwan (Chan *et al*., 2009), the research on the Korean barnacles is relatively poorly studied. Sill, numerous Korean barnacles remained undiscovered and undescribed. Revisions that reflect the latest taxonomic ranks and classification systems are needed.

Historically, morphology of the shell and opercular plates (scutum and tergum) were used to identify barnacles as key characters, but it sometimes cause misidentification because there are some suspected cryptic species or misidentified specimens were discovered and arthropodal characters, including setal types of cirri and mouthparts, were often neglected (Begum *et al*., 2004; Chan *et al*., 2013b). DNA sequencing of the mitochondrial 12S rRNA, cytochrome *c* oxidase subunit I (COI), and the first internal transcribed spacer (ITS1) of nuclear rRNA has been proposed to be an effective systems to analyze the differentiation and evolution of species (Hebert *et al*., 2003; Chan *et al*., 2007). Especially, DNA sequencing is a useful tool for identification in many animal groups including some crustaceans (Radulovici *et al*., 2009). Thus, additional molecular taxonomic approaches will have a potential to serve as a supplemental tool for the resolution of taxonomic problems by presenting additional valuable characters, where morphological identification is challenging.

The purpose of this study is to reconsider the geographical distribution and classification of the Korean barnacles by identifying the new species and considering the previous literatures. To accomplish this, all the studied specimens were collected along the coastal regions of Korea including Korean marine national park areas from 2016 to 2018. The species are illustrated with color photographs, and the morphology of shell, cirri and, mouthparts were also illustrated by light microscopy or line drawing. For further evaluation and efficient morphological description of shell parts of coral-associated barnacles, scanning electron microscopy (SEM) was used. The studies of each chapter in this dissertation were conducted based on geographical, morphological and molecular data.

The following contents of each chapter are summarized here below.

1) Chapter 1 provides geographical distribution in different marine ecosystems and reconsideration of the classification.

2) Chapter 2 focuses on the diversity and host usage of coral-associated barnacles in Korea by identifying the new and unreported species.

3) Chapter 3 provides a taxonomic revision of the acorn barnacle *Tetraclitella chinensis*.

Barnacle Morphology and Systematic Characters

Shell

The stalked barnacles consist of the capitulum and peduncle. The number of their plates is various with taxa, and Lepadiformes have five plates, the paired terga and scuta, and the carina in the dorsal midline. The number of plates in the stalked barnacle is key characters to classify of families; capitulum without plates in Heteralepadidae (Nilsson-Cantell, 1921), with four plates in Iblidae Leach, 1825, five in the Oxynaspididae Pilsbry, 1907, Lepadidae Darwin, 1851 and Poecilasmatidae Annandale, 1909. In species of the Poecilasmatidae, the plates are often reducedape to two from zero (Fig. 1).

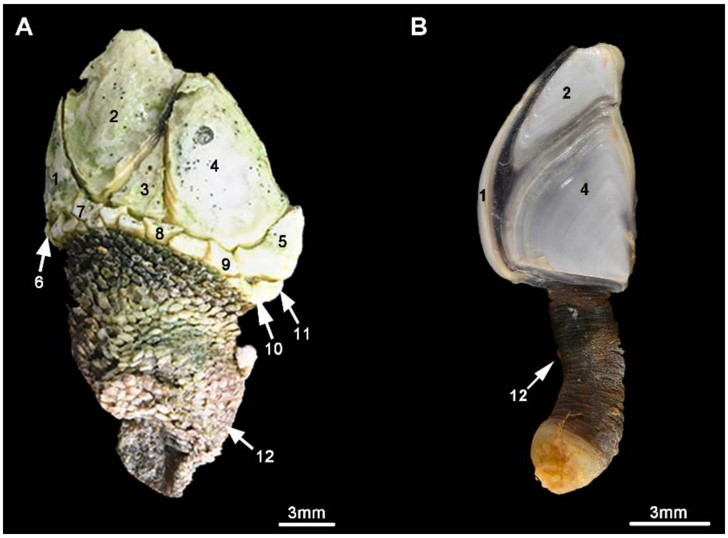

Fig. 1. Morphological terms used in stalked barnacles. A. *Capitulum*; B. *Lepas*. 1, carina; 2, tergum; 3, upper latus; 4, scutum; 5, rostrum; 6, subcarina; 7, carinal latus; 8, median latus; 9, rostral latus; 10, accessory plates; 11, subrostrum; 12, peduncle.

Unlike stalked barnacles, the barnacles of balanomorpha attach to rocks and other permanent structures directly and have no peduncle. There are usually four, six or eight plates surrounding the body symmetrically. The plates consist of two parts: external and inner surface. On the external surface, they are divided into three parts, the pariete, the radii, and the ala. The plates at the front are called the rostrum (near the scutum), that at the back is the carina (near the tergum), and the paired side plates are called laterals and carinolaterals (Fig. 2A, B). The radii and ala provide interlocking devices between the plates. The ala is overlapped by the radii and by part of the parietes. The inner surface of plates lower to the sheath can be smooth or longitudinally ribbed. Usually, it is not easy to see these features if the barnacle is eroded (Fig. 2C, D).

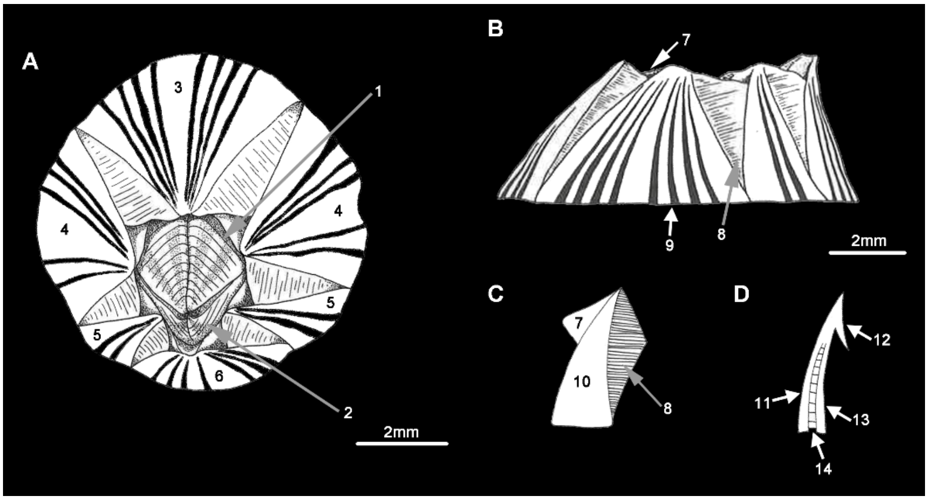

Fig. 2. Morphology of shell (*Amphibalanus amphitrite*). A. upper view; B. lateral view; C. exterior of a plate; D. longitudinal section of plate. 1, scutum; 2, tergum; 3, rostrum; 4, lateral; 5, carinolateral; 6, carina; 7, ala; 8, radii; 9, basis; 10, pariete; 11, outer lamina; 12, sheath; 13, inner lamina; 14, parietal tube. Modified from Kim (1998).

Opercular Plates

The opercular plates, the scuta, and terga, of balanomorph barnacles are movable relative to each other. The scuta are often larger pairs of plates and the terga can be shown at the edge of the operculum. The morphology of operculum plates is useful to distinguish barnacle species (Fig. 3).

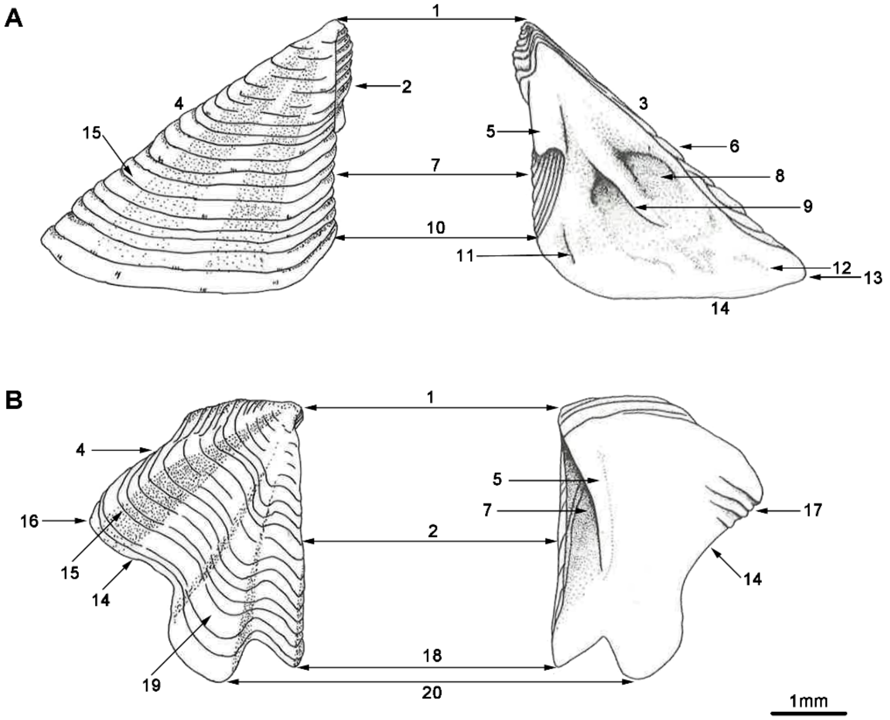

Fig. 3. Morphology of opercular plates. A. Scutum, outer and inner; B. Tergum, outer and inner. 1, apex; 2, articular margin; 3, occludent margin; 4, carinal margin; 5, articular ridge; 6, occludent ridge; 7, articular furrow; 8, adductor muscle pit; 9, adductor ridge; 10, tergal angle; 11, pit for lateral depressor muscle; 12, pit for rostral depressor muscle; 13, basirostral angle; 14, basal margin; 15, growth ridge; 16, carinal angle; 17, crests for depressor muscle; 18, basiscutal angle; 19, spur furrow; 20, spur. Scale bar in mm. Modified from Kim (1998).

Inner Parts (Mouth and Cirri)

The body of the barnacles sits inside the shell plates and consists of the prosoma, thorax, and abdomen but there is no differentiation. The thoracic segments support six pairs of cirri; each cirrus has two-segmented protopods and is ramified into the exopod (posterior ramus) and endopod (anterior ramus). The rami comprise segments that carry two multi-segmented barnacles with long setae or hairs. The first cirrus is located close to the mouthparts and channels food particles from the more posterior cirri to the mouthparts. Cirrus II and III also assist to manipulate food and catch or filter the function of the more posterior cirri. The first three pairs of cirri are smaller than the rami of cirri IV-VI. Cirri IV-VI are generally longer and slender with 2-3 pairs of setae on anterior margin. Cirrus IV shows morphological variations with species. The most significant feature situated between the left and right side of cirrus VI is an elongated penis. It is generally longer than cirrus VI and one of the key characters to distinguish species (Fig. 4A). The prosoma contains mouthparts, comprising labrum, paired maxillules, maxillae, mandibles and madibulatory palps. The labrum usually has a central notch with teeth along each crest. The maxillules is positioned behind the mandibles with some spines and is provided with genera and species of different size. The maxillae are triangular lobes and bilobed conveying food particles to the mouth. The mandibles bear 3-5strong teeth and the arrangement of the teeth is one of the important systematic characters. The mandibulatory palp is located on the upper part of the labrum and helps to guard the anterior ventral part of the mouth (Fig. 4B).

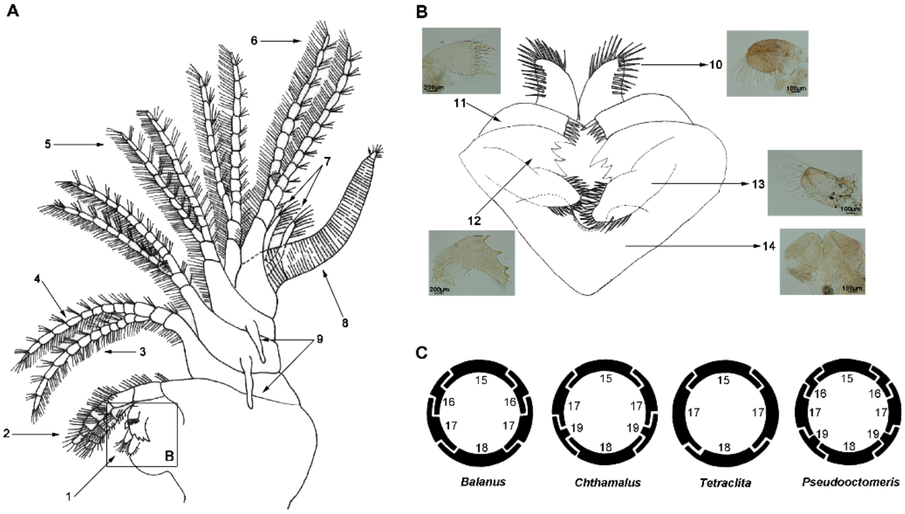

Fig. 4. Inner parts and arrangements of plates in balanomorph barnacles. A. Cirri parts; B. Mouthparts; C. Arrangements of plates. 1, mouthparts; 2, cirri I; 3, anterior ramus of cirri II; 4, posterior ramus of cirri II; 5, cirri IV; 6, cirri VI; 7, caudal appendage; 8, penis; 9, filamentary appendages; 10, maxilla; 11, maxillule; 12, mandible; 13, madibulatory palp; 14, labrum; 15,carina; 16, carinolateral; 17, lateral; 18, rostrum; 19, rostrolateral. Modified from Kim (1998).

Basal Number of Plates

Unlike the stalked barnacle, the balanomorph barnacles have plates arranged symmetrically. The basal number of plates is eight, but the number of plates gets reduced in various groups. The arrangement of basal plates is one of the key characters to classify genera or higher taxa. For example, the genus *Tetraclita* has four plates and there are two fusions of plates: between the carinolateral and carina and between rostrolateral and rostrum. However, the genus *Balanus* having six plates fuse between rostrum and rostrolateral (Fig. 4C).

Chapter 1.

Biogeography of Barnacles on Different Marine Ecosystems in Korea

1.1 Biogeography of intertidal and shallow water barnacles in Korea in relation to oceanographic current systems

1.1.1 Introduction

In the marine environment, global climatic changes often cause a shift in the geographical distribution and abundance of species (Rivadeneira & Fernandez, 2005; Parmesan, 2006). The intertidal rocky shore fauna provides an excellent model to investigate the effect of global changes to biota because its ecosystem is common worldwide. For intertidal invertebrates, rocky shores represent one of the harshest habitats with strong selection pressure from both physical (*e.g.*, heat stress) and biological factors (*e.g.*, competition for spaces) (Tomanek & Somero, 2002). Intertidal organisms are, thus, sensitive to any changes in the environment and show early responses to climate change. Barnacles are the most representative organisms in rocky shores and are used as an ideal model for studying the biogeography of intertidal assemblages as they are sessile, highly abundant and have wide geographical distribution. The geographical distribution range of adult intertidal barnacles is affected by their planktonic larval dispersal and ocean circulation patterns so that any range shift can be easily detected. For instance, the quantitative comparisons of distribution patterns of intertidal communities in the Western English channel during the past 70 years showed that global warming has enhanced the survival, distribution range and abundance of the warm-water species (*e.g.*, the barnacle *Chthamalus stellatus*) and reduced the abundance of cold-water species (*e.g.*, the barnacle *Semibalanus balanoides*). Likewise, the acorn barnacle *Hexechamaesipho pilsbryi* has been extended the distribution into tropical waters due to an increase in environmental temperature and shifts in ocean currents in the

West Pacific (Chan *et al*., 2008a; Tsang *et al*., 2011). The invasion of non-native species also can be influenced by global climate change and disperses to new habitats. One of the introduced barnacles from the European waters, *Perforatus perforatus*, has been expanding its range with the increase of temperature and has recently been discovered on the east coast of Korea (Choi *et al*., 2013). These comparable changes in species composition result in a shift of the vertical zonation, geographical distribution and gene flow between populations of intertidal organisms (Southward, 1991; Southward *et al*., 1995; Thompson *et* al., 2002; Helmuth et al., 2006; Mieszkowska et al., 2006).

The Indo-West Pacific region has the highest marine biodiversity in the world, but the patterns of marine diversity were poorly documented and have remained problematic because global warming has caused changes to the distribution of species. Previous studies have surveyed the geographical distribution of intertidal barnacles with different species compositions among Japan, Okinawa, Taiwan and Southern China (Chan *et al*., 2008a, b, 2009, 2012). In Korea, 63 barnacle species have been reported by Kim (1998), however, there is no study on the distribution of barnacle species concerning oceanographic currents system. The seas surrounding the Korean Peninsula are the Yellow Sea, East China Sea and Eastern coast, which are marginal seas in the northwestern Pacific Ocean and affected by different major ocean currents: the Yellow Sea Current, Kuroshio Current and Tsushima Current (Fig. 5). Seasonal variation of the water circulation in the Yellow and East China seas (YECS) are large as their water depth is so shallow (with depth < 200m) and influenced by heat transfer through the sea surface, salinity, and tidal environments. The main YECS circulation system consists of the Kuroshio and coastal currents (the Taiwan Current and the Korean Strait Current). The Kuroshio transports warm saline water into the YECS through the northern waters of Taiwan in the East China Sea and flows into Yellow sea when the

Taiwan current moves up to north. In contrast to the YECS, the Sea of Japan is connected with the East China Sea through the Tsushima Current which originated from the branching of Kuroshio west of Kyushu. The Tsushima transports warm and saline equatorial waters from the Pacific Ocean to the Sea of Japan and issues the East Korea Warm Current as a northern branch.

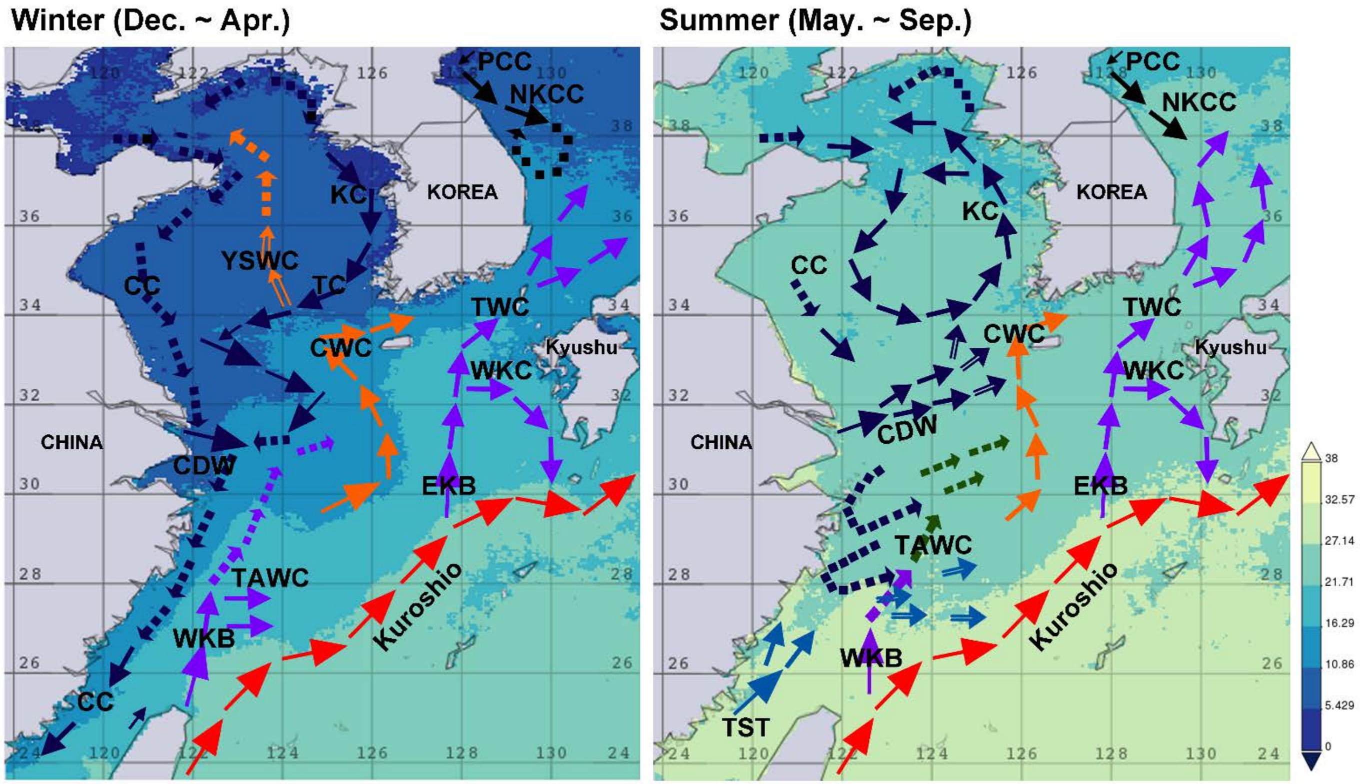

Fig. 5. Seasonal surface circulation for winter and summer in Korea. Modified from Lie & Cho (2016). CC:Chinese Coastal Current, CDW:Changjiang Diluted Water, CWC:Cheju Warm Current, EKB:Eastern Kuroshio Branch, KC:Korean Coastal Current, TAWC:Taiwan Warm Current, TC:Yellow Sea Transversal Current, TWC:Tsushima Warm Current, WKB:Western Kuroshio Branch, WKC:Western Kyushu Current, YSWC:Yellow Sea Warm Current, PCC:Primorye Cold Current, NKCC:North Korea Coastal Current. Modified form Lie & Cho (2016).

The western coast of the Korean Peninsula is affected by the Yellow Sea Warm Current (YSWC), which is thought to be a branch of the Tsushima Current originating from the Kuroshio west of Kyushu (Nitani, 1972; Guan, 1994), and two seasonal coastal currents (Korean coastal current, KC; Chinese coastal current, CC) along the coasts of Korea and China determining the annual mean YSWC. In the winter, warm and saline water is introduced to the Yellow Sea through YSWC and northward Kuroshio branch current, Cheju Warm Current (CWC), extends westward in a counterclockwise circulation from the surface to the bottom. The coastal currents KC and CC change their direction by contact with the Kuroshio Current and northerly monsoon winds. The compensation of KC in winter is very weak, but the CC contributes to flow southward and induces a northward flow along the Yellow Sea. Between 2017 and 2018, the average sea surface temperature in the western coast was below 10°C due to an inflow of cold coastal water from the southward KC and CWC water (Giovanni database, NASA, USA, Fig. 6). In the summer, counterclockwise circulations are developed at the surface and middle layer and induced by the sea surface heating affected by the vertical mixing of tidal currents. The YSWC vanishes and turns eastward instead of intruding into the Yellow Sea and the CC flows northward. The salinity of the CC also drops down due to the freshwater discharge from Changjiang river. KC is weaker in the summer due to a decrease in strength with monsoon wind stress (Jacobs *et al.*, 2000; Wu *et al.*, 2014; Koh & Khim, 2014; Lie & Cho, 2016). Average sea surface temperature ranged from 27 °C to 38°C in 2017-2018 (Giovanni database, NASA, USA, Fig. 6). The CC also has high nutrients and productively, resulting in the waters affected by this current having slightly higher chlorophyll a concentration than the other two seas around the Korean Peninsula.

The southern coast and Jeju Island in Korea are under the influence of both Kuroshio Current (KUC) with high salinity and high temperature through the branching of the Kuroshio at the northern waters of Taiwan in the East China Sea. The winter monsoon weakens the KUC and strengthens south-flowing coastal currents so that sea surface temperatures drop. Then counterclockwise circulation can set up from the surface to the bottom. The Kuroshio branch current in the west of Kyushu, the Tsushima Warm Current (TWC), transports a mixture of Kuroshio water and also flows diluted water into Changjiang River southward in the winter. This flow is related to the part of the northward Western Kuroshio Branch (Taiwan Warm Current; TAWC) strength. During the summer, however, the northward expansion of TAWC transportation is much stronger. Most of the freshwater discharge is directed northeast toward Jeju Island, and the remaining part flows southward along the coast. The summer monsoon winds from the South are much weaker and shorter than winter (Jacobs *et al*., 2000; Yuan *et al*., 2004; Yuan & Hsueh, 2010). In 2017–2018, variation in the sea surface temperature along the southern coastlines of Korea was over 10°C in the winter and ranged from 32°C to 38°C in the summer (Giovanni database, NASA, USA, Fig. 6).

The eastern part of the Korean seas is connected with the East China Sea through the Korea/Tsushima straight (KTS) and is affected by the Asian monsoon system (Chu *et al*., 2005). The southern region of the East Sea is influenced by transport of Tsushima Warm Current (TWC) and its branch current, the East Korea Warm Current (EKWC), whereas the northern part is influenced by Primorye Cold Current (PCC) and its branch current, the North Korea Cold Current (NKCC). The winter northwesterly monsoon and summer southeasterly monsoon have made a remarkable contribution to the seasonal interchange of cold and warm currents. In the winter, the PCC, coming from the Okhotsk Sea through the Tartar/Mamiya Strait along the Siberian coast, is greater and transport of TWC including the EKWC is weaker. However, the southward current underneath the EKWC encounters the NKCC and strengthens due to heat losses and positive northwesterly winds stress (Chang *et al*., 2004). Low-salinity water is provided from the East China Sea and the maximum volume transport through TWC occurs during the summer (Takikawa *et al*., 2005). The reason is that the outflow through Soya Strait becomes bigger, and the northward branch of inflow through the KS becomes stronger. In the summer, the coastal upwelling takes place under the influence of the southwesterly monsoon, and main axis of the EKWC moves farther offshore (Liu & Chai, 2009). NKCC originating from PCC also develops in the summer, but it is hardly seen in the winter (Morimoto & Yanagi, 2001). Between 2017 and 2018, the average sea surface temperature varied from 10°C in winter to 30°C in summer (Giovanni database, NASA, USA, Fig. 6). Changes in oceanographic currents in Korea relevant to climatic change or anthropogenic activities have been reported. On the Japanese Pacific Coast, the Oyashio Current flowing along the Pacific coastline has been intruded further south compared with the current patterns in past centuries (Ishizaka *et al*., 1992). The construction of the Three-Gorge Dam in Changjiang contributes to reducing the run-off of the Yangtze River and thus the flow rate of the China Coastal Current (CCC) in the East China Sea might be changed (Lee & Chao, 2003). Such temporal variation in the oceanographic patterns could affect the patterns of abundance and geographic distribution of intertidal assemblages in the Korean waters. Under the effect of global warming, increased in temperature can enhance the northward expansion of the warm-water species and the introduction of non-native species (Thompson *et al*., 2002). However, no detailed survey the geographical distribution of barnacles in relation to current systems in Korea yet exists. Kim (1998) only reviewed and reported on the description of Korea barnacles including four introduced species in the southern sea of the Korean peninsula. The present study conducted a survey of the presence or absence of intertidal and shallow water barnacles in 28 locations in South Korea, covering different marine ecosystems including the Yellow Sea Marine System, South Sea Marine System and East Sea Marine System. Sea surface temperature, chlorophyll *a* concentration and salinity related to introduced species from satellite data were included sea to provide baseline pattern oceanographic information of different marine systems in Korea (Fig. 6).

The biogeography of barnacle species assemblages may be different among different marine systems in the Korean Peninsula.

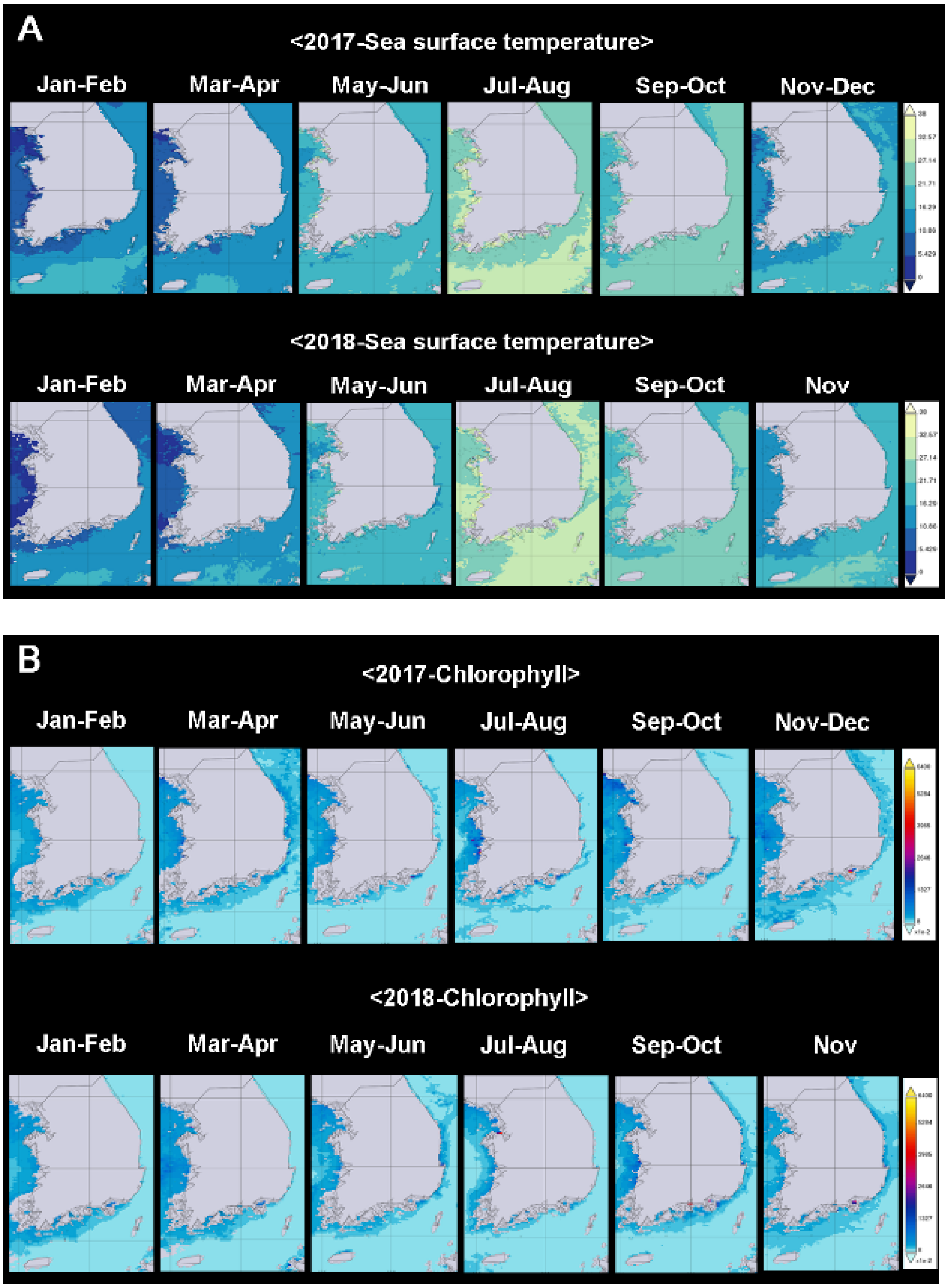

Fig. 6. Sea surface temperature and Chlorophyll *a* concentration derived from satellite images from January 2017 to November 2018. A, Sea surface temperature; B, Chlorophyll *a* concentration.

1.1.2 Materials and Methods

Study Sites and Sampling

Barnacles were collected from 28 locations, 44 subdivisions in Korea from 2016 to 2018 (Fig. 7., Table 1). Sampling sites covered three different large marine ecosystems of Korea. 22 sites were located in the western coast of Korean Peninsula, including Gwanmae, Cheongsan, Hyeol, and Geomun Islands, which are protected by Korea Marine National Park Service, and are affected by the Yellow Sea Warm Current (YSWC), Cheju Warm Current (CWC) and two seasonal coastal currents. The southern coast in Korea, including Jeju Island, 16 sampling sites were selected influenced by the warm Kuroshio Current (KUC) and its branch. Six sites were selected in the eastern waters of Korea, which are affected by the transport of Tsushima Warm Current (TWC) and its branch current. Intertidal barnacles were collected during low tide and shallow water barnacles were sampled through scuba diving at depths of 5–20m using hammer and chisel. All barnacle specimens were preserved in 95% ETOH.

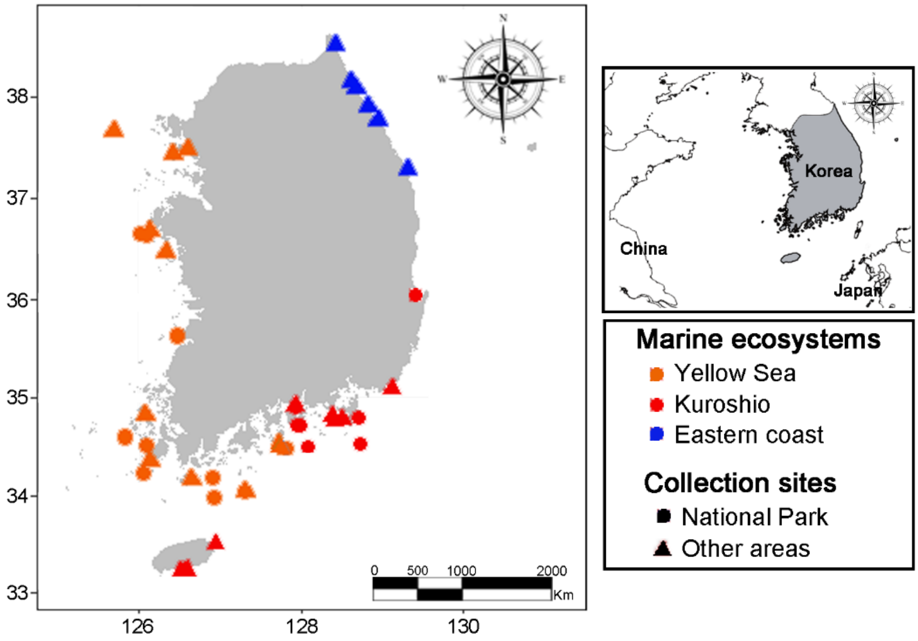

Fig. 7. Collection sites located in different marine ecosystems.

Table 1. Detailed collection sites from 2016 to 2018 in Korea

	Collection site	Latitude	Longitude
	Incheon		
1	Yeonpyeong-eup, Ongjin-gun	37°39'31.28" N	125°40'57.94" E
2	Jung-gu, Incheon	37°25'54.68" N	126°24'57.53" E
3	Wolmi Is., Jungu	37°28'33.20" N	126°35'50.70" E
	Chungcheongnam-do		
4	Sinjin Is.,Geunheung-myeon, Taean-gun,	36°40'50.5" N	126°8'02.7" E
4-1	Ong Is., Gauidoli, Geunheung-myeon, Taean-gun	36°38'55.2" N	126°00'28.3" E
4-2	Jeongjok Is., Gauidoli, Geunheung-myeon, Taean-gun	36°38'14.8" N	126°05'09.1" E

5	Ammyeon Is., Taean-gun	36°28'15.21" N	126°20'24.82" E
	Jellabuk-do		
6	Chaeseokgang, Byeonsan-myeon, Buan	35°37'39.4" N	126°28'06.4" E
6-1	Jeokbyeokkgang, Byeonsan-myeon, Buan	35°28'15.0" N	126°27'44.9" E
	Jellanam-do		
7	Aphae-eup, Sinan-gun	34°49'23.58" N	126°4'31.32" E
7-1	Mokke, Uidodoli, Docho-myeon, Sinan-gun	34°36'09.1" N	125°49'43.0" E
7-2	Seongchon beach,Uidodoli, Docho-myeon, Sinan-gun	34°37'06.2" N	125°49'47.2" E
8	Seomanghang, Jindo-gun	34°21'50.9" N	126°07'56.5" E
9	Hyeol Is., Jodomyeon, Jindo-gun	34°31'0.21" N	126°5'11.75" E
10	Gwanmae Is., Jodomyeon, Jindo-gun	34°14'37.49" N	126°3'6.61" E
11	Soan-myeon, Wando-gun	34°10'19.47" N	126°38'59.35" E
12	Cheongsan Is., Cheongsan-myeon, Wando-gun	34°11'16.94" N	126°54'41.88" E
12-1	Yeoseli, Cheongsan-myeon, Wando-gun	33°59'03.1" N	126°56'00.4" E
13	Geomun Is., Samsan-myeon, Yeosu-si	34°2'51.85" N	127°18'41.02" E
14	Geumo Is., Nam-myeon, Yeosu-si	34°31'38.96" N	127°43'51.68" E
14-1	Ando beach, Andoli, Nam-myeon, Yeosu-si	34°29'22.8" N	127°48'51.9" E
14-2	Jikpo beach, Dumoli, Nam-myeon, Yeosu-si	34°30'28.9" N	127°44'21.7" E
	Gyeongsangnam-do		

15	Wolgokli ,Seolcheon-myeon, Namhae-gun	34°55'25.3" N	127°51'29.0" E
15-1	Geumeumli, Seolcheon-myeon, Namhae-gun	34°55'23.4" N	127°55'40.5" E
16	Sangjubeach, Sangjuli, Sangju-myeon, Namhae-gun	34°43'03.8" N	127°59'28.1" E
16-1	Sejon Is., Sangjuli, Sangju-myeon, Namhae-gun	34°29'57.4" N	128°04'58.3" E
16-2	Yangali, Sangju-myeon, Namhae-gun	34°43'42.5" N	127°57'07.4" E
17	Pungwhali, Sanyang-eup, Tongyeong-si	34°49'10.0" N	128°22'56.3" E
17-1	Yeonwhali, Sanyang-eup, Tongyeong-si	34°46'04.1" N	128°24'26.7" E
18	Hansan Is.,Hansan-myeon, Tongyeong-si	34°46'59.71" N	128°30'19.99" E
18-1	Hong Is., Hansan-myeon, Tongyeong-si	34°32'17.3" N	128°43'48.8" E
19	Irun-myeon, Geoje	34°48'06.1" N	128°42'53.2" E
20	Haeundae-gu, Busan	35°5'58.76" N	129°7'19.05" E
	Gyeongsangbuk-do		
21	Guryongpo-eup, Pohang	36°0'47.0" N	129°28'04.1" E
	Gangwon-do		
22	Janghohang-gil, Geundeok-myeon, Samcheok-si	37°17'20.44" N	129°19'3.10" E
23	Changhae-ro, Jumunjin-eup, Gangneung-si	37°46'20.028" N	128°57'5.922" E
23-1	Jumumli, Jumunjin-eup, Gangneung-si	37°54'22.9"N	128°49'48.5"E

24	Susangil, Sonyang-myeon, Yangyang-gun	38°04'44.5" N	128°40'49.0" E
25	Yongho-gil, Ganghyeon-myeon, Yangyang-gun	38°08'08.4" N	128°37'18.4" E
26	Daejinhang-gil, Hyeonnae-myeon, Goseong-gun	38°30'00.2" N	128°25'36.8" E
	Jeju Island		
27	Beophwan-dong, Seogwipo-si	33°13'25.72" N	126°30'57.45" E
27-1	Bomok-dong, Seogwipo-si	33°13'53.43" N	126°35'50.43" E
27-2	Seogwi-dong, Seogwipo-si	33°13'40.13" N	126°33'54.42" E
28	Udo Is., Jeju-si	33°30'7.97" N	126°56'35.33" E

Morphological Examination

The identification of species was facilitated by dissection of the specimens under a stereomicroscope (Leica MZ8, Germany; SMZ1500, Japan) and a light microscope (Olympus BX60, Japan). The individuals were dissected using the dissecting pins made of 0.2 mm diameter of tungsten wire under stereomicroscope (SMZ1500, Japan). All dissected appendages including cirri and Mouth parts were mounted in the small vial. Images were taken with a digital camera (Model D7000; Nikon, Tokyo, Japan), and produced with Helicon Focus software. For the dissection and setal classification follows Chan *et al*. (2008c).

Environmental Factors

The bimonthly variation in sea surface temperature, chlorophyll *a* concentration and salinity were derived from Giovanni and NASA database. Seasonal variation of the sea surface circulation patterns in winter and summer were modified from Lie and Cho, 2016.

Multivariate Analysis in Different Marine Ecosystems

To compare whether the distribution patterns of barnacle assemblages affected by different marine ecosystems, multivariate analysis were performed in the PRIMER package (v6, Plymouth Routine in Multivariate Analysis, PRIMER-E Ltd; Clake, 1993). Data on species abundances were square-root transformed prior to analysis and the matrix of distance calculated with the Bray-Curtis similarity index for the 21 species and sites as replicate (n = 28). Non-metric Multidimensional Scaling (nMDS; Clark, 1993) was conducted to generate two-dimensional plates on the species composition in all sites. Analysis of

Similarity Percentage (SIMPER) was used to identify the species primarily providing the average percent dissimilarity in the contribution of barnacle assemblages among the sites.

1.1.3 Results

Species Composition and Diversity

A total number of 21 barnacle species belonging to 14 genera were recorded in the study site from all marine ecosystems in Korea (Table 2). The diversity of barnacles was sensitive to alteration in coastal oceanographic ecosystem patterns. Twelve species were recorded in the Yellow Sea ecosystem and 18 species were recorded in the Kuroshio ecosystem. Between the two marine ecosystems, overlap in the distribution of 10 species was detected. The stalked barnacle *Capitulum mitella* and the acorn barnacle *Tetraclita japonica* were common on the mid-littoral zone between the two ecosystems; these species are rare in eastern coast. The mangrove barnacle *Fistulobalanis albicostatus* was also recorded, which is mainly attached to the rocks or on other marine crustacean shells of intertidal mudflats and competes with the introduced barnacle *Amphibalanus amphitrite* in ports of the southern coast. The barnacle *Striatobalanus amaryllis* and *A. reticulatus* were only recorded in the Yellow Sea ecosystem. These species distributes from the low intertidal zone to shallow water (up to 15m depth). Three coral associated barnacles, *Catellius arcuatus*, *Cantellius* sp. and *Pyrgomina oulastreae* were recorded only in the Kuroshio ecosystems. These species are tropical or subtropical, and the known coral-associated barnacles in Korea is smaller than that of Japan and Taiwan. In the Eastern Coast ecosystem, seven species were recorded. Of these, *Hesperibalanus hesperius hesperius* and *Amphibalanus improvisus* were found attached on the surfaces of molluscan shells. Both species have tolerance for cold waters.

There are four common barnacles occurring on all coasts of Korea: *Chthamalus challengeri*, *Balanus rostratus, B. trigonus,* and *Megabalanus rosa*.

The intertidal barnacle, *C. challengeri*, is common from the mid-littoral to the supra-littoral zones of the rocky shore. The remaining three species were found not in the intertidal zone but on buoys attached or the surfaces of molluscan shells.

Table 2. Summary of presence and absences of barnacle species collected in the different marine ecosystems of Korea (+ : presence, - : absence)

Species	**Yellow Sea**	**Kuroshio**	**Eastern coast**
Capitulum mitella (Linnaeus, 1758)	+	+	-
Chthamalus challengeri Hoek, 1883	+	+	+
Tetraclitella chinensis (Nilsson-Cantell, 1921)	-	+	-
Striatobalanus amaryllis (Darwin, 1854)	+	-	-
Tetraclita japonica Pilsbry, 1916	+	+	-
Euacasta dofleini (Kruger, 1911)	+	+	-
Cantellius arcuatus (Hiro, 1938)	-	+	-
Cantellius sp.	-	+	-
Pyrgomina oulastreae (Utinomi, 1962)	-	+	-
Fistulobalanus albicostatus (Pilsbry, 1916)	+	+	-
Fistulobalanus kondakovi (Tarasov and Zevina, 1957)	+	+	-
Amphibalanus amphitrite (Darwin, 1854)	+	+	-
Amphibalanus eburneus (Gould, 1841)	-	+	-
Amphibalanus improvisus (Darwin, 1854)	-	+	+
Amphibalanus reticulatus (Utinomi, 1967)	+	-	-
Balanus rostratus Hoek, 1883	+	+	+
Balanus trigonus Darwin, 1854	+	+	+
Megabalanus rosa (Pilsbry, 1916)	+	+	+
Megabalanus volcano (Pilsbry, 1916)	-	+	-
Perforatus perforatus (Bruguière, 1789)	-	+	+
Hesperibalanus hesperius hesperius (Pilsbry, 1916)	-	-	+
Total	**12**	**18**	**7**

Introduced Barnacles

The distribution of four introduced species that dominate native species and disrupt marine ecosystems was observed in this study:*Amphibalanus amphitrite*, *A. eburneus*, *A. improvisus* and *Perforatus perforatus*. *A. amphitrite*, one of the most successful marine invaders worldwide, was found at six sites examined affected by the Yellow Sea ecosystem and Kuroshio ecosystem. Its abundance varied from occasional to common. At four sites (Namhae, Tongyeong, Geoje and Busan), it was found to be common in the Kuroshio ecosystem. Its presence was occasional at the remaining two sites:Buan (Yellow Sea ecosystem) and Seogwipo (Kuroshio ecosystem). *A. eburneus*, introduced to the eastern Pacific from the northwest Atlantic Ocean, was found on buoys attached or the bottom of ships in two sites (Tongyeong and Geoje) with high temperature and salinity distributed in the Kuroshio ecosystem. The bay barnacle, *A. improvisus*, was found at four sites on a port structure, and molluscan shells attached in a relatively low salinity area (salinity : 8‰): two sites of Namhae (Yellow Sea ecosystem), Busan (Yellow Sea ecosystem) and Gangneung (Eastern Coast ecosystem). The other introduced barnacle species, *P. perforatus*, was mostly found at six sites: Busan and Pohang (Kuroshio ecosystem) and the remaining four sites (Eastern Coast ecosystem) where some of the important international shipping ports in Korea. It has been expanding its distribution with the increase of sea temperature and port facilities (Fig. 8).

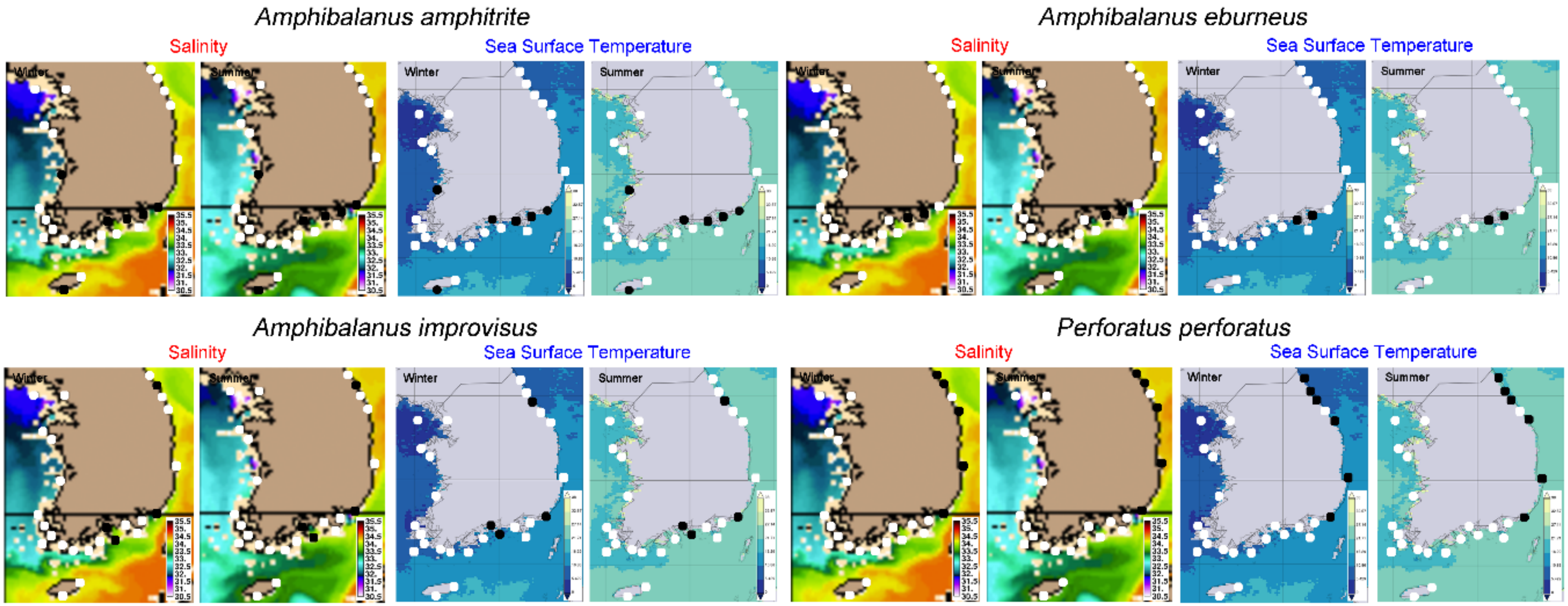

Fig. 8. Distribution of four introduced barnacles related to salinity and sea surface temperature.

Species Abundance in Relation to Different Marine Ecosystems

The non-metric multidimensional scaling (nMDS) ordination plots of the species abundance in relation to different marine ecosystems using Bray-Curtis similarity formed distinct clades. Between the Yellow Sea and Kuroshio ecosystems formed overlapping clusters, but the clusters of Eastern Coast ecosystem were distinct and clearly separated from other ecosystems (Fig. 9).

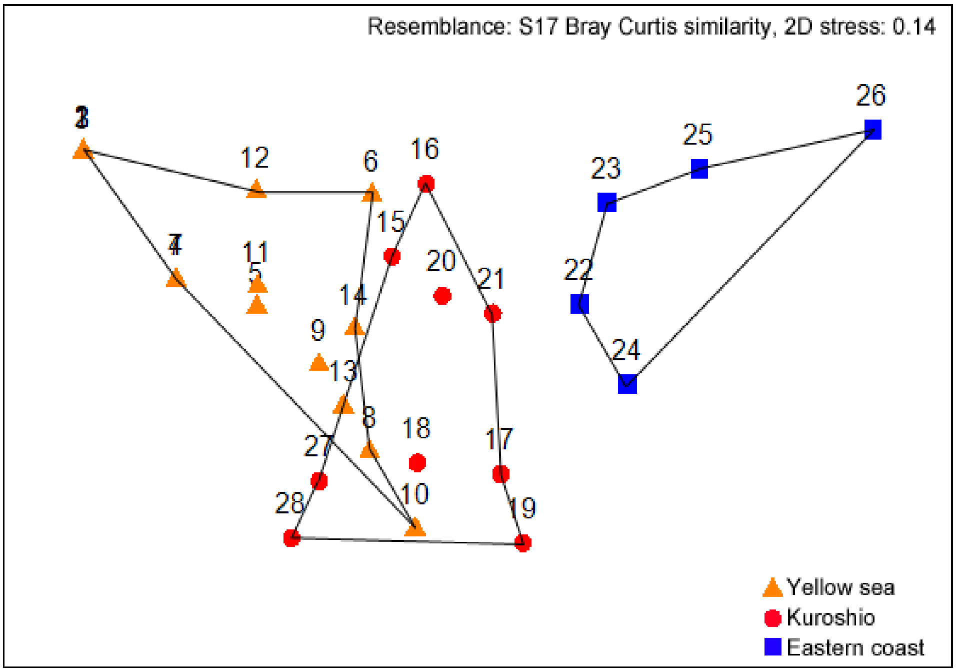

Fig. 9. Non-metric nMDS plots on the species compositions in all collecting sites from different marine ecosystems in Korea.

The patterns visible in the nMDS plots were statistically supported by the ANOSIM analysis, which showed significance differences in barnacle assemblages among the marine ecosystems ($R = 0.498$, $P < 0.001$). From the Similarity Percentage, one way analysis (SIMPER), which computed the average dissimilarity between pairs of species contribution on all sites from three different marine ecosystems, the average dissimilarities among oceanographic current ranged from 66.85% (Yellow Sea versus Kuroshio ecosystem) to 88.78% (Yellow sea versus Eastern coast ecosystem). *Fistulobalanus albicostatus*, *Balanus trigonus*, *Capitulum mitella*, *Tetraclita japonica*, and *Amphibalanus amphitrite* contributed a total of 41% differences between the Yellow Sea and Kuroshio ecosystems. *Eucasta dolfleini* and *Fistulobalanus knodakovi* are more abundant in the Kuroshio ecosystem and contribute to reduced abundance in the Yellow Sea ecosystem. By comparing the Yellow Sea and Eastern Coast ecosystem, *Fistulobalanus albicostatus, Perforatus perforatus*, *Balanus rostratus*, *Chthamalus challengeri*, and *Balanus trigonus* contributed a total of 66% differences.

From the cluster analysis, the similarity of the barnacle assemblages between the Yellow Sea and Kuroshio mingled together. For example, three species, *F. albicostatus, B. trigonus* and *C. mitella*, with higher percentage, determining the differences in the species composition between two marine ecosystems, were found on both Gwanmae Island, influenced by the Yellow Sea ecosystem and on Hansan Island, influenced by the Kuroshio ecosystem. Results support that these two ecosystems have similar species compositions. However, the Eastern coast ecosystem had < 20% similarity from other ecosystems and clearly formed a distinct clade. This means the composition of barnacle species in the eastern coast ecosystem are strongly different (Fig. 10).

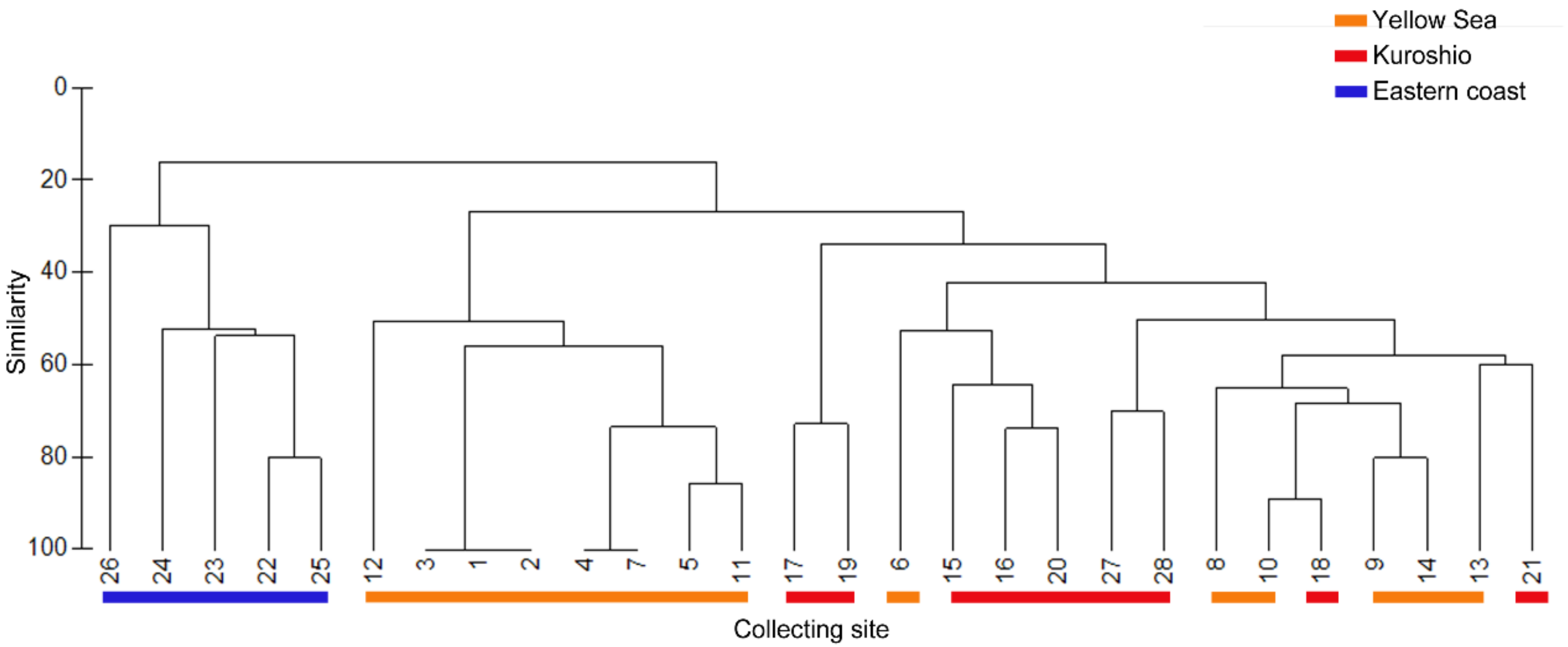

Fig. 10. Cluster dendogram showing the similarity based on the species compositions on all collecting sites from different marine ecosystems.

Systematic Accounts

Based on the shell and opercular plates morphology, total 21 species (14 genera) of barnacles from Korea were identified. The information on distribution, depth and literature records for investigated barnacles, as well as detailed description for four introduced barnacles are provided.

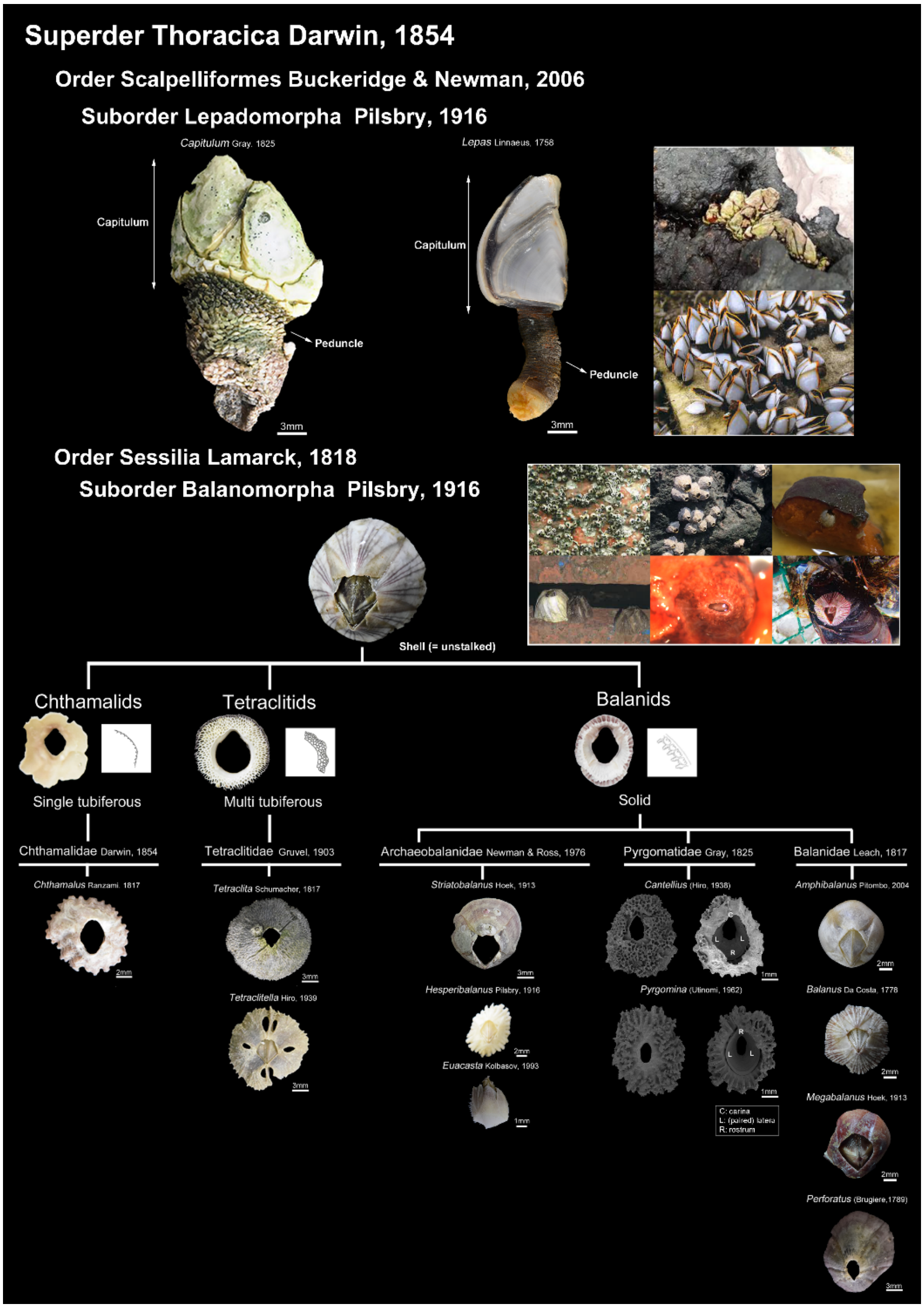

Fig. 11. Morphological classification of collected barnacles based on the shell structure. The ridged goose barnacle, *Lepas anserifera* Linnaeus, 1767, was used only for molecular phylogenetic analysis as their floating habitat.

Superorder Thoracica Darwin, 1854

Order Scalpelliformes Buckeridge & Newman, 2006

Family Pollicipedidae Leach, 1817

Genus *Capitulum* Gray, 1825

Capitulum mitella (Linnaeus, 1758)

Lepas mitella Linnaeus, 1758:668.

Pollicipes mitella.—Darwin, 1851:316, pl. 7, fig. 3.—Nilsson-Cantell, 1921:163, pl. 3, figs. 7, 8.—Utimomi, 1970:340.—Rosell, 1972:148.—Zevina, 1978:1002.—Dong *et al*., 1980:124.

Mitella mitella.—Pilsbry, 1907:6.—Krüger, 1911:8, pl. 2, figs. 10, 11.—Annandale, 1916:128, pl. 12, fig. 1.—Broch, 1922:258, fig. 20; 1931:27.—Hiro, 1932b:546; 1937a:23, fig. 16; 1939 b:202.—Withers, 1953:102.—Dong & Mao, 1956:287, fig. 2.—Tarasov & Zevina, 1957:121, fig. 33.—Shen *et al*., 1962:59.—Zevina & Tarasov, 1963:77.—Gordon, 1970:44, fig. 14.

Capitulum mitella.—Foster, 1980:209.—Liu & Ren, 2007:218, fig. 92.

Previous records in Korea. In clear waters of all coasts of Korea, except for Gyeonggi-do (Kim, 1998).

Materials Examined. 8 specimens (Seomanghang, Jindo-gun); 5 specimens (Hyeol Island, Jodomyeon, Jindo-gun; 4 specimens (Gwanmae Island, Jodomyeon, Jindo-gun); 3 speciemens (Geomun Island; Nam-myeon; Yeosu-si); 2 specimens (Ando beach; Nam-myeon; Yeosu-si); 5 specimens (Jikpo beach; Nam-myeon; Yeosu-si); 12 spcimens (Sangju beach, Sangju-myeon, Namhae-gun); 8 specimens (Sejon Island, Sangju-myeon, Namhae-gun); 3 specimens (Yangali, Sangju-myeon, Namhae-gun); 5 specimens (Hansan Island, Hansan-myeon, Tongyeong-si); numerous specimens (Hong Island, Hansan-myeon, Tongyeong-si); 7 specimens (Haeundae-gu, Busan); 2 specimens (Guryongpo-eup, Pohang); numerous specimens (Beopwhan-dong, Seogwipo-si, Jeju); 3 specimens (Bomok-dong, Seogwipo-si, Jeju); 4

spcimens (Seogwi-dong, Seogwipo-si, Jeju); nemerous specimens (Udo Island, Jeju).

Diagnosis. *Capitulum* roughly triangular, with 8 plates, base with more than 18 smaller plates. All plates yellow, longer than wide, with distinct growth lines. Peduncle covered with numerous fine scales (Fig. 12). Maxilla globular; mandibulatory palp elongated; labrum with minute denticles on each side; mandibles with 4 teeth; small spinules on above forth tooth; maxillule with enlarged uppermost spine, slightly notched (Fig. 13).

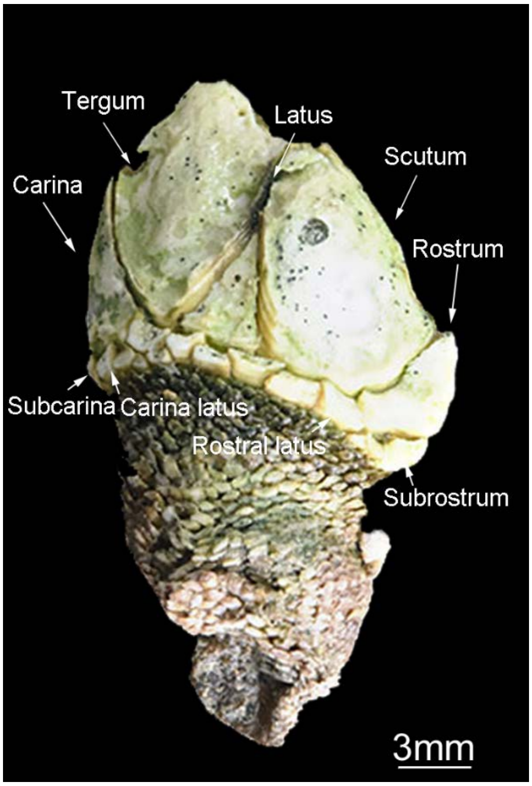

Fig. 12. *Capitulum mitella* (Linnaeus, 1758), side view.

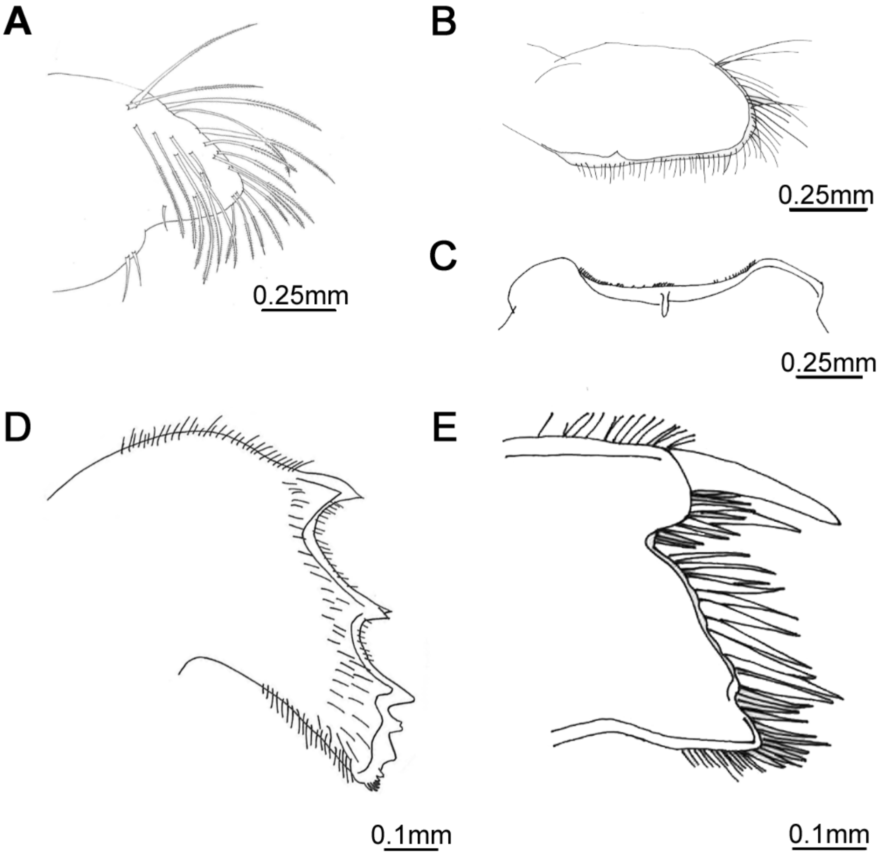

Fig. 13. Mouth parts of *Capitulum mitella* (Linnaeus, 1758). A, Maxilla; B, Mandibulatory palp; C, Labrum; D, Mandible; E, Maxillule.

Distribution. Indo-Pacific Region (Including Japan, Korea, China, Taiwan) (Fig. 14).

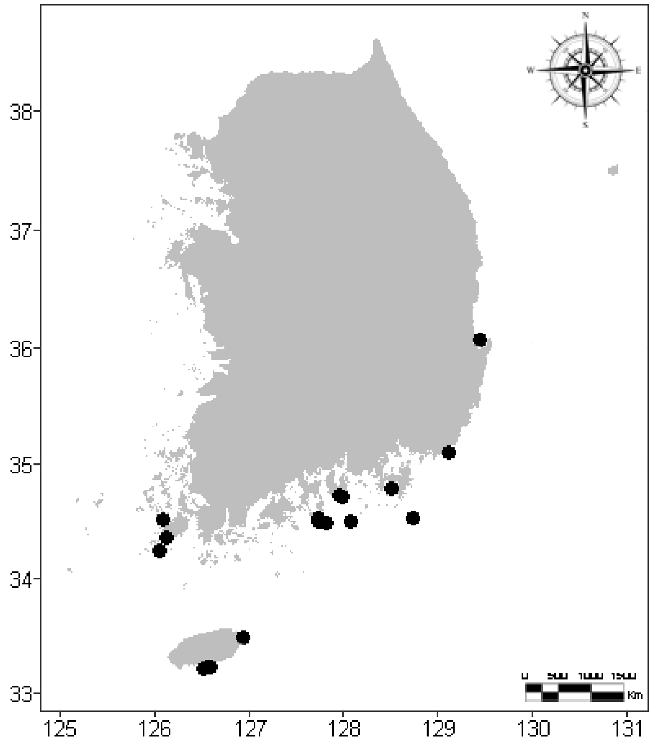

Fig. 14. Distribution of *Capitulum mitella* (Linnaeus, 1758) in Korea.

Remarks. *Capitulum mitella* is a common barnacle in Indo-Pacific regions. This species lives rocky shores in the mid-littoral zone of almost all coast of Korea. They are rare on the western coast influenced by freshwater and the eastern coast. In some countries (Japan, China, etc.), it is sold as food.

Order Sessilia Lamarck, 1818

Family Chthamalidae Darwin, 1854

Genus *Chthamalus* Ranzani, 1817

Chthamalus challengeri Hoek, 1883

Chthamalus challengeri Hoek, 1883:165, pl. 3, figs. 35-38.—Pilsbry, 1916:307, pl. 72, figs. 1-4a.—Nilsson-Cantell, 1921:279, figs. 51c, d; 1927:781, pl. 1, fig. 13; 1932:8.—Hiro, 1932b:546, figs. 1, 2.—Utinomi, 1949:21; 1962:215; 1970:345.—Tarasov & Zevina, 1957:256, fig. 103.—Zevina & Tarasov, 1963:79, fig. 2.—Utinomi, 1970:345.—Newman & Ross, 1976:41.—Yamaguchi, 1979:39, fig. 2.—Kim & Kim, 1980:167, pl. 1, figs. 7-11.—Southward & Newman, 2003:803, fig. 6.

Chthamalus challengeri forma *krakatauensis* Broch, 1931:54.

Chthamalus pilsbryi.—Kim, 1978:14.—Kim *et al*., 1979:109.

Previous records in Korea. On all coasts excluding northern part of Korea coast (Kim, 1998).

Materials Examined. numerous specimens (Sinjin Island, Geunheung-myeon, Taean-gun); numerous specimens (Ong Island, Geunheung-myeon, Taean-gun); numerous specimens (Jeongjok Island, Geunheung-myeon, Taean-gun); numerous specimens (Anmyeon Island, Taean-gun); 18 specimens (Chaeseokgang, Byeonsan-myeon, Buan); 22 specimens (Jeokbyeokgang, Byeonsan-myeon, Buan); numerous specimens (Aphae-eup, Sinan-gun); 8 specimens (Mokke, Uidoli, Docho-myeon, Sinan-gun); 4 specimens (Seongchon beach, Uidoli, Docho-myeon, Sinan-gun); 4 specimens (Seomanghang, Jindo-gun); numerous specimens (Hyeol Island, Jodomyeon, Jindo-gun); numerous specimens (Gwanmae Island, Jodomyeon, Jindo-gun); nemerous specimens (Soan-myeon, Wando-gun); 7 specimens (Geomun Island, Samsan-myeon, Yeosu-si); 4 spcimens (Geomun Island; Nam-myeon; Yeosu-si); 3 specimens (Ando beach; Nam-myeon; Yeosu-si); 2 specimens (Jikpo beach; Nam-myeon; Yeosu-si); 13 specimens (Wolgokli, Seolcheon-myeon, Namhae-gun); 15 specimens (Geumeumli, Seolcheon-myeon, Namhae-gun); numerous specimens (Pungwhali, Sanyang-eup, Tongyeong-si); numerous specimens (Yeonwhali, Sanyang-eup, Tongyeong-si); numerous specimens (Hansan Island, Hansan-myeon, Tongyeong-si); numerous specimens (Hong Island, Hansan-myeon, Tongyeong-si); numerous specimens (Haeundae-gu, Busan); 21 specimens (Guryongpo-eup, Pohang); numerous specimens (Changhae-ro, Jumunjin-eup, Gangneung-si); numerous specimens (Jumunli, Jumunjin-eup, Gangneung-si); numerous specimens (Beopwhan-dong, Seogwipo-si, Jeju); numerous specimens (Bomok-dong, Seogwipo-si, Jeju); numerous spcimens (Seogwi-dong, Seogwipo-si, Jeju); nemerous specimens (Udo Island, Jeju).

Diagnosis. Parietes white to grey, with 4-6 plates. Scutum triangular; tergum higher than wide (Fig. 15). Maxilla bilobed; mandibulatory palp slightly concave, with numerous setae on margin; labrum with small denticles scattered on each crest; mandible with 4 teeth, lower margin with small spines; maxillule notched, with 7-15 spines (Fig. 16).

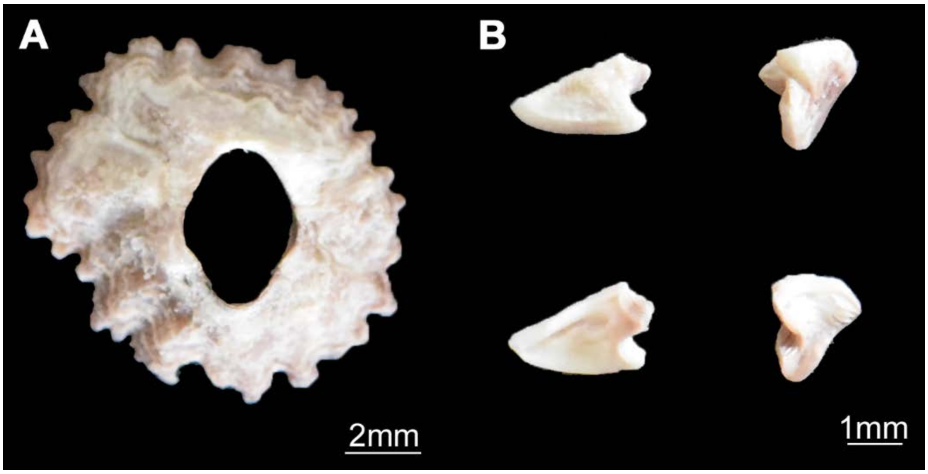

Fig. 15. *Chthamalus challengeri* Hoek, 1883. A, Pariests, top view; B, External and internal view of scutum and tergum.

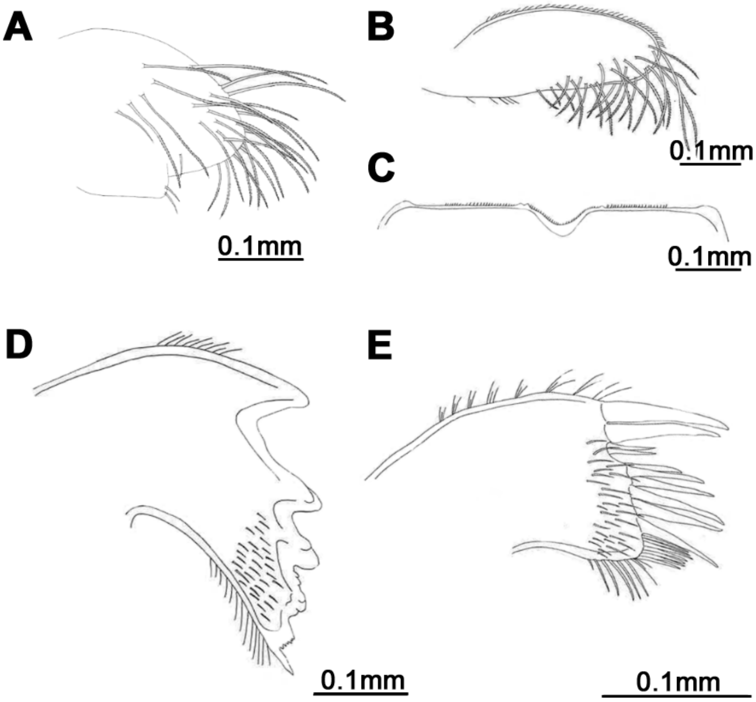

Fig. 16. Mouth parts of *Chthamalus challengeri* Hoek, 1883. A, Maxilla; B, Mandibulatory palp; C, Labrum; D, Mandible; E, Maxillule.

Distribution. Indo-West Pacific Region (Including Red Sea, Japan, Korea, N. China, Taiwan) (Fig. 17).

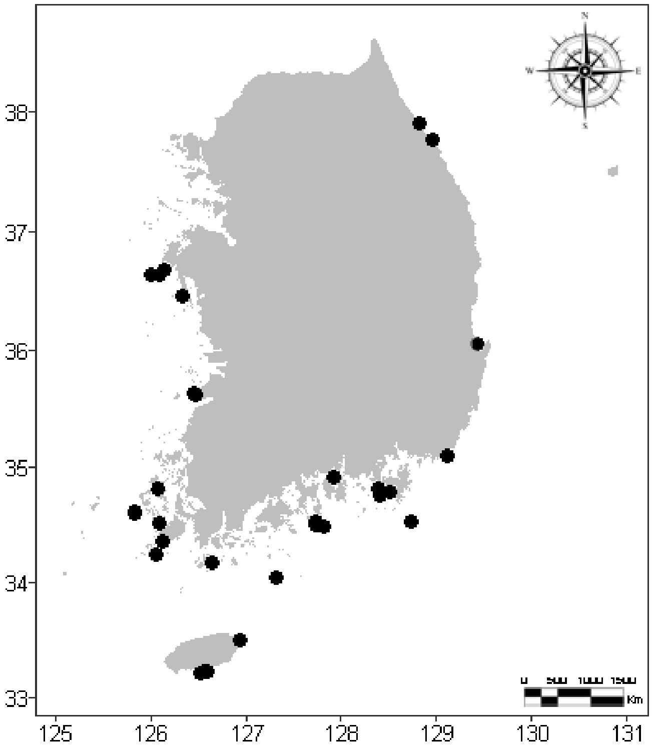

Fig. 17. Distribution of *Chthamalus challengeri* Hoek, 1883 in Korea.

Remarks. *Chthamalus challengeri* occurs on nearly all coasts of Korea. It distributes from mid littoral to supralittoral zones of the intertidal zone. The shell form depends on population density of colony. The orifice is less than basal margin, but larger in overcrowding during growth (Fig. 18).

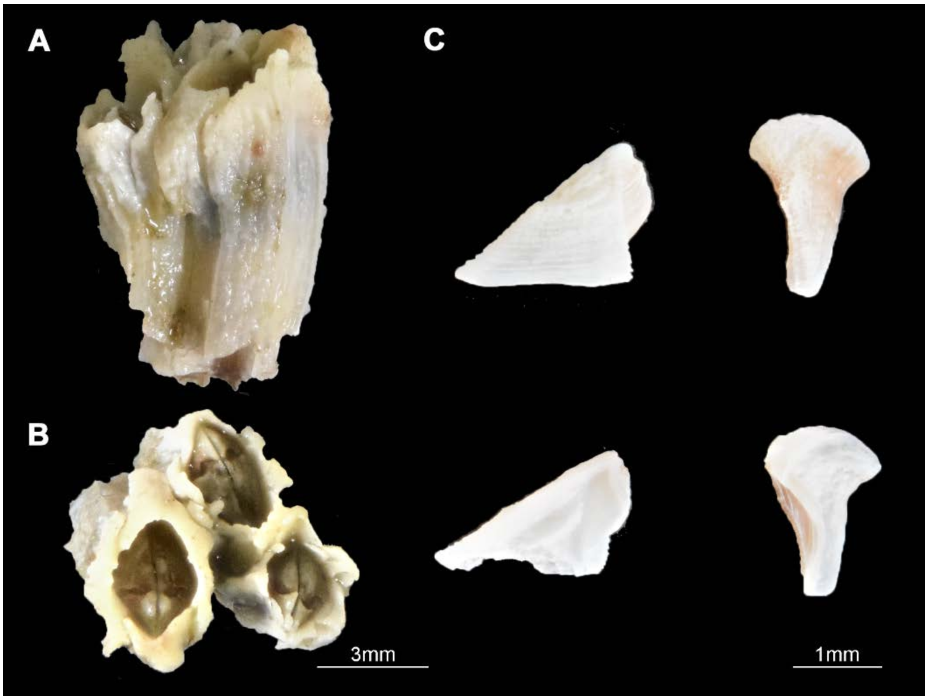

Fig. 18. *Chthamalus challengeri* Hoek, 1883 from Anmyeon Island, Taean-gun, showing etiolated growth through overcrowding. A, Pariests, lateral view; B, Pariests, top view; C, External and internal view of scutum and tergum.

Family Tetraclitidae Gruvel, 1903

Genus Tetraclitella Hiro, 1939

Tetraclitella chinensis (Nilsson-Cantell, 1921)

Tetraclita purpurascent chinensis Nilssom-Cantell, 1921:359, text-figs. 81, 82, pl. 3, fig. 12.—Hiro, 1937b:469; 1939b:273.

Tetraclita purpurascens nipponensis Hiro, 1931:155, fig. 11, pl. 14, fig. 3-3d; 1937b, 469.

Tetraclita (*Tetraclitella*) *chinensis*.—Utinomi, 1949:36; 1954:23; 1962, pl. 231.

Tetraclitella chinensis.—Utinomi, 1970:347, pl. 8, fig. 5.—Ross, 1971:217.—Newman & Ross, 1976:46.—Ren & Liu, 1979:347, pl. 3, figs. 5-9.—Foster, 1980:209.—Kim & Kim, 1980:168, pl. 2, figs. 5-10.

Previous records in Korea. Gyeongsangbuk-do; Jeju-do; Jeollanam-do (Kim, 1998).

Materials Examined. numerous specimens (Beopwhan-dong, Seogwipo-si, Jeju).

Diagnosis. Parietes flat, with 2 major forms (hollowed and multicostate form) (Fig. 19). Maxilla bilobed; mandibulatory palp elongated; labrum notched; mandible with 5 teeth, second and third teeth bidentated; maxillule notched, with 7-11 spines on cutting edge.

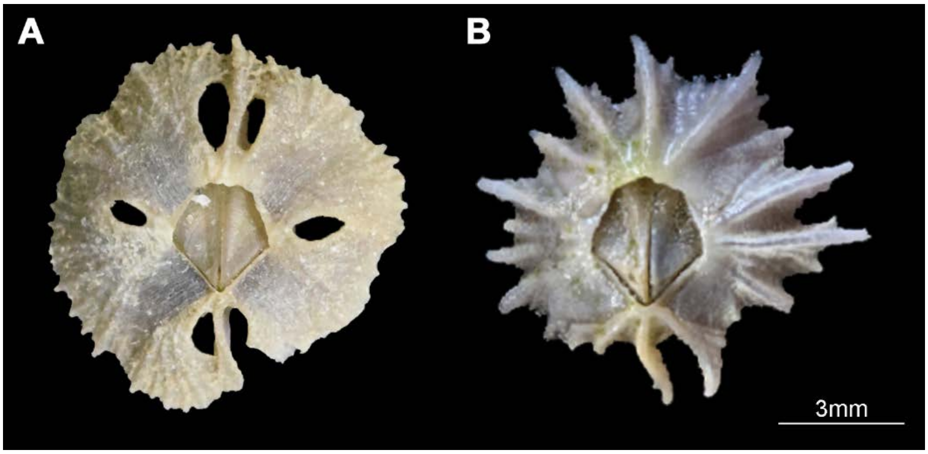

Fig. 19. *Tetraclitella chinensis* (Nilsson-Cantell, 1921). A, Hollowed form, pariests, top view; B, Multicostate form, pariets, top view.

Distribution. Indo-Pacific Region (Including Hongkong, Japan, Korea, N. China, Taiwan) (Fig. 20).

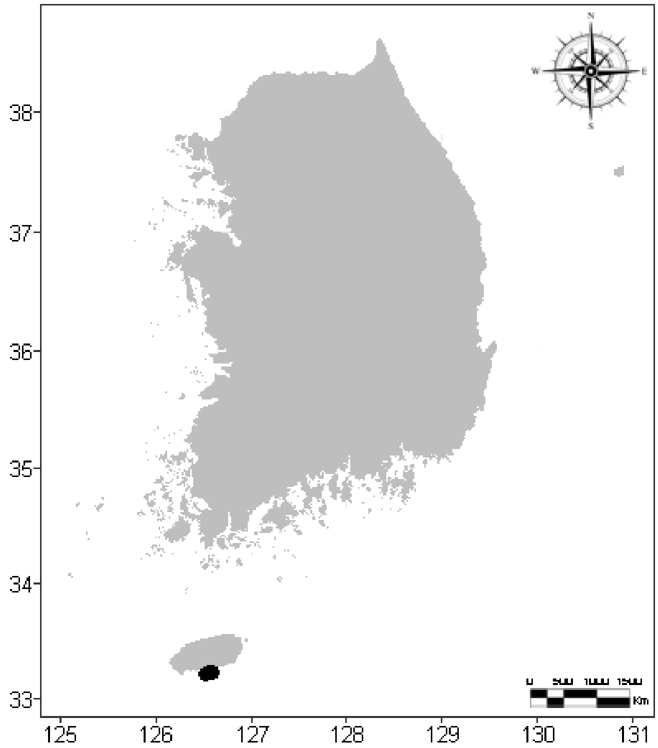

Fig. 20. Distribution of *Tetraclitella chinensis* (Nilsson-Cantell, 1921) in Korea.

Remarks. *Tetraclitella chinensis* is characterized by six large, lunnule-like hollows on plates. Specimens are occasionally found that characters of both *T. chinensis* and *T. multicostata* have fewer than six hollows. In contrast, the shell of *T. multicostata* (Nilsson-Cantell, 1930) has no such hollows. This species is re-described to include the morphological variation in shell form (hollowed and multicostate), and the two nominal species are formally synonymized by the author. Detailed information of remarks is suggested in Chapter 3: Taxonomic revision of two acorn barnacles.

Genus *Tetraclita* Schumacher, 1817

Tetraclita japonica (Pilsbry, 1916)

Tetraclita japonica Pilsbry, 1916:252, pl. 58, figs. 1-3a.—Nilsson-Cantell, 1927: 786.—Hiro, 1932b:551; 1937b:469; 1939b:213.—Tarasov & Zevina, 1957:236, fig. 94.—Newman & Ross, 1976:48.—Yamaguchi, 1979:42, figs. 2,3.—Kim & Kim, 1980:170, pl. 2, fig. 108.

Tetraclita japonica.—Ren & Liu, 1979:339, pl. 1, figs. 1-11.

Previous records in Korea. Gangwon-do; Gyeongsangbuk-do; Gyeongsangnam-do; Jeju-do; Jeollanam-do; Jeollabuk-do; Chungcheongnam-do (Kim, 1998).

Materials Examined. 4 specimens (Chaeseokgang, Byeonsan-myeon, Buan); 2 specimens (Jeokbyeokgang, Byeonsan-myeon, Buan); 7 specimens (Seomanghang, Jindo-gun); numerous specimens (Hyeol Island, Jodomyeon, Jindo-gun); numerous specimens (Gwanmae Island, Jodomyeon, Jindo-gun); 8 specimens (Geomun Island, Samsan-myeon, Yeosu-si); 5 spcimens (Geomun Island; Nam-myeon; Yeosu-si); numerous specimens (Hansan Island, Hansan-myeon, Tongyeong-si); numerous specimens (Hong Island, Hansan-myeon, Tongyeong-si); 25 specimens (Irun-myeon, Geoje); numerous specimens (Haeundae-gu, Busan); 21 specimens (Guryongpo-eup, Pohang); numerous specimens (Beopwhan-dong, Seogwipo-si, Jeju); numerous specimens (Bomok-dong, Seogwipo-si, Jeju); numerous spcimens (Seogwi-dong, Seogwipo-si, Jeju); nemerous specimens (Udo Island, Jeju).

Diagnosis. Parietes brown, dark gray, or blueish gray, with 4 plates; orifice small. Scutum triangular, occludent margin with distinct teeth, adductor muscle pit deep and large; tergum elongated, basi scutal angel rounded (Fig. 21). Cirrus III with multicuspidate setae (Fig. 22); cirri IV-VI bearing 3 pairs of setae. Mandible with 4 teeth, second to forth tooth with extra denticle, lower margin consisting of 15 spines; maxillule notched, broad; labrum slightly notched, with

1-2 teeth (Fig. 23).

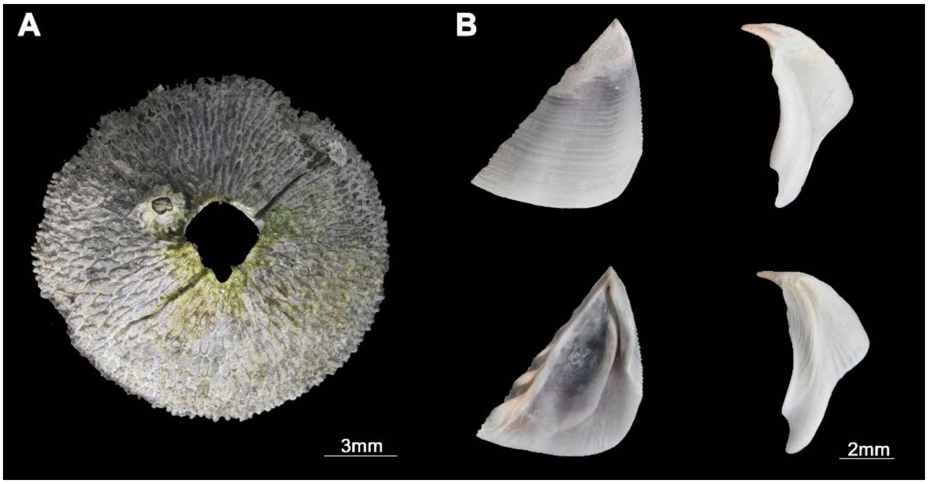

Fig. 21. *Tetraclita japonica* (Pilsbry, 1916). A, Pariests, top view; B, External and internal view of scutum and tergum.

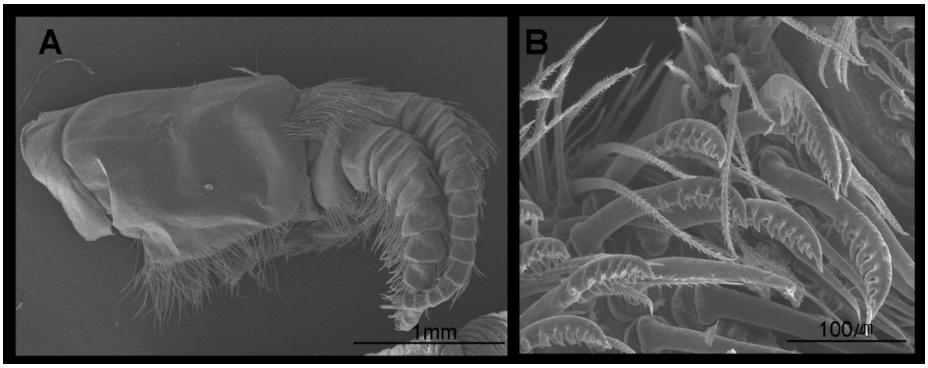

Fig. 22. Cirrus III of *Tetraclita japonica* (Pilsbry, 1916). A, Scanning electron microscopy on cirrus III; B, Cuspidate setae on cirrus III. Modified from Chan *et al*., 2007b.

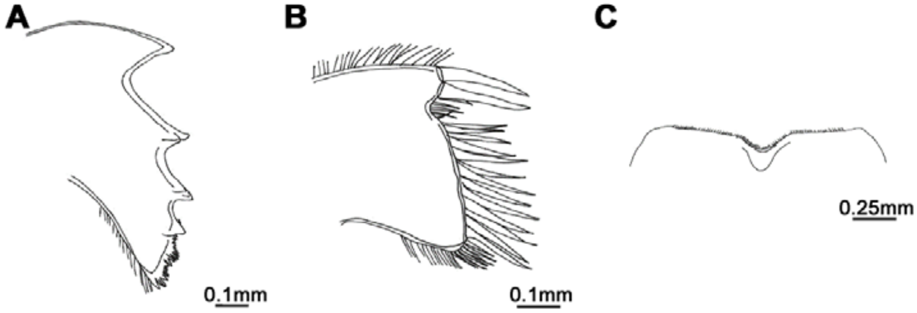

Fig. 23. Mouth parts of *Tetraclita japonica* (Pilsbry, 1916). A, Mandible; B. Maxillule; C. Labrum.

Distribution. Taiwan, Hongkong, Japan, China, Taiwan, Korea (Fig. 24).

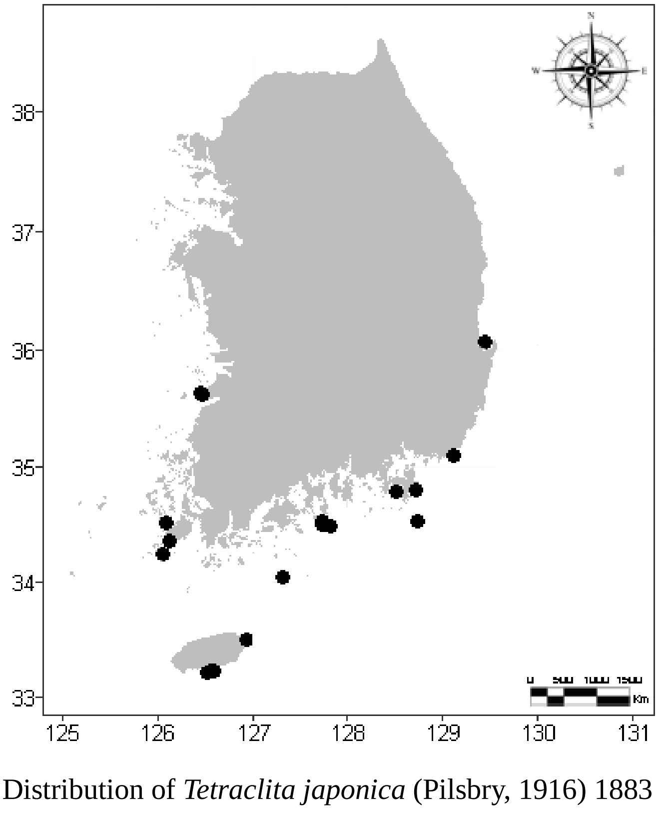

Fig. 24. Distribution of *Tetraclita japonica* (Pilsbry, 1916) 1883 in Korea.

Remarks. The distribution of *Tetraclita japonica* relates to high salinity in warm waters. It is most common along the southern coast of Korea and attached to exposed rocks in the mid-intertidal and lower littoral zone. It is rare on the eastern coast and has been started to expand habitats into the western coast due to climate change. *T. japonica* exhibits phenotypic plasticity in cirral length and morphological variation in scutum and tergum in response to the degree of wave exposure and habitats (Fig. 25). This species is considered as an indicator species for detecting the ecological effects of a climate-changing. Monitoring abundance and recruitment of warm-water barnacle species, *T. japonica*, is necessary.

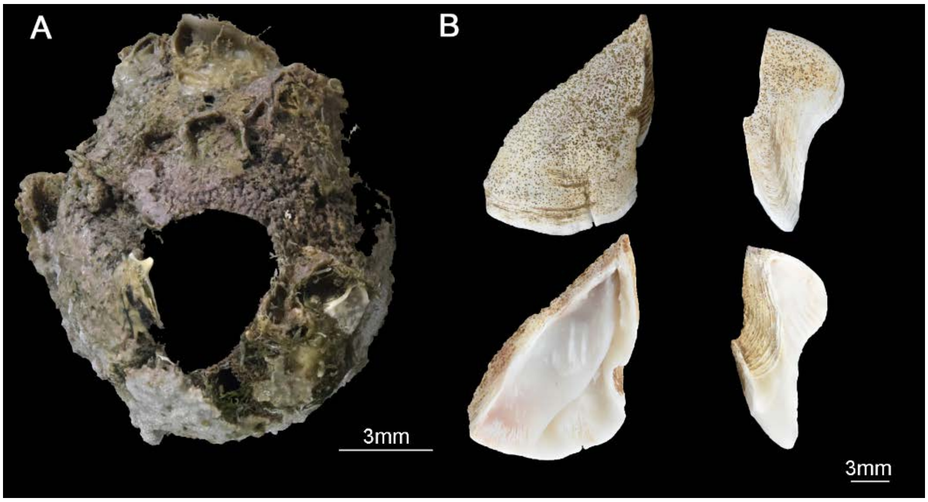

Fig. 25. *Tetraclita japonica* (Pilsbry, 1916) from Seomanghang, Jindo-gun, showing phenotypic plasticity in morphology of opercular plates. A, Pariests; B, External and internal view of scutum and tergum.

Family Archaeobalanidae Newman & Ross, 1976

Genus *Striatobalanus* Hoek, 1913

***Striatobalanus amaryllis* (Darwin, 1854)**

Balanus amaryllis Darwin, 1854:279, pl. 7, fig. 6a-6c.—Hoek, 1883:153, pl. 7, figs. 4, 5; 1913:179, pl. 15, figs. 17-21, pl. 16, figs. 1-4.

Balanus (*Chirona*) *amaryllis*.—Pilsbry, 1916:217.—Hiro, 1936:624; 1939a: 243.— Utinomi, 1962:216.—Ren & Liu, 1978:159, fig. 21, pl. 7, figs. 1-5.

Balanus (*Chirona*) *amaryllis* forma *euamaryllis* Broch, 1922:321.

Balanus (*Chirona*) *amaryllis laevis* Broch, 1931:67.

Chirona (*Striatobalanus*) *amaryllis*.—Newman & Ross, 1976:50.—Foster, 1980:209.—Kim & Kim, 1980:171, pl. 3, figs. 9-15.—Lewis, 1981:6, figs. 5b, 6d, pl. 2a, b.

Striatobalanus amaryllis.—Chan, Prabowo & Lee, 2009.

Previous records in Korea. Gyeonggi-do; Gyeongsangnam-do; Jeollabuk-do (Kim, 1998).

Materials Examined. 2 specimens (Chaeseokgang, Byeonsan-myeon, Buan); 4 specimen (Jeokbyeokgang, Byeonsan-myeon, Buan); 3 specimens (Seomanghang, Jindo-gun).

Diagnosis. Parietes solid, surface with pink. Scutum triangular, basal margin strongly convex; tergum longer than wide, spur long, spur furrow deep (Fig. 26). Mandible with 5 teeth, forth and fifth teeth small; maxillule slightly notched, with pairs of spines; labrum notched, with 3-4small teeth on each crest (Fig. 27).

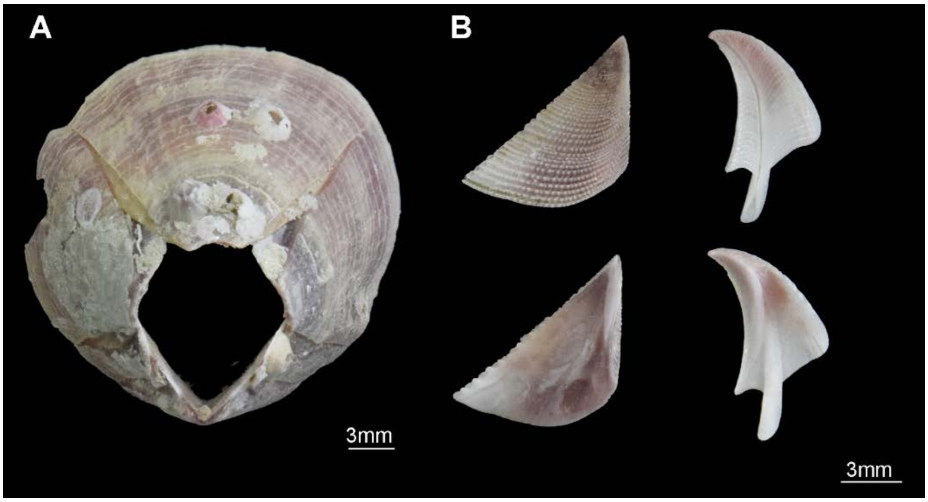

Fig. 26. *Striatobalanus amaryllis* (Darwin, 1854). A, Pariests, top view; B, External and internal view of scutum and tergum.

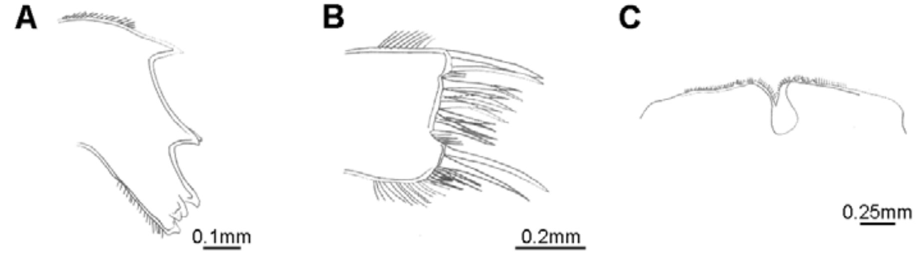

Fig. 27. Mouth parts of *Striatobalanus amaryllis* (Darwin, 1854). A, Mandible; B, Maxillule; C, Labrum.

Distribution. East Africa to Philippines, Indo-West Pacific, Northeast Australia and Korea (Fig. 28).

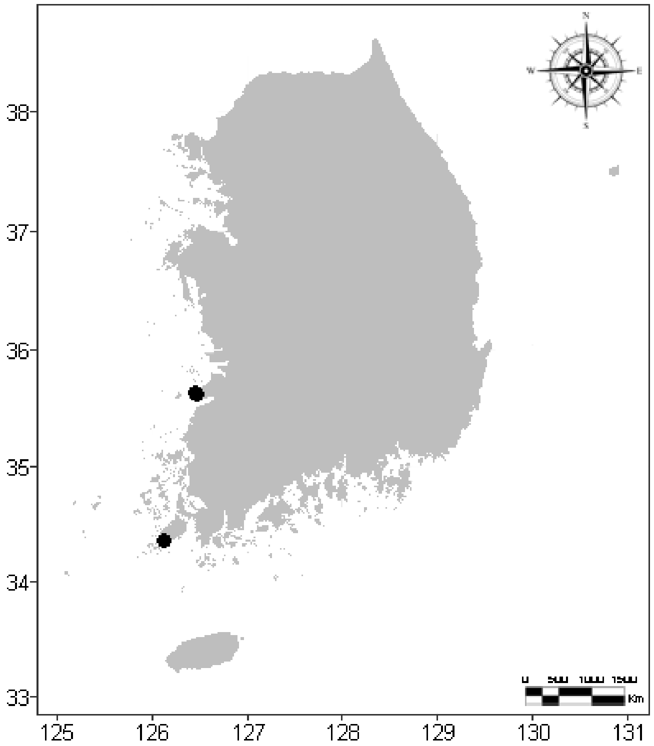

Fig. 28. Distribution of *Striatobalanus amaryllis* (Darwin, 1854) in Korea.

Remarks. Darwin (1854) described *Balanus amaryllis* and the genus *Striatobalanus* was later established by Liu and Ren (2007) for this species. The present specimens agree with the description and illustrations of *Balanus amaryllis* (*e.g.*, Darwin, 1854, p. 279, pl. 7, fig. 6a-6c; Hoek, 1883, p. 153, pl. 7, figs. 4, 5; 1913, p. 179, pl. 15, figs. 17-21, pl. 16, figs. 1-4).

Striatobalanus amaryllis is found in warm clear waters at shallow depths (up to 10m).

Genus *Hesperibalanus* Pilsbry, 1916

Hesperibalanus hesperius hesperius (Pilsbry, 1916)

Balanus (*Hesperibalanus*) *hesperius* Pilsbry, 1916:193, pl. 49, figs. 1-1d, 7-7b.

Balanus (*Hesperibalanus*) *hesperius* forma *laevidomus* Pilsbry, 1916:196, pl. 49, figs. 2-5, pl. 50.

Balanus (*Hesperibalanus*) *hesperius nipponensis* Pilsbry, 1916:199, pl. 49, fig. 6.

Balanus (*Solidobalanus*) *hesperius*.—Henry & McLaughlin, 1967:47.—Utinomi, 1970:359.

Balanus (*Solidobalanus*) *hesperius nipponensis* Henry & McLaughlin, 1967:47.

Solidobalanus (*Hesperibalanus*) *hesperius nipponensis* Newman & Ross, 1976:51.

Solidobalanus (*Hesperibalanus*) *hesperius hesperius* Newman & Ross, 1976:51.—Kim & Kim, 1980:172, pl. 4, figs. 1-6.

Solidobalanus (*Hesperibalanus*) *hesperius alevidomus* Newman & Ross, 1976:51.

Solidobalanus (*Hesperibalanus*) *hesperius*.—Yamaguchi, 1977:187, text-fig. 22, pl. 27, figs. 1-18.

Previous records in Korea. Gangwon-do; Gyeongsangbuk-do (Kim, 1998).

Materials Examined. numerous specimens (Daejinhang fish market, Hyeonnae-myeon, Goseong-gun), on a gastropod shell.

Diagnosis. Pariets conical, surface with white. Scutum triangular, adductor ridge short, lateral muscle pit small; tergum with weak growth ridges, articular ridge well developed (Fig. 29). Mandible with 5 teeth, fifth tooth nearly fused with inferior angle; maxillule faint or without notch; labrum with 3 teeth on each crest (Fig. 30).

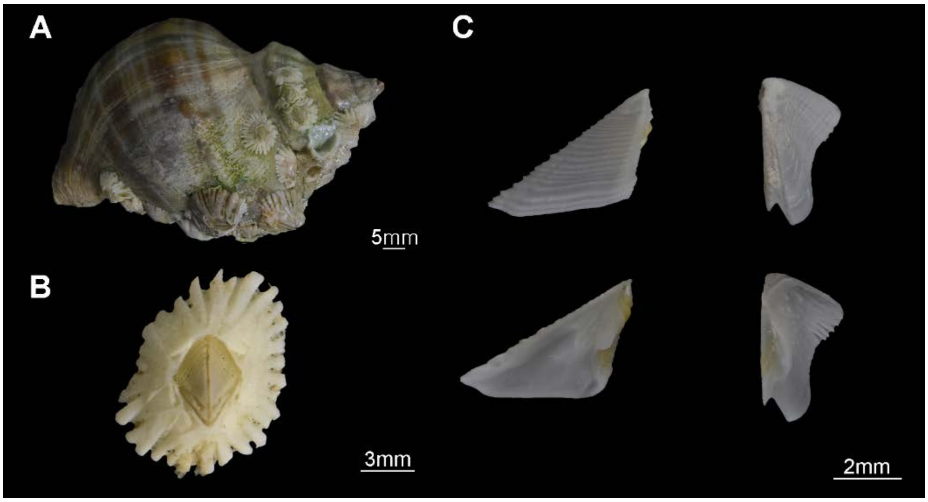

Fig. 29. *Hesperibalanus hesperius hesperius* (Pilsbry, 1916). A, Pariests on gastropod shells , top view; B, Pariests, top view; C, External and internal view of scutum and tergum.

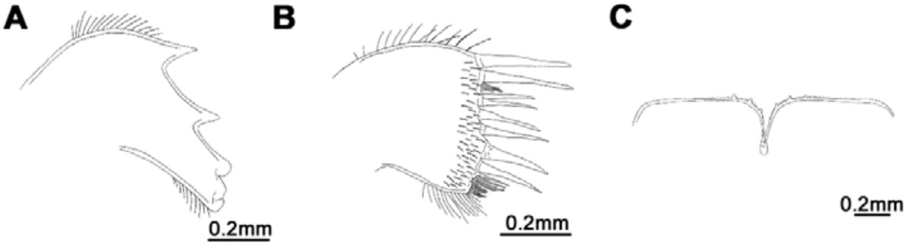

Fig. 30. Mouth parts of *Hesperibalanus hesperius hesperius* (Pilsbry, 1916). A, Mandible; B, Maxillule; C, Labrum.

Distribution. Alaska, Bering Sea, Japan, northwest coast of United States, and Korea (Fig. 31).

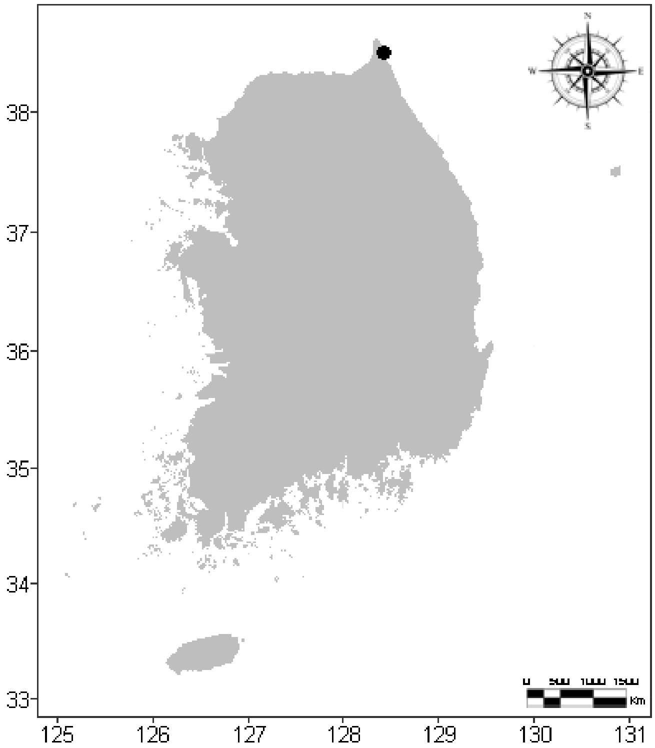

Fig. 31. Distribution of *Hesperibalanus hesperius hesperius* (Pilsbry, 1916) in Korea.

Remarks. Pilsbry (1916) described *Hesperibalanus* as a new subgenus of *Balanus*. The genus *Hesperibalanus* was recently upgraded to the genus level and there are 4 subspecies in *Hesperibalanus hesperius*. The present specimens agree with the description and illustrations of *Balanus* (*Hesperibalanus*) *hesperius* (*e.g.*, Pilsbry, 1916:193, pl. 49, figs. 1-1d, 7-7b).

All were found attaching to gastropod shells and hermit crab shells in the Eastern coast. As a cold-water species, this species cannot be found in the western and southern coasts in Korea.

Genus *Euacasta* Kolbasov, 1993

Euacasta dofleini (Kruger, 1911)

Acasta dofleini Kruger, 1911:56, pl. 4, fig. 39.—Pilsbry, 1916:247.—Broch, 1922:330, figs. 67, 68.—Utinomi, 1958:309.—Rosell, 1972:198, pl. 23, figs. 3, 4, pl. 25, figs. 1-8.—Newman & Ross, 1976:53.—Lewis, 1981:7, fig. 4d, pl. 2e, f.—Kim, 1998:205, pl. 19C, D, fig. 58.

Acasta aperta Hiro, 1931:151, fig. 7, pl. 12, fig. 2-2c.

Euacasta dofleini.—Kolbasov, 1993:409, fig. 8.

Previous records in Korea. Gangwon-do; Gyeongsangbuk-do; Gyeongsangnam-do (Kim, 1998).

Materials Examined. 3 spcimens (Cheongsan Island, Cheongsan-myeon, Wando-gun), in depths between 5-15m; 2 specimens (Geomun Island, Samsan-myeon, Yeosu-si), in depth 10m; 6 specimens (Sejon Island, Sangjuli, Sangju-myeon, Namhae-gun), in depths between 5-15m; 4 specimen (Haeundae-gu, Busan), in depths between 5-15m; 3 specimens (Guryongpo-eup, Pohang), in depths between 5-15m; 10 specimens (Beopwhan-dong, Seogwipo-si, Jeju), in depths between 10-15m; 4 specimens (Bomok-dong, Seogwipo-si, Jeju), in depths between 10-15m; 3 spcimens (Seogwi-dong, Seogwipo-si, Jeju), in depths between 10-15m; 5 specimens (Udo Island, Jeju), in depths between 10-15m.

Diagnosis. Parietes conical, white, with some pores, carinolateral with a row of longitudinal spines in the middle. Scutum triangular, basi-tergal rounded, articular ridge long; tergum without longitudinal setae, spur wider than long, spur furrow indistinct (Fig. 32). Cirri IV with teeth on posterior ramus (Fig. 33). Mandible with 5 teeth, second and third tooth bidentated, fifth tooth nearly fused with inferior angle; maxillule without notch; labrum with distinct notched, 0-2 small teeth on each crest (Fig. 34).

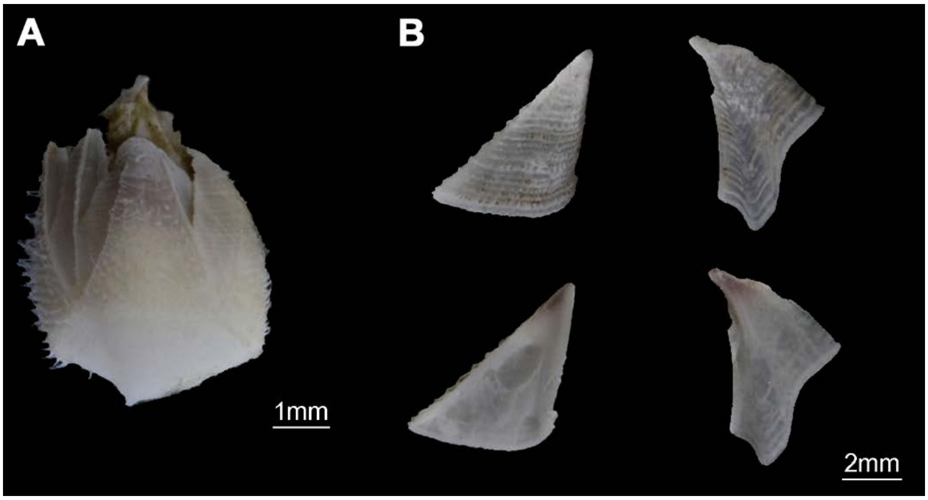

Fig. 32. *Euacasta dofleini* (Kruger, 1911). A, Pariests, lateral view; B, External and internal view of scutum and tergum.

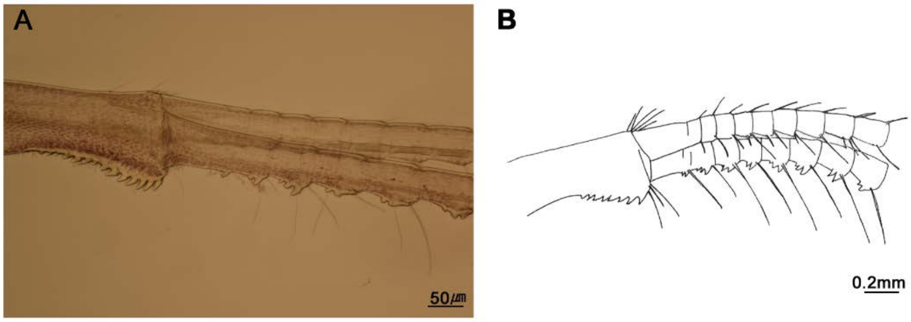

Fig. 33. Cirrus IV of *Euacasta dofleini* (Kruger, 1911). A, Light microscopy on cirrus IV, teeth on posterior ramus; B, Line drawing of teeth on cirrus IV.

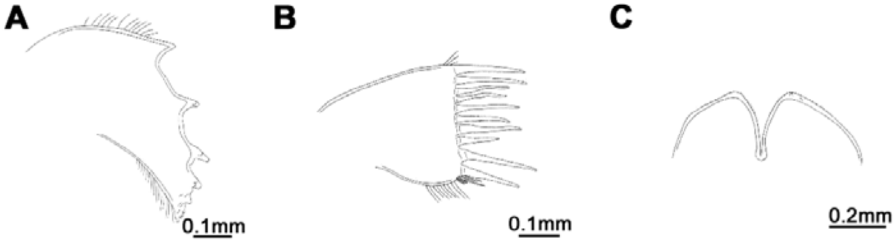

Fig. 34. Mouth parts of *Euacasta dofleini* (Kruger, 1911). A, Mandible; B, Maxillule; C, Labrum.

Distribution. Japan, Hong Kong, Singapore, the Philippines, Malay Archipelago and Korea (Fig. 35).

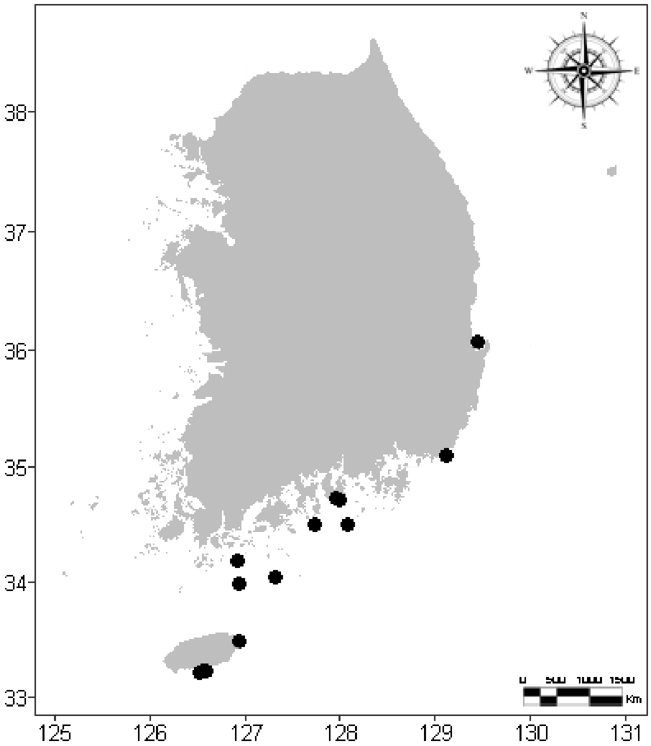

Fig. 35. Distribution of *Euacasta dofleini* (Kruger, 1911) in Korea.

Remarks. Kruger (1911) described the *Acasta dofleini* and Kolbasov (1993) divided into 5 genera: *Archiacasta*, *Neoacasta*, *Euacasta*, *Acasta*, and *Pectinoacasta*, distinguished from the original genus *Acasta* on the basis of morphological characteristics. *Euacasta dofleini* is characterized by some pores on the external surface of plates after removing curly hairs. This species is the most common sponge-inhabiting barnacles in Korea.

Family Pyrgomatidae Gray, 1825

Genus *Cantellius* Ross and Newman, 1973

Cantellius arcuatus (Hiro, 1938)

Creusia spinulosa forma *arcuata* Hiro, 1938:395, 403, fig. 3a-c, tab. II.—Kolosváry, 1947a:426-428; 1947b:364-367.—Utinomi, 1949a:69.

Cantellius arcuatum Ross & Newman, 1973:150, fig. 7d-e.—Newman & Ross, 1976:57.—Foster, 1980, tab. 5.

Cantellius arcuatus Galkin, 1986:1290.—Ogawa, 1992:app. tab.—Asami & Yamaguchi, 1997:14, figs. 1-2.—Ogawa, 1998:12, fig. 11.—Chan, Chen & Achituv, 2013:12.

Materials Examined. numerous specimens (Bomok-dong, Seogwipo-si, Jeju) in depths between 5-15m; numerous spcimens (Seogwi-dong, Seogwipo-si, Jeju), in depths between 5-15m; numerous specimens (Udo Island, Jeju), in depths between 5-15m.

Diagnosis. Base of shell with 25 longitudinal septa, shell conical with 4 plates (Fig. 36). Scutum triangular, without a rostral tooth, width equal to height; tergum thin, outer surface with distinct growth ridges, spur furrow shallow. Mandible with 5 teeth; maxillule without notch; labrum with distinct notched, 0-2 teeth on each crest (Fig. 37). Serrulate setae present on cirri I and II; cirrus III with sharp teeth on each segment of both rami. Penis longer than cirrus VI with acute basidorsal point.

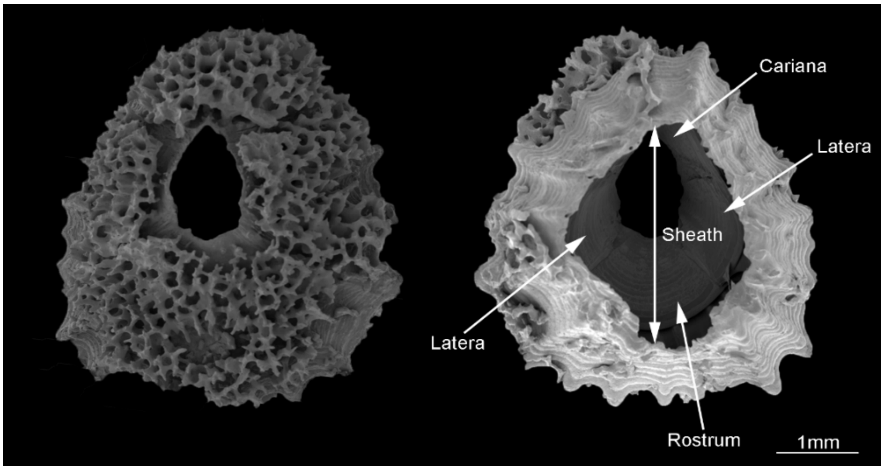

Fig. 36. *Cantellius arcuatus* (Hiro, 1938), top and internal view of pariets.

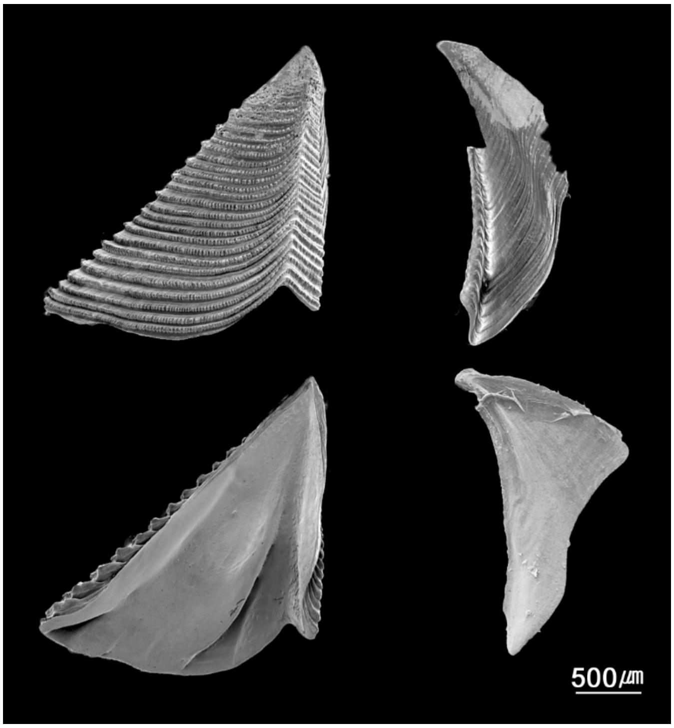

Fig. 37. *Cantellius arcuatus* (Hiro, 1938), external and internal view of scutum and tergum. Scale bar in μm.

Distribution. Hong Kong, Japan, Taiwan, Mauritius, Palau Island and Korea (Fig. 38).

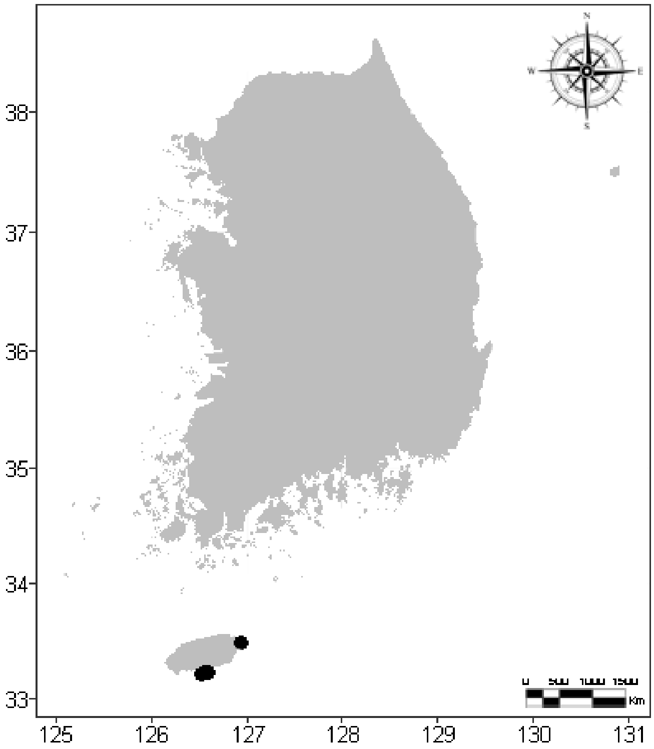

Fig. 38. Distribution of *Cantellius arcuatus* (Hiro, 1938) in Korea.

Remarks. *Cantellius arcuatus* Hiro, 1938 is the first report in the present study from Korean waters. The genus *Cantellius* have been recorded 26 species in the world. Of these, only two species have been reported in Korea from Jeju Island. This species can be distinguished from *C. euspinulosum* by the morphology of scutum. *C. arcuatus* has no rostral tooth in basal margin while *C. euspinulosum* has a rostral tooth. Detailed information is suggested in Chapter 2: Biodiversity and host specificity of coral-associated barnacles in Korea, with descriptions.

***Cantellius* sp.**

Materials Examined. numerous specimens (Bomok-dong, Seogwipo-si, Jeju), in depths between 5-15m; numerous specimens (Bomok-dong, Seogwipo-si, Jeju), in depths between 5-15m; numerous spcimens (Seogwi-dong, Seogwipo-si, Jeju), in depths between 5-15m; numerous specimens (Udo Island, Jeju), in depths between 5-15m.

Diagnosis. Base of shell with 29 longitudinal septa, shell conical with 4 plates (Fig. 39). Scutum triangular, with rostral tooth, width equal to height, occludent margin straight with strong teeth; tergum flat, thin, spur blunt (Figs. 40). Mandible with 5 teeth, fifth tooth fused with inferior angle; maxillule without notch; labrum with slightly notched, 3 teeth on each crest. Serrulate setae present on cirrus I to III; cirrus IV to VI long, slender. Penis annulated, longer than cirrus VI.

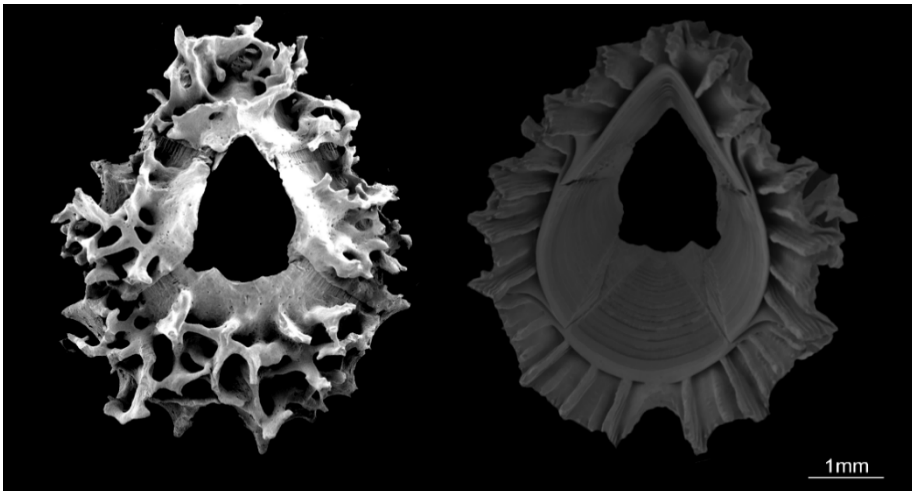

Fig. 39. *Cantellius* sp., top and internal view of pariets.

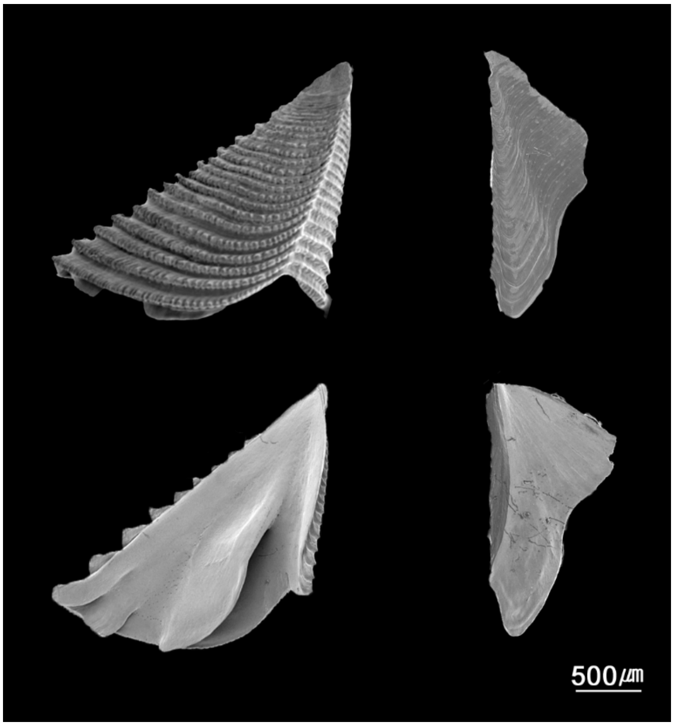

Fig. 40. *Cantellius* sp., external and internal view of scutum and tergum.

Distribution. Korea (Fig. 41).

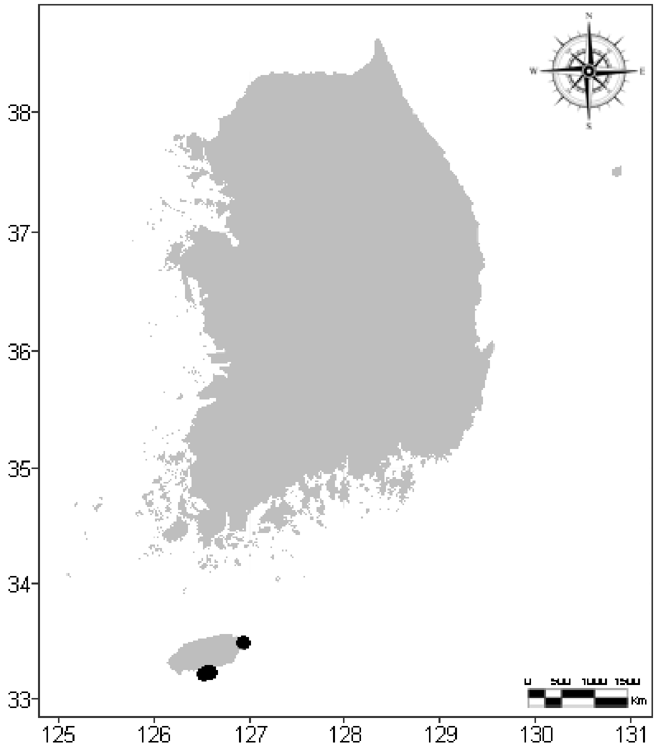

Fig. 41. Distribution of *Cantellius* sp. in Korea.

Remarks. This species is similar to *Cantellius euspinulosum* (Broch, 1931), but do not have an oval-shaped lateral depressor muscle on the basal margin of the scutum and tergal apex does not curve towards scutal margin. On the basis of these differences, this species is assigned to be a new species. Detailed information is suggested in Chapter 2: Biodiversity and host specificity of coral-associated barnacles in Korea, with descriptions.

Genus *Pyrgomina* Baluk & Radwanski, 1967

Pyrgomina oulastreae (Utinomi, 1962)

Pyrgoma oulastreae Utinomi, 1962:227, figs. 6-8.

Creusia spinulosa forma *quarta* Utinomi, 1949b:35.

Megatrema oulastreae.—Utinomi, 1967:229.—Kim, 1998:107, fig. 58.

Boscia oulastreae.—Ross & Newman, 1973:164.—Newman & Ross, 1976:59.—Foster, 1980:209.

Pyrgomina oulastreae.—Ross & Pitombo, 2002:61.

Previous records in Korea. Gyeongsangnam-do; Jeju-do. On the corals *Psammocora profundacella* Gardiner, 1898 and *Dichopsammia granulosa* Somg, 1994 (Kim, 1998).

Materials Examined. numerous specimens (Haeundae-gu, Busan), in depths between 5-15m; numerous specimens (Beophwan-dong, Seogwipo-si, Jeju), in depths between 5-15m; numerous specimens (Bomok-dong, Seogwipo-si, Jeju), in depths between 5-15m; numerous spcimens (Seogwi-dong, Seogwipo-si, Jeju), in depths between 5-15m; numerous specimens (Udo Island, Jeju), in depths between 5-15m.

Diagnosis. Base of shell with 30 longitudinal septa, shell low conical, with 2 plates (Fig. 42). Scutum triangular, wider than high, outer surface with distinct growth ridges; tergum flat, spur short, blunt. Mandible with 5 teeth, second and third teeth bidentated; maxillule notched; labrum with deep notched, 2-3 teeth on each crest (Fig. 43). Serrulate setae present on cirri I and II; cirrus III with 1-3 hooks and sharp teeth on each segment of both ramus. Penis long, with acute basidorsal point.

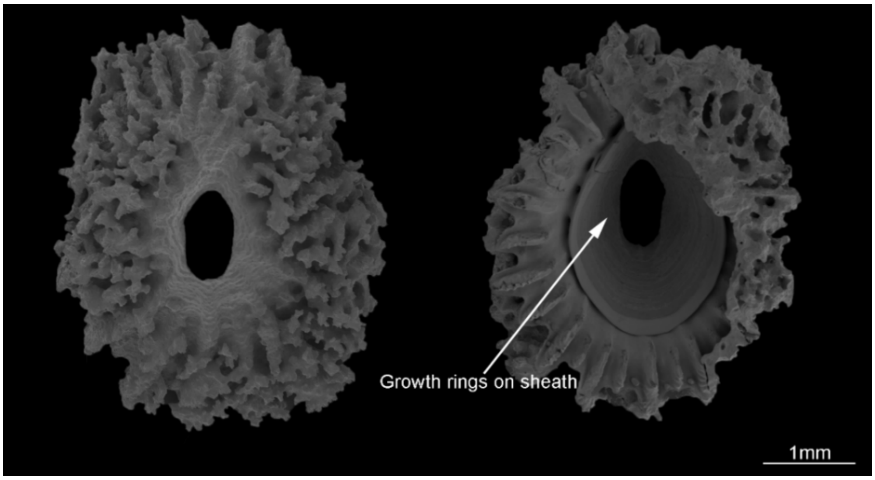

Fig. 42. *Pyrgomina oulastreae* (Utinomi, 1962), top and internal view of pariets.

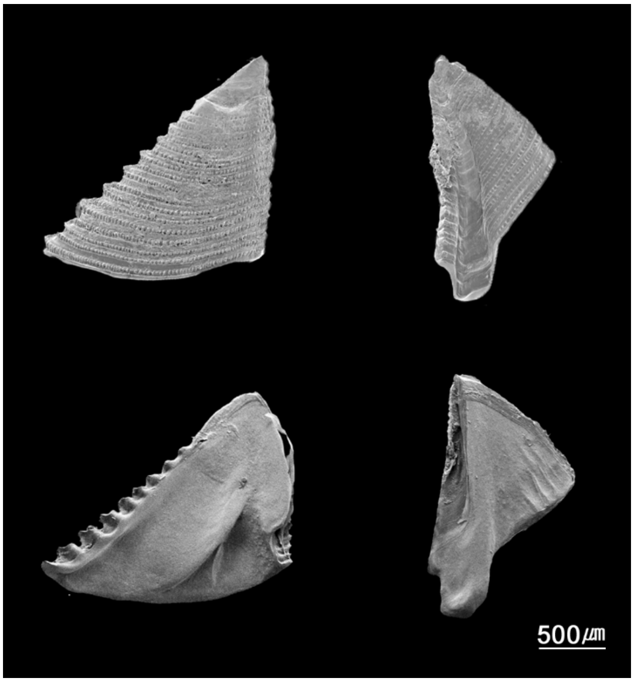

Fig. 43. *Pyrgomina oulastreae* (Utinomi, 1962), external and internal view of scutum and tergum. Scale bar in μm.

Distribution. Japan and Korea (Fig. 44).

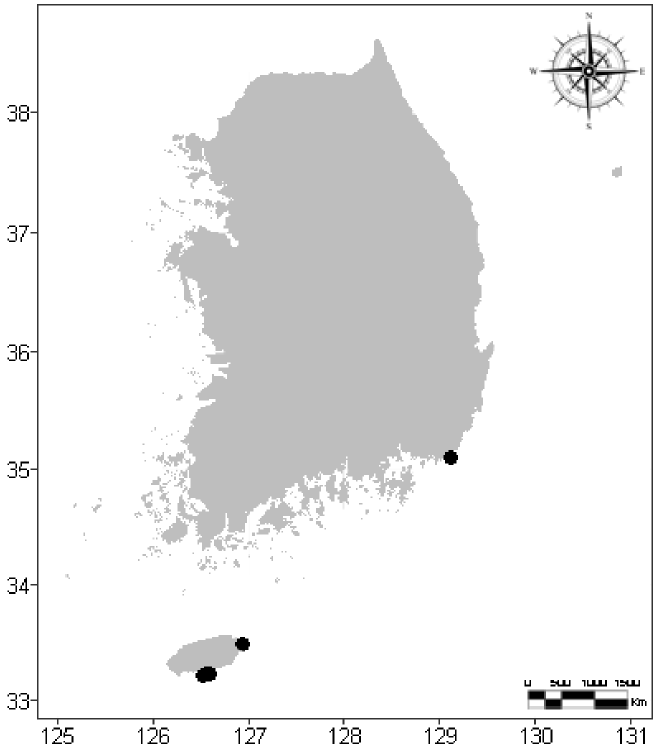

Fig. 44. Distribution of *Pyrgomina oulastreae* (Utinomi, 1962) in Korea.

Remarks. This species is symbiotic on two species of corals *Oulastrea crispate* and *Psammocora* sp. in Jeju. Kim (1998) suggested that specimens from different hosts reveal morphological differences in basis, cirri, and mouth parts. Detailed information is suggested in Chapter 2: Biodiversity and host specificity of coral-associated barnacles in Korea, with descriptions.

Family Balanidae Leach, 1817

Genus *Fistulobalanus* Zullo, 1984

Fistulobalanus albicostatus (Pilsbry, 1916)

Balanus amphitrite albicostatus Pilsbry, 1916:90, pl. 20, figs. 1-4.—Utinomi, 1949b:22; 1962:216.

Balanus albicostatus albicostatus.—Utinomi, 1967:209, text-figs. 4,5; 1970: 356.—Newman & Ross, 1976:62.

Balanus albicostatus formosanus.—Utinomi, 1967:212, figs. 6a-c, 7a-d, pl. 6, fig. 3.

Balanus albicostatus.—Henry & McLaughlin, 1975:108, text-figs. 20, 20a.—Yamaguchi, 1977:176, text-fig. 16, pl. 19, figs. 3, 4, pl. 20, figs. 2, 6, 10, pl. 21, fig. 2, pl. 22, figs. 1-5.—Foster, 1980:210.—Kim & Kim, 1980:174, pl. 5, figs. 1-7.

Fistulobalanus albicostatus.—Zullo, 1984:1330.—Pitombo, 2004:275.

Previous records in Korea. All coasts of Korea except for the eastern coast north to Pohang (Kim, 1998).

Materials Examined. numerous specimens (Yeonpyeong-eup, Ongjin-gun); 17 specimens (Jung-gu, Incheon); numerous specimens (Wolmi Island, Jungu); 12 specimens (Sinjin Island, Geunheung-myeon, Taean-gun); 4 specimens (Ong Island, Geunheung-myeon, Taean-gun); numerous specimens (Jeongjok Island, Geunheung-myeon, Taean-gun); 20 specimens (Anmyeon Island, Taean-gun); 23 specimens (Chaeseokgang, Byeonsan-myeon, Buan); 22 specimens (Jeokbyeokgang, Byeonsan-myeon, Buan); numerous specimens (Aphae-eup, Sinan-gun); 5 specimens (Hyeol Island, Jodomyeon, Jindo-gun); 8 specimens (Soan-myeon, Wando-gun); 7 specimens (Cheongsan Island, Cheongsan-myeon, Wando-gun); 3 specimens (Geumo Island, Nam-myeon, Yeosu-si); 14 specimens (Wolgokli, Seolcheon-myeon, Namhae-gun); numerous specimens (Sangjubeach, Sangjuli, Sangju-myeon, Namhae-gun); 2

specimens (Haeundae-gu, Busan); 6 specimens (Seogwi-dong, Seogwipo-si, Jeju).

Diagnosis. Parietes conical, surface with gray or purple; radii wide, with transverse ridges. Scutum triangular, basal margin convex, adductor muscle pit faint; tergum narrow, spur round, articular furrow deep (Fig. 45). Maxilla slightly protrude; labrum deep notched, with 2 teeth on each crest; mandible with 5 teeth excluding inferior angle; maxillule not notched, with fine spines (Fig. 46).

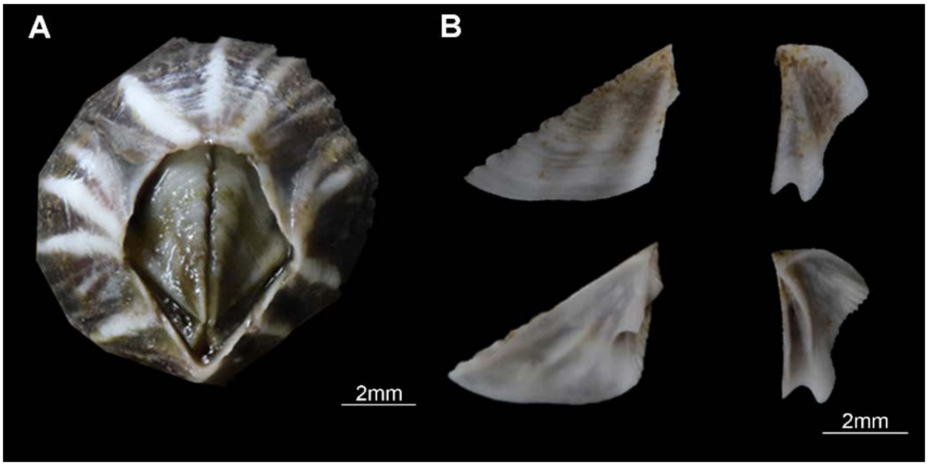

Fig. 45. *Fistulobalanus albicostatus* (Pilsbry, 1916). A, Pariests, top view; B, External and internal view of scutum and tergum.

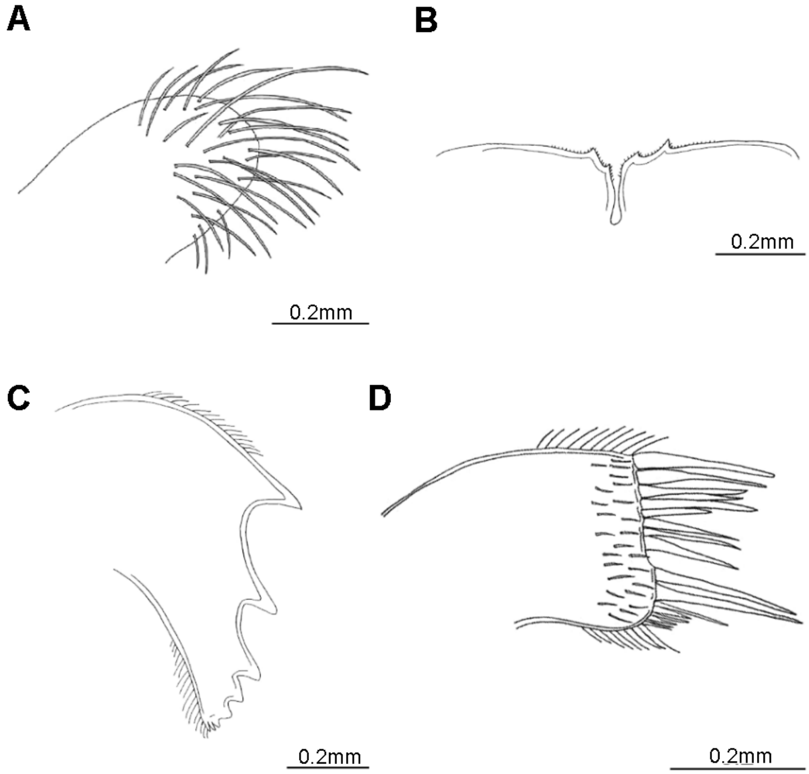

Fig. 46. Mouth parts of *Fistulobalanus albicostatus* (Pilsbry, 1916). A, Maxilla; B, Labrum; C, Mandible; D, Maxillule.

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

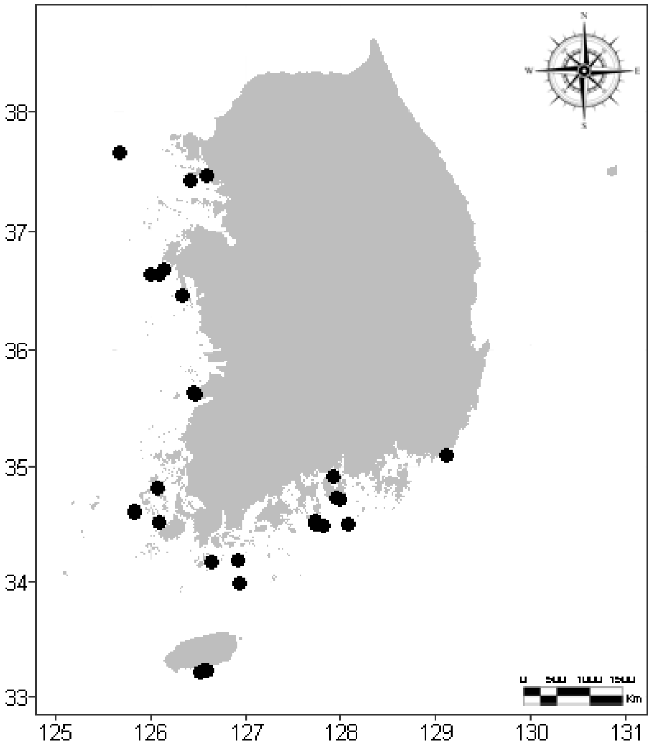

Fig. 47. Distribution of *Fistulobalanus albicostatus* (Pilsbry, 1916) in Korea.

Remarks. *Fistulobalanus albicostatus* is an intertidal form restricted to brackish waters and is very common in the western and southern coast of Korea. Its vertical distribution overlaps with *Chthamalus challengeri* Hoek (1883), but it can be easily distinguished by eyes.

In ports of the southern coast, this species competes with the introduced barnacle species *Amphibalanus amphitrite*. When corroded, *F. albicostatus* may be confused with *A. amphitrite*, due to the presence of stripes on the shell. However, they can be distinctly differentiated by morphological differences of the outer surface, with thick longitudinal ridges.

***Fistulobalanus kondakovi* (Tarasov & Zevina, 1957)**

Balanus Amphitrite krugeri Nilsson-Cantell, 1932:24, text-fig. 10, pl. 1, figs. 5-7.—Hiro, 1939b:263.—Utinomi, 1949b:22; 1962:216.—Rosell, 1972:86.

Balanus amphitrite kondakovi Tarasov & Zevina, 1957:191, fig. 76.—Rosell, 1972:88, fig. 8.—Newman & Ross, 1976:63.

Balanus uliginosus Utinomi, 1967:202, figs. 1, 2, pl. 6, figs. 4-6; 1970:356.

Balanus kondakovi.—Henry & McLaughlin, 1975:114, text-figs. 21, 22b, c, f, pl. 11, figs. a-m.—Yamaguchi, 1977:176, text-fig. 18, pl. 19, figs. 6,7, pl. 20, figs. 13-18.—Kim & Kim, 1980:276, pl. 6, figs. 1-8.

Fistulobalanus kondakovi.—Zullo, 1984:1330.—Pitombo, 2004:275.

Previous records in Korea. Gyeonggi-do; Chungcheongnam-do; Jeollabuk-do; Jeollanam-do; Gyeongsangnam-do (Kim, 1998).

Materials Examined. 2 specimens (Chaeseokgang, Byeonsan-myeon, Buan); 3 specimens (Sangjubeach, Sangjuli, Sangju-myeon, Namhae-gun); numerous specimens (Haeundae-gu, Busan).

Diagnosis. Parietes conical, surface with pale purple or gray; radii wide. Scutum triangular, basal margin straight, adductor muscle pit distinct; tergum arrow-shaped, with concave scutal margin, spur long, articular furrow deep (Fig. 48). Maxilla concave; labrum deep notched, with 3 or 4 teeth on each crest; mandible with 5 teeth excluding inferior angle; maxillule slightly notched, with well-developed spines (Fig. 49).

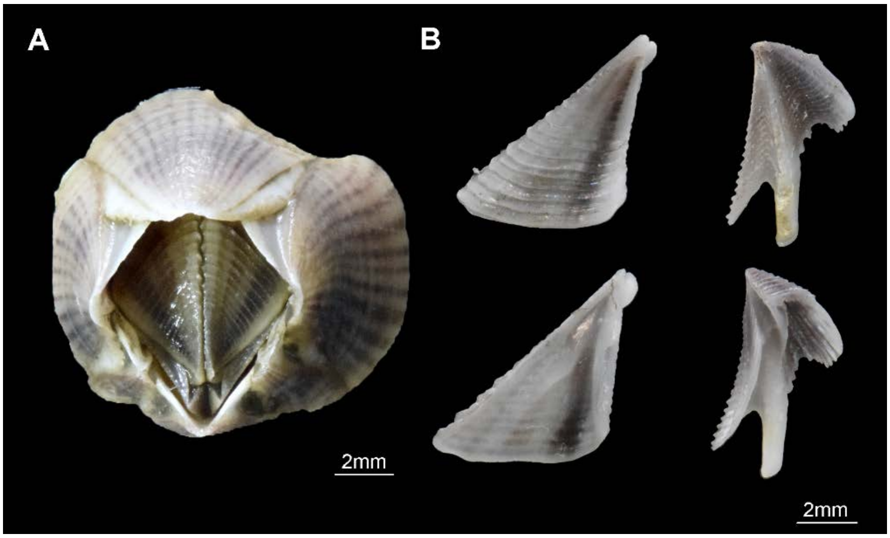

Fig. 48. *Fistulobalanus kondakovi* (Tarasov & Zevina, 1957). A, Pariests, top view; B, External and internal view of scutum and tergum.

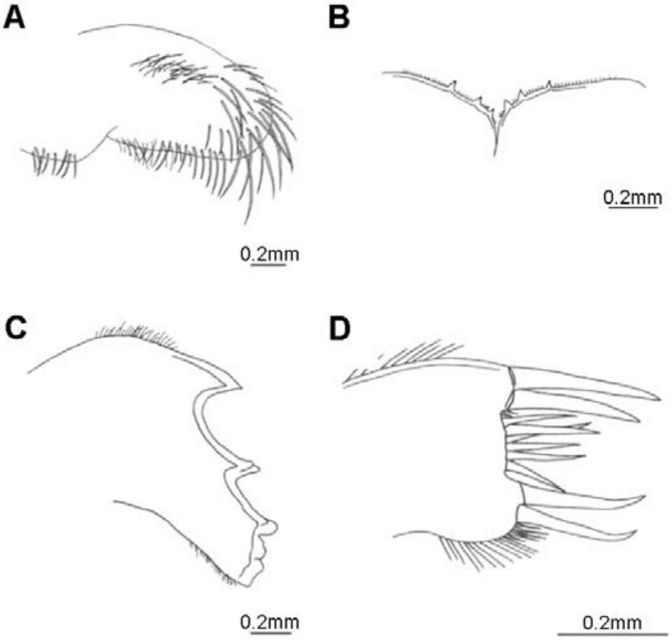

Fig. 49. Mouth parts of *Fistulobalanus kondakovi* (Tarasov & Zevina, 1957). A, Maxilla; B, Labrum; C, Mandible; D, Maxillule.

Distribution. Indian Union, Japan, New Zealand, southwest Australia to Sumatra, Yellow Sea coasts of China and Korea (Fig. 50)

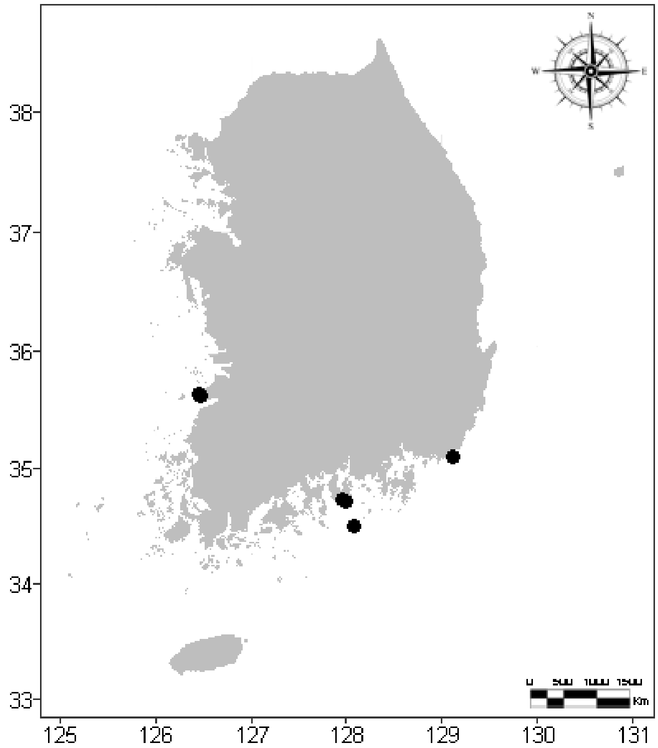

Fig. 50. Distribution of *Fistulobalanus kondakovi* (Tarasov & Zevina, 1957) in Korea.

Remarks. The distribution of *Fistulobalanus kondakovi* is in the western and southern coast in Korea, occurring in freshened closed inner parts of bays and estuaries of rivers.

The parietes marked with pale purple or gray with narrow longitudinal stripes on the outer surface. The large individual usually has coarse surface or erased longitudinal stripes.

This species is found in brackish waters, on the shell surface and shore installations, especially muddy regions. *F. kondakovi* is easy to distinguish from other barnacles having a deeply clefted carinal side of the basal margin.

Genus *Amphibalanus* Pitombo, 2004

Amphibalanus reticulatus (Utinomi, 1967)

Balanus reticulatus Utinomi, 1967:216, figs. 9-12, pl. 6, figs. 7, 8; 1970:356.—Henry & McLaughlin, 1975:88, text-figs. 11, 18, pl. 7, fig. 7, fig. d, pl. 9, figs. a-c.—Southward, 1975:11, pl. 1, figs. 4-15.—Yamaguchi, 1977:176, text-fig. 17, pl. 19, fig. 5, pl. 20, figs. 3, 7, 11, pl. 21, fig. 3, pl. 22, figs. 6-12.—Kim & Kim, 1980:177, pl. 6, figs. 9-15.—Lewis, 1981:9, figs. 5e, 6b, e, pls. 3c-f, 4f.

Amphibalanus reticulatus.—Pitombo, 2004:274.

Previous records in Korea. Gyeongsangnam-do; Jeollanam-do; Jeollabuk-do; Chungcheongnam-do; Gyeonggi-do (Kim, 1998).

Materials Examined. 7 specimens (Ammyeon Island, Taean-gun), on a gastropod shell; 2 specimens (Chaeseokgang, Byeonsan-myeon, Buan), on the bottom of port structure; 3 specimens (Seomanghang, Jindo-gun), on the bottom of buoys.

Diagnosis. Parietes conical, surface with longitudinal and horizontal reddish purple stripes; radii wide. Scutum triangular, basal margin straight, adductor muscle pit distinct; tergum with long spur, articular ridge distinct, basi-scutal angle acute (Fig. 51). Maxilla bilobed; labrum deep notched, with 3-4 teeth on each crest; mandible with 4-5 teeth excluding inferior angle; maxillule not notched, with well-developed spines (Fig. 52).

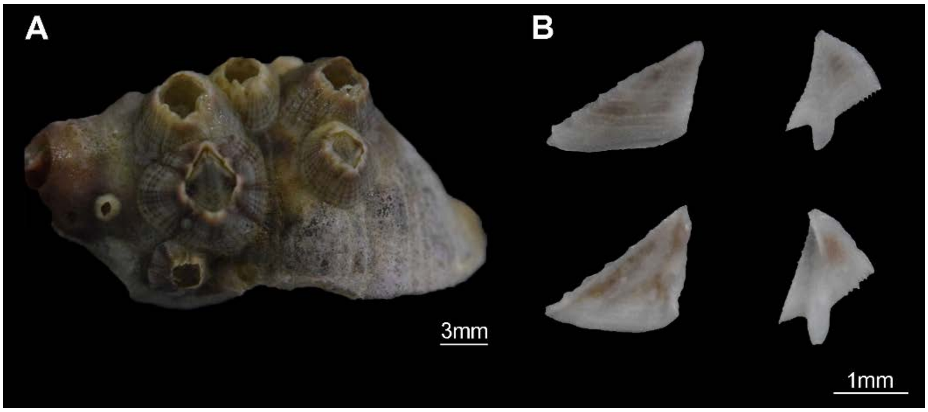

Fig. 51. *Amphibalanus reticulatus* (Utinomi, 1967). A, Pariests on gastropod shells , top view; B, External and internal view of scutum and tergum.

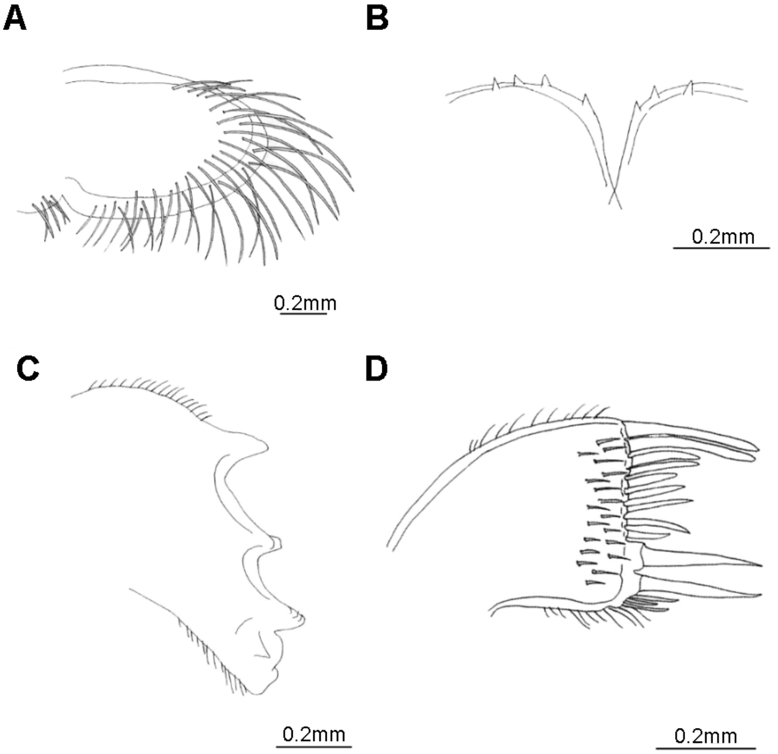

Fig. 52. Mouth parts of *Amphibalanus reticulatus* (Utinomi, 1967). A, Maxilla; B, Labrum; C, Mandible; D, Maxillule.

Distribution. East Asia from the Yellow Sea to the Gulf of Siam, Japan and Hawaii to Malay Archipelago, Malaysia to southeast Africa, Mediterranean Sea, West Africa, southeast United States to West Indies and Korea (Fig. 53).

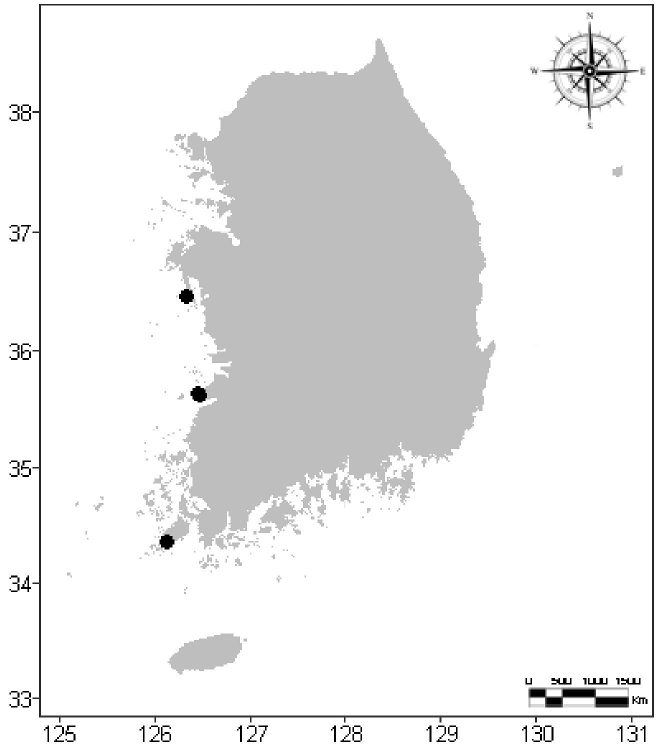

Fig. 53. Distribution of *Amphibalanus reticulatus* (Utinomi, 1967) in Korea.

Remarks. *Amphibalanus reticulatus* has a conical or subcylindrical shell, with a toothed orifice and more conical than *A. amphitrite*. Also, the tergum has a more pointed apex than two introduced barnacles, *A. amphitrite* and *A. improvisus*. This species is widely distributed from Japan, the Indo-West Pacific to Australia. *A. reticulatus* distributes in the shallow water (the most abundant up to 5m depth) and found on buoys attached in the lowest intertidal zone.

***Amphibalanus amphitrite* (Darwin, 1854)**

Balanus amphitrite var. *communis* Darwin, 1854:240.—Stubbings, 1936:41-42.

Balanus amphitrite forma *hawaiiensis* Broch, 1922:314, figs. 56, 57.

Balanus amphitrite hawaiiensis.—Nilsson-Cantell, 1938:40, text-fig. 9.—Rosell, 1972:82, figs. 5, 6.

Balanus amphitrite communis.—Nilsson-Cantell, 1921:311, fig. 64a-e; 1938:36, text-fig. 7.—Utinomi, 1949b:22.

Balanus amphitrite.—Hoek, 1913:167, pl. 14, figs. 8-17.—Pilsbry, 1916:89.—Yamaguchi, 1977:174, text-fig. 15, pl. 19, figs. 1, 2, pl. 20, figs. 1, 5, 9, pl. 21, fig. 1; 1979:41, figs. 2, 6.

Balanus amphitrite amphitrite.—Broch, 1947:5.—Utinomi, 1967:200, pl. b, fig. 1; 1970:355.—Rosell, 1973:79, fig. 4.—Foster, 1974:47, fig. 8A-G.—Henry & McLaughoin, 1975:6, text-fig. la, pl. 1, figs. 1-3.—Kim & Kim, 1980:175, pl. 5, figs. 8-16.

Balanus amphitrite saltonensis.—Henry & McLaughoin, 1975:46, text-figs. 12, 13, pl. 2.

Amphibalanus amphitrite.—Pitombo, 2004:274.

Previous records in Korea. Daeheuksan Island, Jeollanamdo; Joomoonjin, Gangreung-si, Gangwondo; Yokji Island, Geongsangnamdo; Jookbyeon, Uljin-gun, Gyeongsangbukdo; Seogwipo, Jeju; Mipo, Haeundae-gu, Busan; Jeodong, Uleung; Geojin, Goseung-gun, Gangwondo (Kim, 1998).

Materials Examined. numerous specimens (Chaeseokgang, Byeonsan-myeon, Buan), on the bottom of port structure; 4 specimens (Wolgokli, Seolcheon-myeon, Namhae gun); numerous specimens (Pungwhali, Sanyang-eup, Tongyeong-si), on the bottom of buoys; 8 specimens (Yeonwhali, Sanyang-eup, Tongyeong-si), on the surface of macro algae; numerous specimens (Irun-myeon, Geoje); 5 specimens (Haeundae0gu, Busan), on the surface of the molluscan shell; 12 specimens (Seogwi-dong, Seogwipo-si, Jeju).

Diagnosis. Parietes conical, white; radii white, narrow with transverse stripe. Scutum triangular, occludent margin straight, articular ridge distinct; tergum with distinct growth lines, spur blunt. Mandible with 5 teeth excluding inferior angle, second tooth bidentated; maxillule without notch; labrum with deep notched, with 2-3 teeth on each crest.

Description. Shell conical, about 10-20mm basal diameter; 6 plates (rostrum, carina, paired lateral and paired rostral-lateral), externally white, smooth with longitudinal purple striations from apex to base, interior surface with black horizontal striations, radii wide; lateral base with radial tubes and transverse septa (Fig. 54).

Scutum triangular, flat, external surface of scutum with distinct growth line, 2 or 3 broad and longitudinal pale purple stripes, occludent margin straight, articular ridge distinct, adductor ridge distinct, short, adductor muscle pit distinct, lateral depressor muscle pit variously developed (Fig. 54).

Tergum broad, outer surface with distinct growth line, scutal articular margin distinct, straight, extending down to spur, spur blunt, wide, with tip rounded or truncate, articular furrow wide, basal margin slightly concave, 4-5 fine depressor crests at basal margin, external surface striated (Fig. 54).

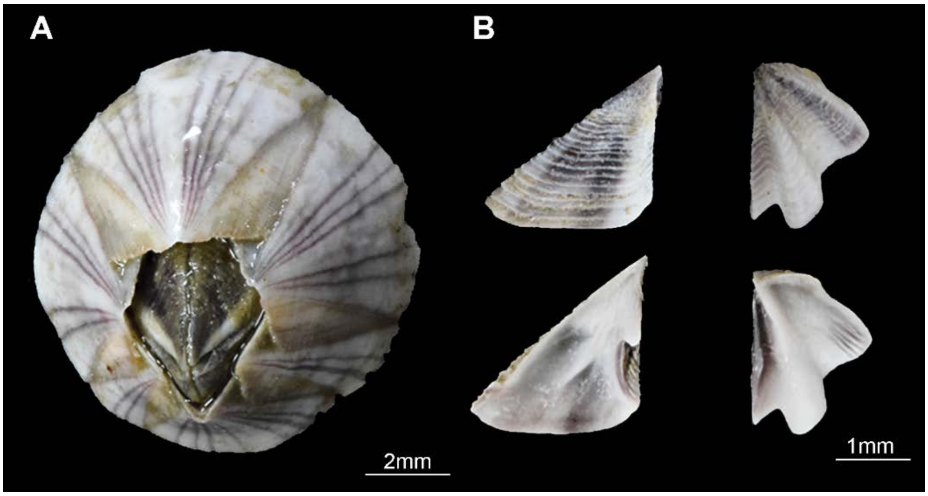

Fig. 54. *Amphibalanus amphitrite* (Darwin, 1854). A, Pariests, top view; B, External and internal view of scutum and tergum.

Cirrus I with unequal rami; anterior ramus long, slender with 14 segments; posterior ramus short with 11 segments, bearing serrulate setae. Cirrus II with subequal rami; 12 segments on anterior ramus and 11 segments on posterior ramus bearing serrulate setae. Cirrus III anterior ramus with 14 segments, slightly longer than posterior ramus (11 segments) with some spines on the segments. Cirri IV-VI long, slender, rami of equal size (Fig. 55).

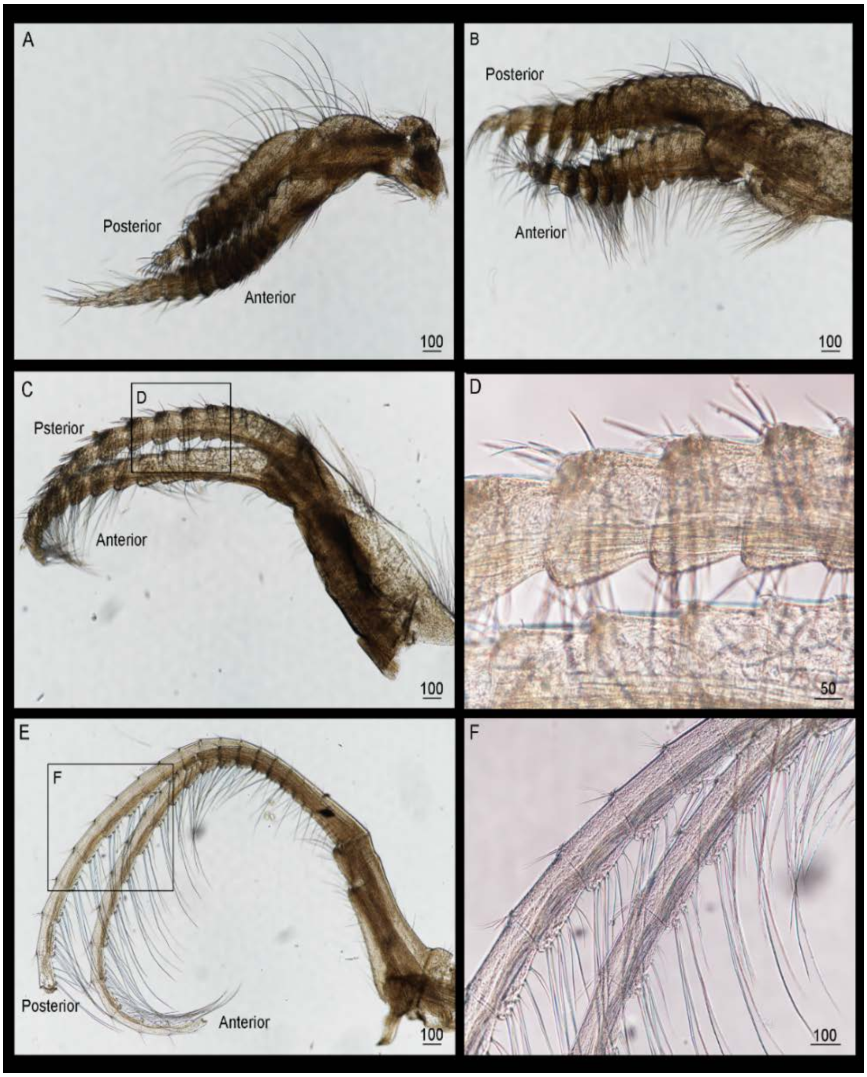

Fig. 55. Cirri of *Amphibalanus amphitrite* (Darwin, 1854). A, Cirrus I; B, Cirrus II; C, Cirrus III; D, Cirrus III with serrulate setae distally on posterior ramus; E, Cirrus IV; F, Cirrus IV with serrulate setae distally on both ramus. Scale bars in μm.

Maxilla bilobed with dense serrulate setae on both margins. Mandibular palp ovate bearing simple setae. Mandible with 5 teeth excluding inferior angle, second tooth bidentated, fourth tooth blunt, inferior angle with fine spinules.

Maxillule without notch below upper pair of spines, spines well- developed, lower angle with fine spinules. Labrum with deep notched, 2-3 teeth on each side crest (Fig. 56).

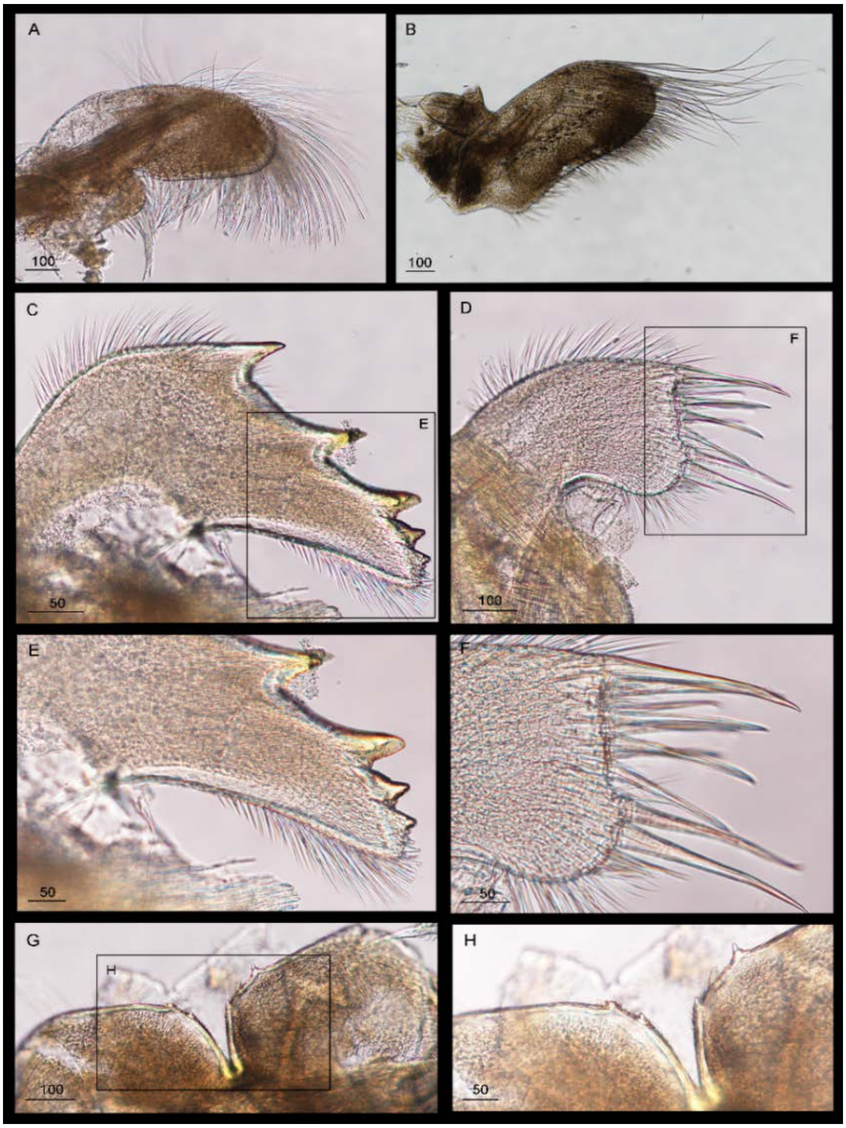

Fig. 56. Mouth parts of *Amphibalanus amphitrite* (Darwin, 1854). A, Maxilla; B, Mandibulatory palp; C, Mandible; D, Maxillule; E, Lower margin and inferior angle of mandible; F, Cutting edge of maxillule; G, Labrum; H, Teeth on the labrum. Scale bars in µm.

Distribution. Distributed worldwide (Fig. 57).

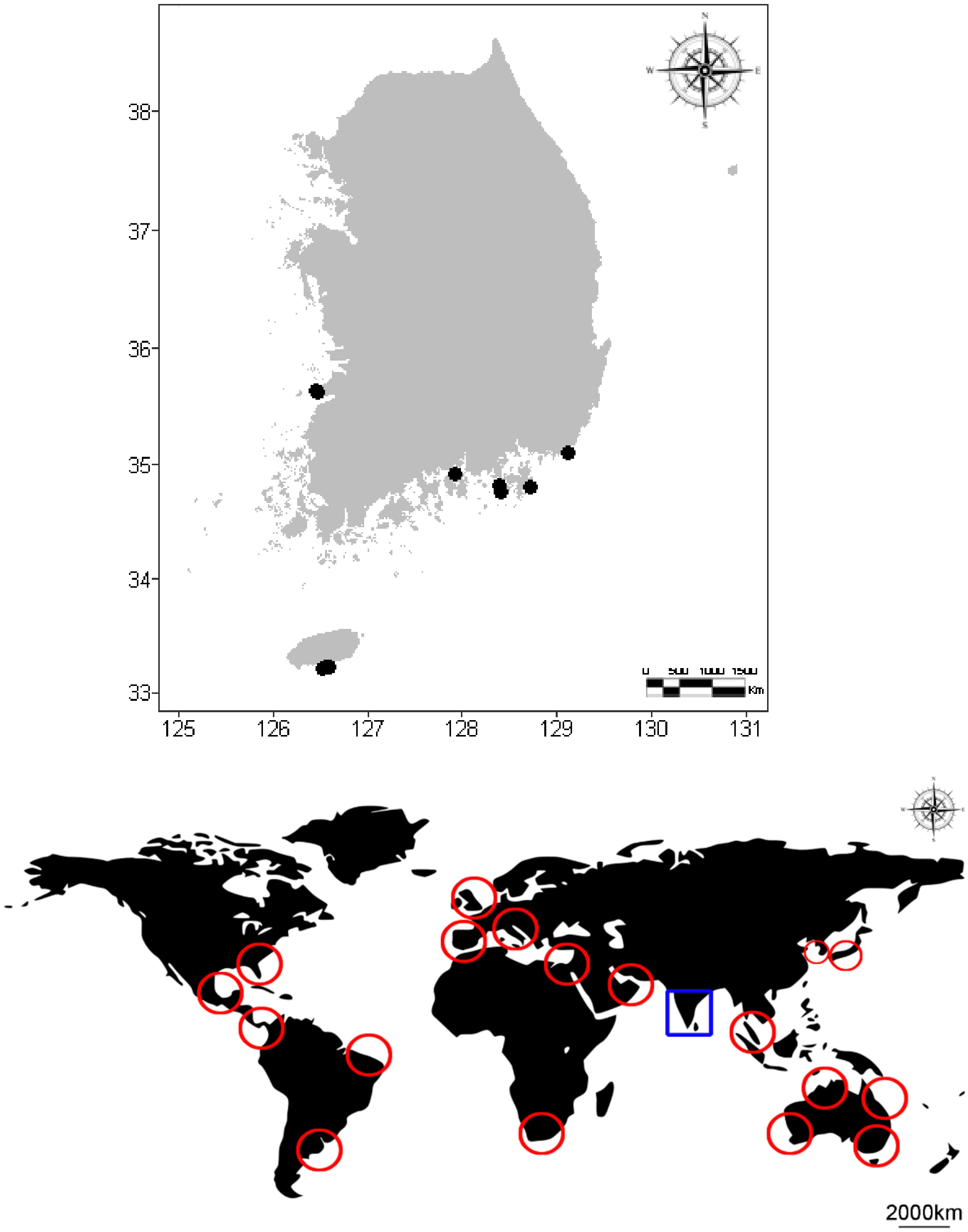

Fig. 57. Distribution of *Amphibalanus amphitrite* (Darwin, 1854). Legend: black circle = collected locality in Korea; red circle = distribution in world-wide; blue square = type locality.

Remarks. *Amphibalanus amphitrite* is a common fouling barnacle. The settlement patterns are various. The morphology of this species is also variable from habitats.

This species has longitudinal purple stripes on the surface. The interface between longitudinal stripes is wider. *A. amphitrite* may be confused with *A. reticulatus* due to the distinct vertical and longitudinal stripes on the external surface of the shell. However, the settlement type is totally different: *A. amphitrite* is found mostly on the bottom of a ship and the other one is found on the molluscan shells. It is also misidentified with *Fistulobalanus kondakovi* due to the purple striations on the shell surface, but it is distinguished by the morphology of tergum.

***Amphibalanus eburneus* (Gould, 1841)**

Balanus eburneus Darwin, 1854:248, pl. 5, fig. 1a-d.—Pilsbry, 1916:80, figs. 1-1c, 2, 14, 16b, 24.—Broch, 1924:112.—Utinomi, 1970:353, text-figs. 8-10.—Bacon, 1976:13.—Henry & McLaughlin, 1975:60-68, fig. 15.

Amphibalanus eburneus.—Pitombo, 2004:274.

Previous records in Korea. Joomoonjin, Gangreung-si, Gangwondo; Guryongpo, Pohangsi, Gyeongsangbukdo (Kim, 1998).

Materials Examined. numerous specimens (Pungwhali, Sanyang-eup, Tongyeong-si), on the bottom of buoys; 8 specimens (Yeonwhali, Sanyang-eup, Tongyeong-si), on the bottom of the ship; 12 specimens (Irun-myeon, Geoje), on the bottom of the ship.

Diagnosis. Parietes conical, smooth, white; radii wide without stripe. Scutum triangular, occludent margin straight, toothed, articular ridge distinct; tergum with distinct growth lines, spur blunt. Mandible with 4-5 teeth; maxillule without notched; labrum with deep notched, with 10 teeth on each crest.

Description. Shell conical, about 10-30mm basal diameter, outer surface of shell smooth, white, without any striations. Radii wide; orifice ovate or slightly toothed, about 1/2 of height; inner lamina ribbed extending to sheath. Parietal tubes in single row, with transverse septa (Fig. 58).

Scutum triangular. Growth ridges on outer surface widely spaced and crossed with many longitudinal striae. Inner surface with irregular tubercles at upper part. Occludent margin toothed and straight. Basal margin weakly toothed. Basi-tergal angle concave, blunt. Articular ridge distinct. Articular furrow deep, high. Adductor ridge short, weak. Adductor muscle pit and lateral depressor muscle pit faint (Fig. 58).

Tergum white, scutal articular margin slightly concave on upper part. Outer surface of tergum with distinct growth line. Carinal margin with arrow-like protrusion in apical 50% part. Basal margin concave, 3-4 distinct depressor crests at basal margin. Articular ridge low, indistinct. Articular furrow wide. Spur straight, blunt, spur furrow shallow (Fig. 58).

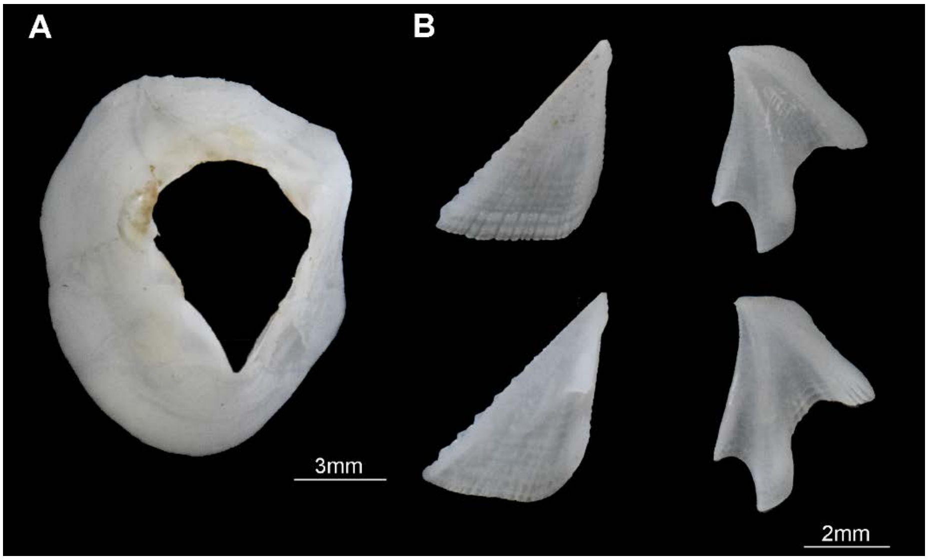

Fig. 58. *Amphibalanus eburneus* (Gould, 1841). A, Pariests, top view; B, External and internal view of scutum and tergum.

Cirrus I with unequal rami, stout. Cirrus II with subequal rami; anterior ramus with 14 segments, posterior ramus with13 segments bearing some simple spines on the segments. Cirrus III with many small spines on anterior ramus segments. Cirri IV-VI long, slender, rami of equal size (Fig. 59).

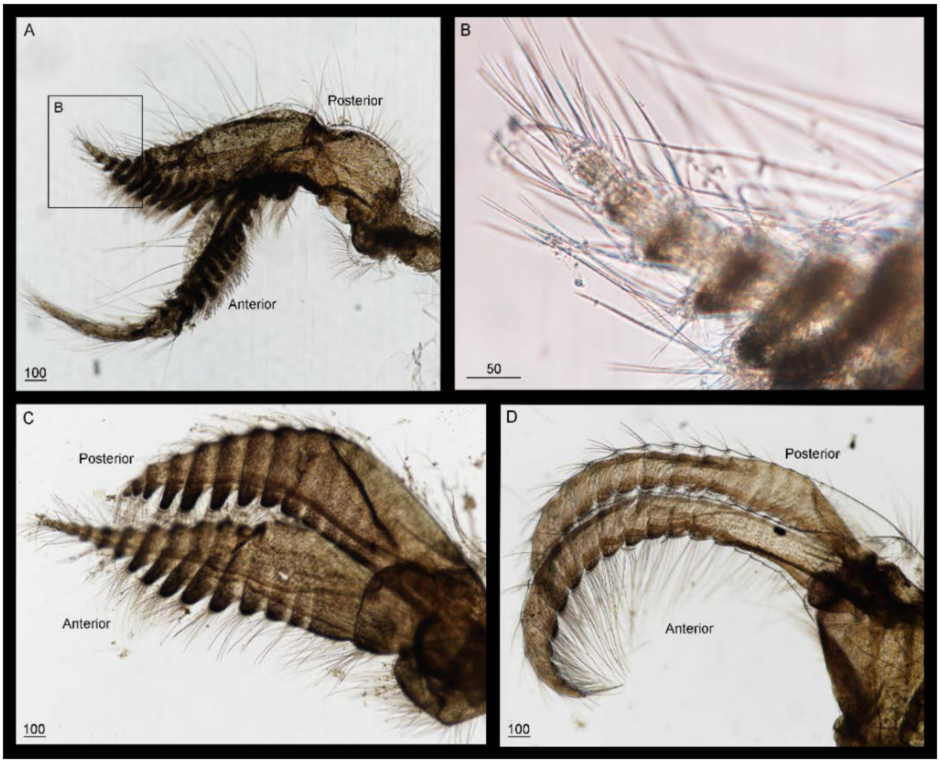

Fig. 59. Cirri of *Amphibalanus eburneus* (Gould, 1841). A, Cirrus I; B, Tip of cirrus I, showing the serrulate setae; C, Cirrus II; D, Cirrus III. Scale bars in µm.

Maxilla lobed with dense serrulate setae on margin. Mandibular palp ovate bearing simple setae. Mandible with 4-5 teeth excluding inferior angle, first to third teeth distinct and others blunt and fused with inferior angle. Maxillule without notch, with distinct upper and lower pairs of spines, lower angle with fine spinules. Labrum with deep V shaped, about 10 teeth on each crest (Fig.

60).

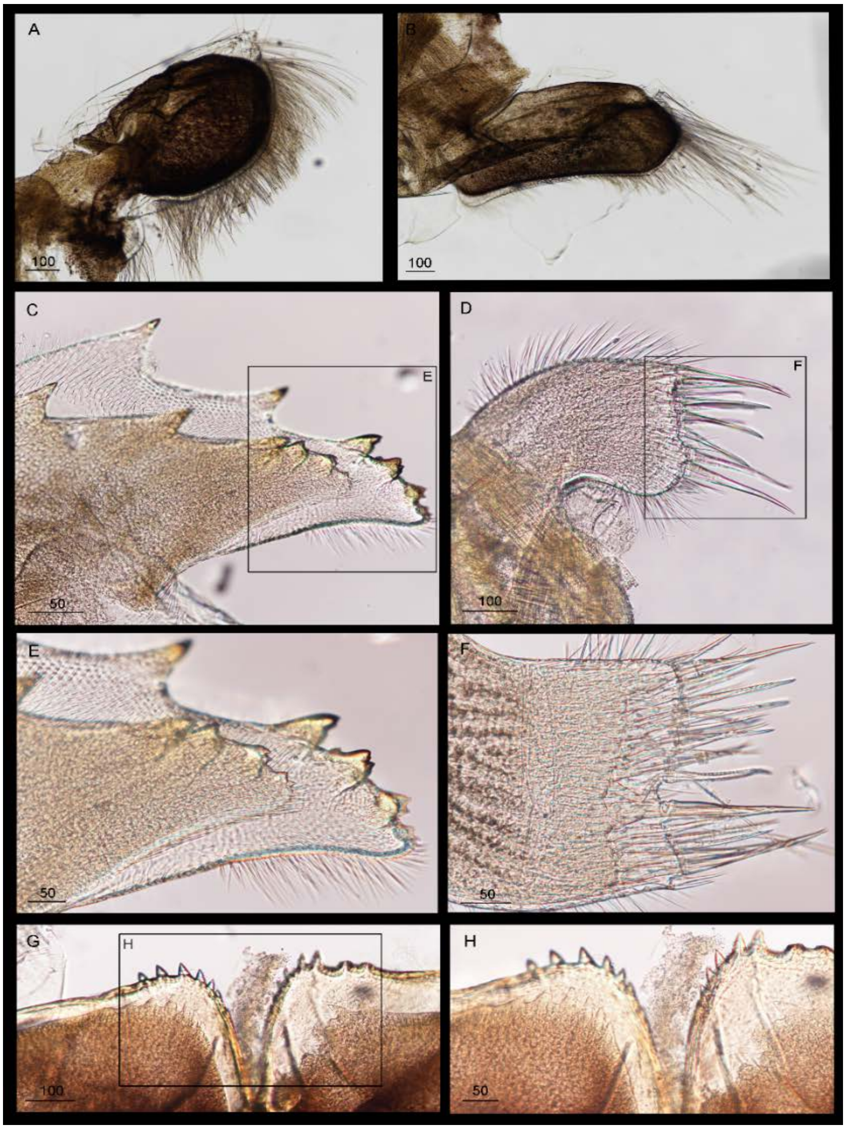

Fig. 60. Mouth parts of *Amphibalanus eburneus* (Gould, 1841). A, Maxilla; B, Mandibulatory palp; C, Mandible; D, Maxillule; E, Lower margin and inferior angle of mandible; F, Cutting edge of maxillule; G, Labrum; H, Teeth on the labrum. Scale bars in μm.

Distribution. Worldwide in subtropical, temperate waters (Fig. 61).

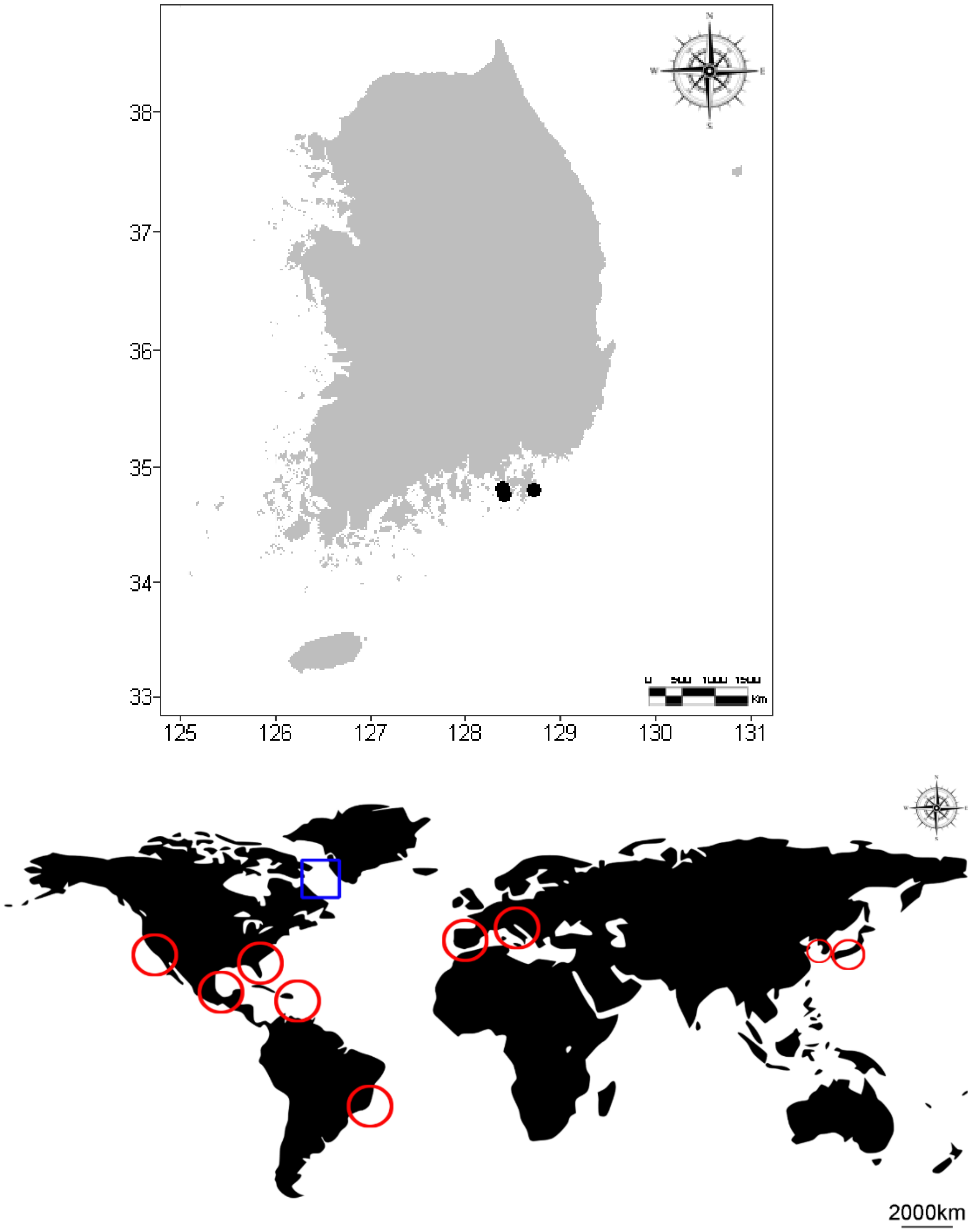

Fig. 61. Distribution of *Amphibalanus eburneus* (Gould, 1841). Legend: black circle = collected locality in Korea; red circle = distribution in world-wide; blue square = type locality.

Remarks. *Amphibalanus eburneus* is native to the Western Atlantic, from the southern Gulf of Maine to Panama, became cosmopolitan due to extensive shipping activities. *A. eburneus* can be confused with another introduced barnacle, *A. improvisus* due to the color of the shell surface is white and smooth in both species. However, it is easily distinguished by the carinal margin of the tergum.

This species is one of the common introduced barnacles in Korea and is not distributed in the northeastern coast of Korea due to the intolerance to low temperature.

***Amphibalanus improvisus* (Darwin, 1854)**

Balanus improvisus Darwin, 1854:250, pl. 6, fig. 1a-c.—Pilsbry, 1916:84, figs. 3-3b, 5-5d.—Nilsson- Cantell, 1978:63, fig. 32.—Broch, 1924:81, fig. 28a-c, pl. 1, fig. 7a, b, pl. 3, fig. 15a-d.—Utinomi, 1970:35, figs. 6, 7.—Henry & McLaughlin, 1975:68, text-fig. 16, pl. 5, figs. a-f.—Newman & Ross, 1976:63.

Balanus improvisus var. *assimilis* Darwin, 1854:250.

Balanus improvisus assmilis.—Bacon, 1976.

Amphibalanus improvisus.—Pitombo, 2004:274.

Previous records in Korea. Joomoonjin, Gangreung-si, Gangwondo (Kim, 1998).

Materials Examined. 7 specimens (Wolgokli, Seolcheon-myeon, Namhae-gun), on the bottom of port structure; 3 specimens (Sangjubeach, Sanjuli, Sangju-myeon, Namhae-gun); 5 specimens (Haeundaegu, Busan); 7 specimens (Jumunli, Jumunjin-eup, Gangeung-si), on the bottom of the ship.

Diagnosis. Parietes low, conical, white; radii narrow. Scutum triangular, occludent margin straight, articular furrow narrow; tergum with indistinct growth lines, spur wide, blunt. Mandible with 5-6 teeth; maxillule without notch; labrum with 7-15 teeth on each crest.

Description. Shell low, conical. Outer surface of shell white, smooth, without any striations. Radii narrow; summits thin, oblique. Sheath without vacuoles, solid, interior surface with longitudinal ribs to sheath, basal end denticulated. Basis with radial tubes and transverse septa (Fig. 62).

Scutum triangular, thin, elongated with straight occludent margin. Growth ridges on outer surface indistinct. Inner surface smooth, with weak tubercles on upper part. Occludent margin straight. Basal margin slightly convex. Articular margin straight, articular ridge distinct. Articular furrow narrow. Adductor muscle pit absent, sometimes small. Pit for lateral depressor muscle indistinct, sometimes absent (Fig. 62).

Tergum triangular, with indistinct growth line. Inner surface with weak irregular tubercles on upper part. Scutal triangular margin straight, carinal margin convex. Carinal side of basal margin slightly concave. Articular ridge low and articular furrow broad. Crest for depressor muscle distinct, several in number at basal margin. Spur furrow open, broad. Spur wide, blunt (Fig. 62).

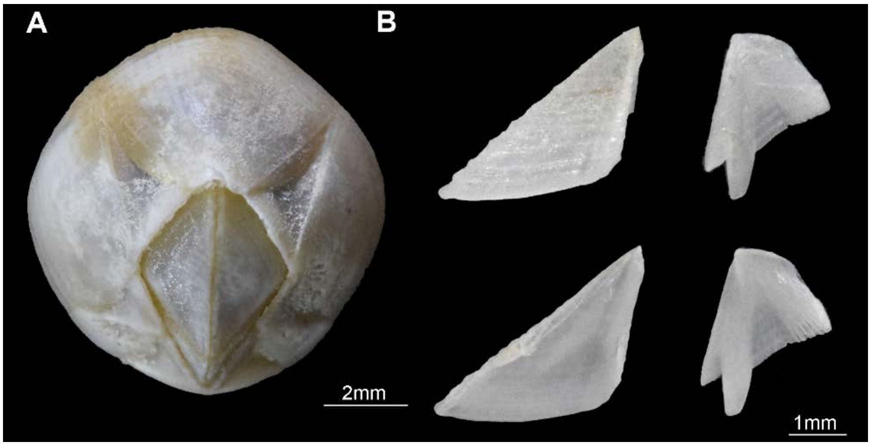

Fig. 62. *Amphibalanus improvisus* (Darwin, 1854). A, Pariests, top view; B, External and internal view of scutum and tergum.

Cirrus I with unequal rami, stout. Cirrus II with subequal rami; anterior ramus with 14 segments, posterior ramus with13 segments bearing some simple spines on the segments. Cirrus III anterior ramus slightly longer than posterior ramus; anterior ramus with small spines on each segments. Cirri IV-VI long, slender, rami of equal size (Fig. 63).

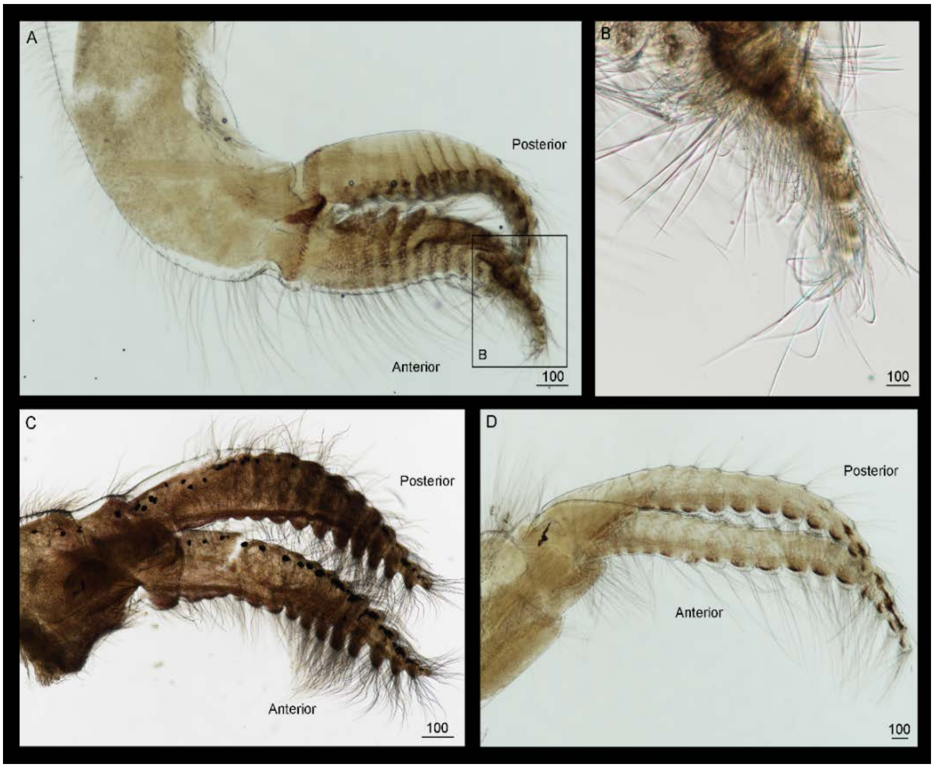

Fig. 63. Cirri of *Amphibalanus improvisus* (Darwin, 1854). A, Cirrus I; B, Tip of cirrus I, showing the serrulate setae; C, Cirrus II; D, Cirrus III. Scale bars in µm.

Maxilla lobed with dense serrulate setae on margin. Mandibular palp ovate bearing short simple setae. Mandible with 5 or 6 teeth; the last 2 teeth closed to inferior angle; inferior angle without spinules; second teeth bidentated, third to sixth teeth blunt, with extra denticles; sixth teeth small. Maxillule without notch below upper pair of spines and slightly straight, spines well-developed, middle spines basically 6-7 in number. Labrum with 7-15 teeth on each crest (Fig. 64).

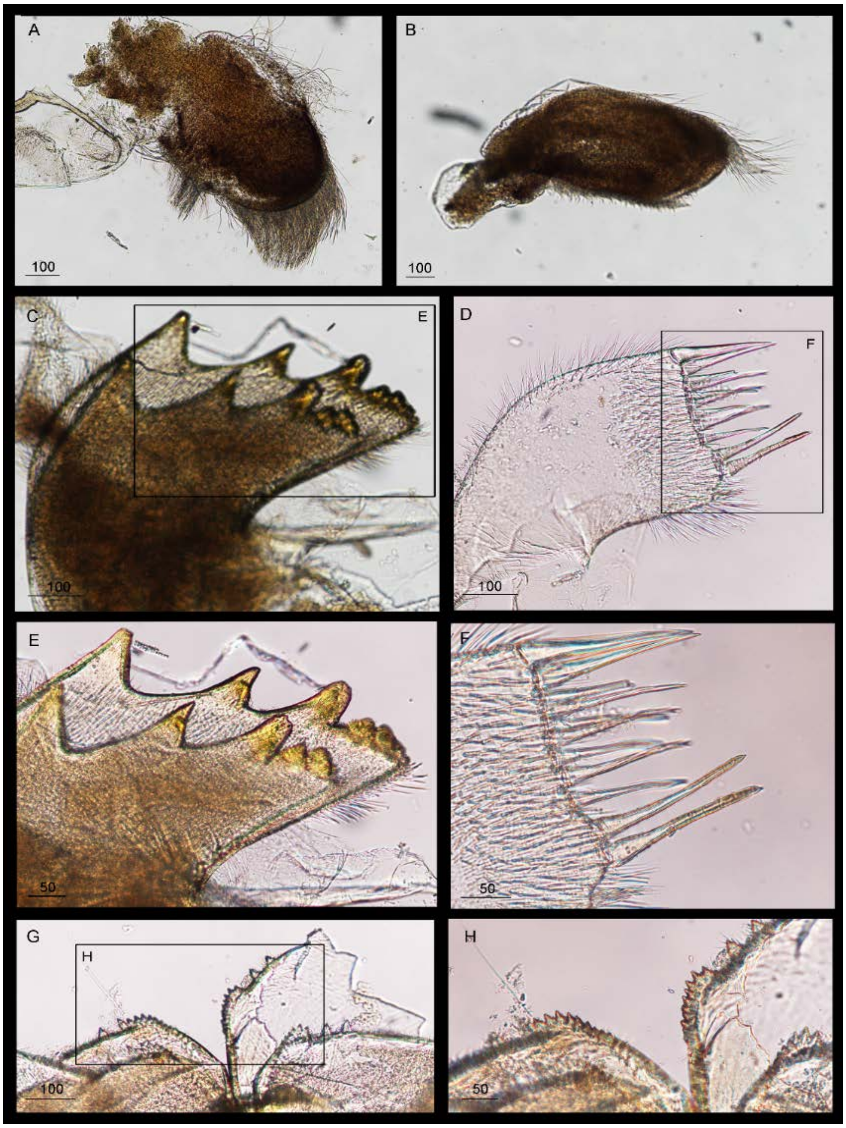

Fig. 64. Mouth parts of *Amphibalanus improvisus* (Darwin, 1854). A, Maxilla; B, Mandibulatory palp; C, Mandible; D, Maxillule; E, Lower margin and inferior angle of mandible; F, Cutting edge of maxillule; G, Labrum; H, Teeth on the labrum. Scale bars in µm.

Distribution. Worldwide tropical to temperate waters (Fig. 65).

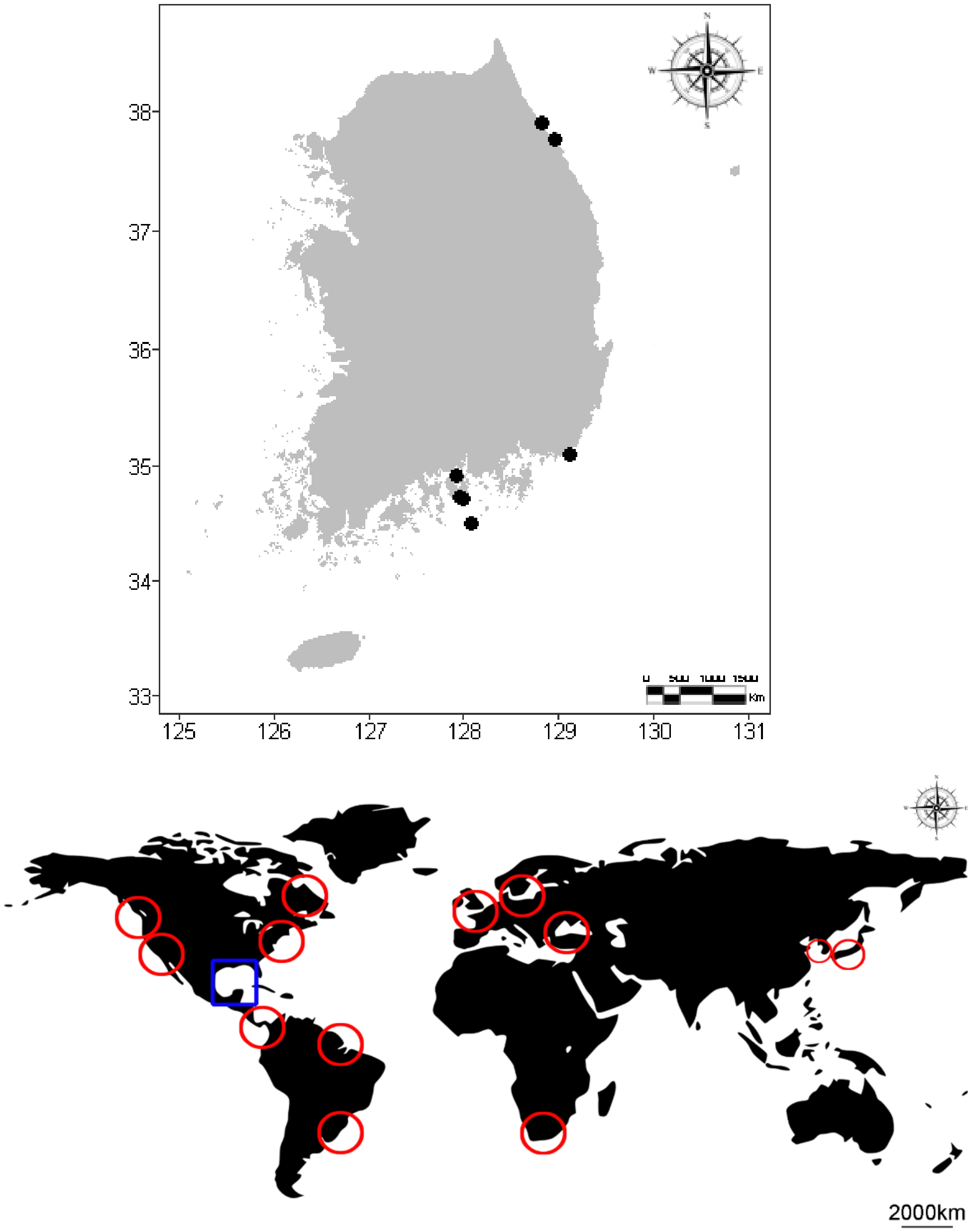

Fig. 65. Distribution of *Amphibalanus improvisus* (Darwin, 1854). Legend: black circle = collected locality in Korea; red circle = distribution in world-wide; blue square = type locality.

Remarks. *Amphibalanus improvisus* introduced from the northwest Atlantic Ocean and has been dispersed by shipment. *A. improvisus is an introduced species in Korea and has* various habitats, easily found on any hard substrate available, such as molluscan shells, on a port structure attached in a relatively low salinity area.

This species is common on the eastern coast of Korea. Based on its range, this barnacle is moderately tolerant of brackish waters and cold waters.

Genus *Balanus* Da Costa, 1778

Balanus trigonus Darwin, 1854

Balanus trigonus Darwin, 1854:223, pl. 3, fig. 7a-f.—Hoek, 1883:149, pl. 12, fig. 20; 1913:152.—Pilsbry, 1916:111, pl. 26, figs. 1-3e.—Nilsson-Cantell, 1927:784.—Hiro, 1932a:551; 1939a:263.—Stubbings, 1961:31, text-fig. 7; 1967:267.— Pope, 1945:361, pl. 29, fig. 6, pl. 30, figs. 9, 10.—Utinomi, 1949b:22; 1970:357.—Newman & Ross, 1976:66.—Foster, 1978:113, fig. 68; 1980:210.—Kim & Kim, 1980:177, pl. 7, figs. 1-7.

Previous records in Korea. Gangwon-do; Gyeongsangbuk-do; Gyeongsangnam-do; Jeju-do; Jeollanam-do (Kim, 1998).

Materials Examined. 8 specimens (Anmyeon Island, Taean-gun), in depths between 5-10m; 14 specimens (Seomanghang, Jindo-gun); numerous specimens (Hyeol Island, Jodomyeon, Jindo-gun), in depths between 5-15m; 5 specimens (Soan-myeon, Wando-gun), in depths between 5–20m; 6 specimens (Cheongsan Island, Cheongsan-myeon, Wangp-gun), on the surface of molluscan shells, in depths between 5–20m; numerous specimens (Geomun Island, Samsan-myeon, Yeosu-si), in depths between 5–20m; 12 specimens (Geumeumli, Seolcheon-myeon, Namhae-gun); numerous specimens (Sejon Island, Sangjuli, Sangju-myeon, Namhae-gun), in depths between 5-15m; 26 specimens (Pungwhali, Sanyang-eup, Tongyeong-si), in depths between 5-

15m; numerous specimens (Hansan Island, Hansan-myeon, Tongyeong-si), in depths between 5-10m; 5 specimens (Irun-myeon, Geoje), in depths between 5-10m; numerous specimens (Haeundae fish market, Busan), on a gastropod shell; numerous specimens (Janghohang-gil, Geundeok-myeon, Sancheock-si); numerous specimens (Susangil, Sonyang-myeon, Yangyang-gun); 5 specimens (Seogwi-dong, Seogwipo-si, Jeju).

Diagnosis. Parietes low conical with white ribs, surface pale pink; radii broad. Scutum narrow, adductor ridge short, adductor muscle pit faint; tergum triangular with short spur, articular ridge distinct, articular furrow wide (Fig. 66). Cirrus I rami unequal, anterior ramus longer; cirrus II rami equal; cirrus III anterior ramus with hooks (Fig. 67). Maxilla with simple setae on all margins; labrum deep notched, with 2-3 teeth on each crest; mandible with 5 teeth excluding inferior angle, second tooth bidentated; maxillule slightly or not notched with well-developed and fine spines (Fig. 68).

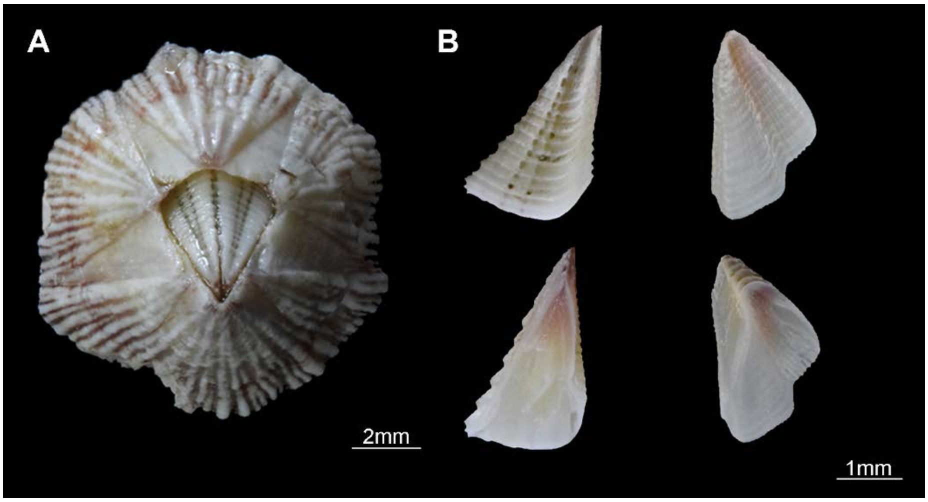

Fig. 66. *Balanus trigonus* Darwin, 1854. A, Pariests, top view; B, External and internal view of scutum and tergum.

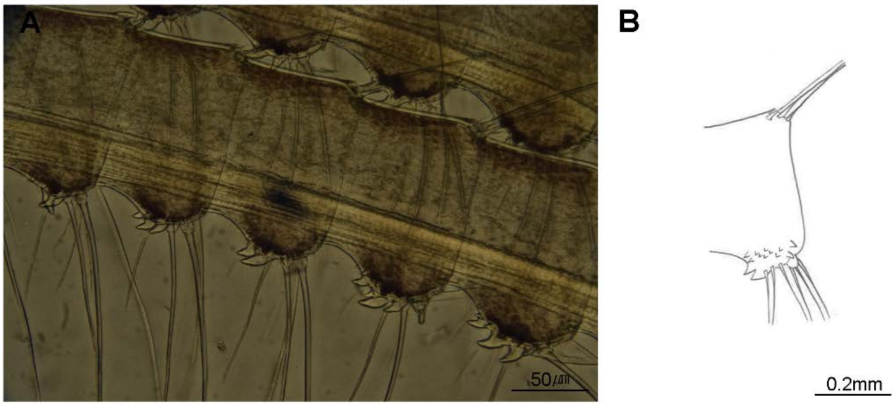

Fig. 67. Cirrus III of of *Balanus trigonus* Darwin, 1854. A, Light microscopy on cirrus III, small spines and teeth on segments; B, Line drawing of small spines and teeth on segment of cirrus III.

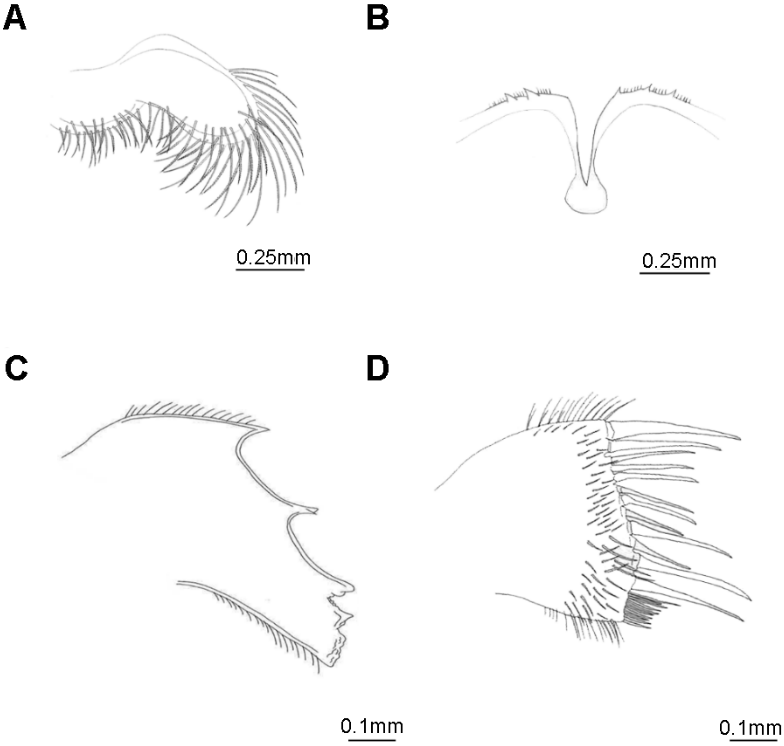

Fig. 68. Mouth parts of *Balanus trigonus* Darwin, 1854. A,Maxilla; B, Labrum; C, Mandible; D, Maxillule.

Distribution. Worldwide in temperate, subtropical water and Korea (Fig. 69).

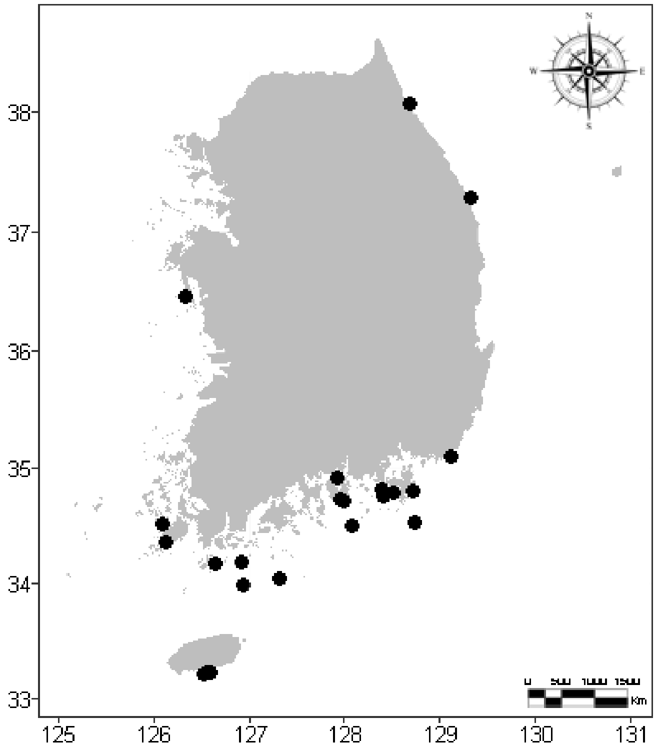

Fig. 69. Distribution of *Balanus trigonus* Darwin, 1854 in Korea.

Remarks. Due to the presence of triangular orifice and one to six longitudinal rows of pits on the outer surface of scutum in *Balanus trigonus*, it can be easily distinguished from other species. This species has various habitats, easily found on bottoms of ships, on floating timbers, on shells and attaching to fish nets. It also lives in deeper waters. The basal diameter is usually less than 10mm.

Balanus rostratus Hoek, 1883

Blanus rostratus Hoek, 1883:152, pl. 13, figs. 16-22.—Pilsbry, 1911:73, pl. 12, fig. 6; 1916:138, pl. 36 figs. 1, 2, 2a.—Hiro, 1935:217.—Utinomi, 1970:357.—Yamaguchi, 1977:178, text-fig. 19, pl. 23, figs. 1-13, pl. 24, figs. 1-3, 7, 8.—Kim & Kim, 1980:172, pl. 3, figs. 1-6.

Blanus rostratus forma *eurostratus* Broch, 1922:320.—Hiro, 1932b:550.

Blanus rostratus alaskensis Pilsbry, 1916:141, pl. 38, figs. 4, 4a, 5.

Blanus rostratus hetetopus Pilsbry, 1916:142, pl. 36, figs. 7, 7a, 8.—Broch, 1922:320

Blanus rostratus dalli Pilsbry, 1916:147, pl. 38, figs. 1-1c, 2.—Hiro, 1935:218, pl. 10, figs. 1, 2.

Blanus rostratus apertus Pilsbry, 1911:73, pl. 12, figs. 4, 7, pl. 13, figs. 1, 2, 8, 9; 1916:144, pl. 36, figs. 3-6, pl. 37, fig. 1-1c.—Utinomi, 1958:295, fig. 5.

Blanus rostratus var. *spinferus* Nilsson-Cantell, 1932:20, text-figs. 8, 9, pl. 1, fig. 4.

Balanus rostratus.—Utinomi, 1958:294.

Previous records in Korea. Gangwon-do; Gyeongsangbuk-do; Gyeongsangnam-do; Jeollanam-do; Chungcheongnam-do (Kim, 1998).

Materials Examined. 2 specimens (Chaeseokgang, Byeonsan-myeon, Buan), on the bottom of port structure; 2 specimens (Jikpo beach; Nam-myeon; Yeosu-si), in depth 5m; 3 specimens (Wolgokli, Seolcheon-myeon, Namhae-gun); 3 specimens (Yangali, Sangju-myeon, Namhae-gun), on the bottom of ship; 6 specimens (Haeundae-gu, Busan); 3 specimens (Guryongpo-eup, Pohang); 4 specimens (Janghohang-gil, Geundeok-myeon, Samchick-si), on the bottom of ship; 2 specimens (Changhae-ro, Jumunjin-eup, Gangeung-si), on the bottom of ship; 1 specimen (Susangil, Soyang-myeon, Yangyang-gun); 1 specimen (Yongho-gil, Ganghyeon-myeon, Yangyang-gun).

Diagnosis. Parietes conical, surface white without any stripe; radii narrow.

Scutum triangular, occludent margin straight, adductor muscle pit deep; tergum narrow with truncated spur, articular ridge distinct, articular furrow shallow (Fig. 70). Cirrus I unequal rami, anterior ramus longer; cirrus III with small spines on segment (Fig. 71). Maxilla with well-developed pair of spines on all margins; labrum without any teeth bearing finely hairs; mandible with 5 teeth, second tooth bidentated; maxillule notched with fine spines (Fig. 72).

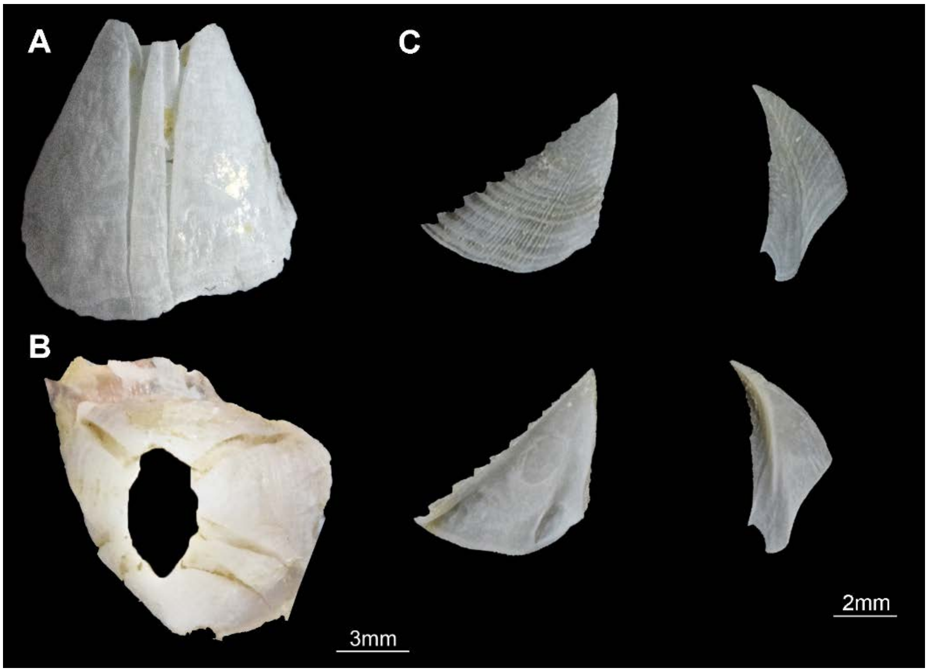

Fig. 70. *Balanus rostratus* Hoek, 1883. A, Pariests, lateral view; B, Pariets, top view; C, External and internal view of scutum and tergum.

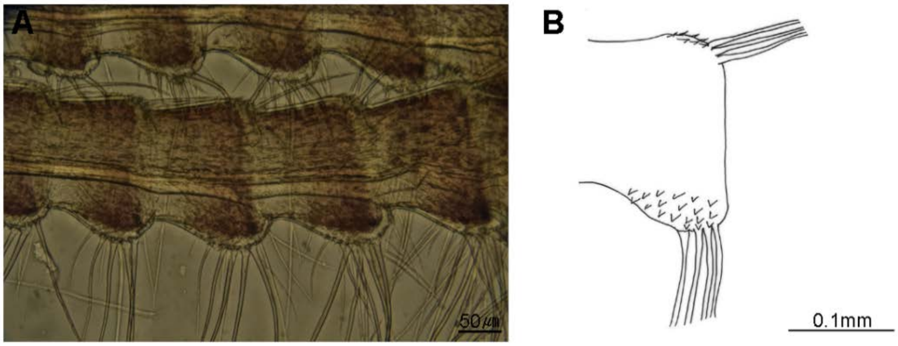

Fig. 71. Cirrus III of *Balanus rostratus* Hoek, 1883. A, Light microscopy on cirrus III, many small spines on segments; B, Line drawing of small spines on segment of cirrus III.

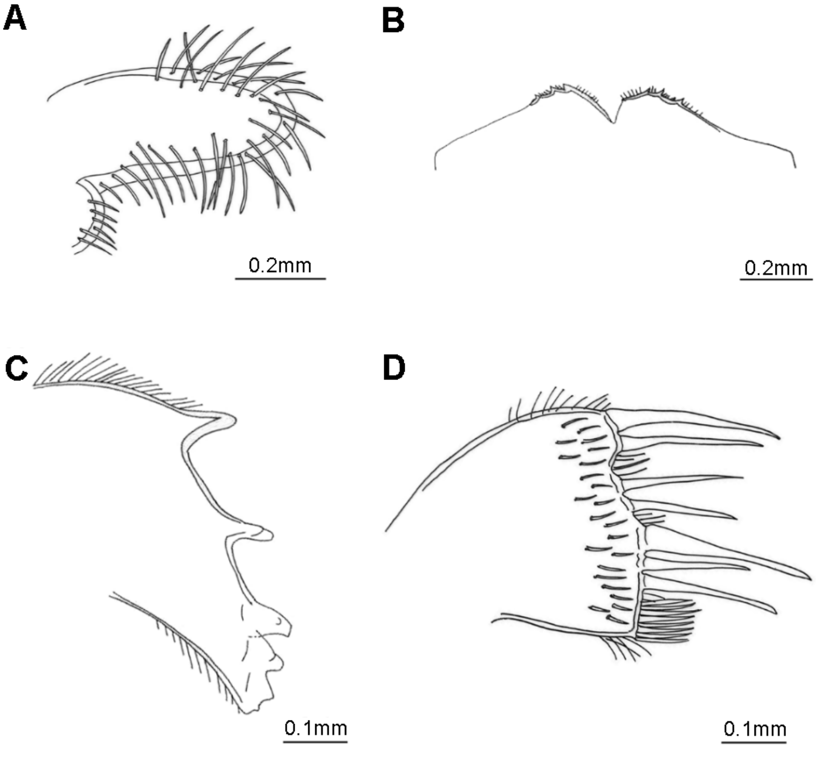

Fig. 72. Mouth parts of *Balanus rostratus* Hoek, 1883. A,Maxilla; B, Labrum; C, Mandible; D, Maxillule.

Distribution. Alaska, Bering Sea, California, Japan, Siberia, west coast of Canada, Yellow Sea and Korea (Fig. 73).

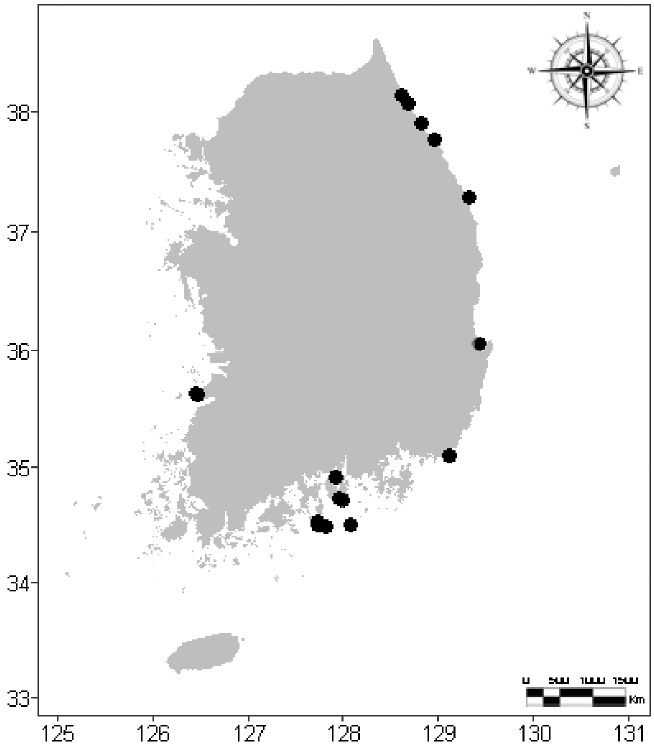

Fig. 73. Distribution of *Balanus rostratus* Hoek, 1883 in Korea.

Remarks. *Balanus rostratus* is cold-water species and has various habitats: on shells, in sponges, on the bottom of ships and on floating timbers, but not found on the rocks. According to Kim (1998), it occured mainly on the western coast and eastern coast of Korea, but now it is rare on the western coast due to climate changes.

Genus *Megabalanus* Hoek, 1913

Megabalanus rosa (Pilsbry, 1916)

Balanus (*Megabalanus*) *tintinnabulum rosa* Pilsbry, 1916:61.—Hiro, 1932b:549, text-fig. 3.—Utinomi, 1970:349, pl. 18, fig. 7.

Megabalanus rosa.—Newman & Ross, 1976:68.—Yamaguchi, 1977:184, pl. 26, figs. 11-13.—Kim & Kim, 1980:178, pl. 7, figs. 8-14.

Previous records in Korea. Gangwon-do; Gyeongsangbuk-do; Gyeongsangnam-do; Jeollanam-do (Kim, 1998).

Materials Examined. 2 specimens (Gwanmae Island, Jodomyeon, Jindo-gun); 5 specimens (Pungwhali, Sanyang-eup, Tongyeong-si), on the bottom of buoys; 6 specimens (Hansan Island, Hansan-myeon, Tongyeong-si); 5 specimens (Irun-myeon, Geoje); 11 specimens (hanghae-ro, Jumunjin-eup, Gangeung-si), on the sufrace of molluscan shell; 2 specimen (Susangil, Soyang-myeon, Yangyang-gun), on the bottom of buoys; 8 specimens (Beopwhan-dong, Seogwipo-si, Jeju), in depth 18m; 4 specimens (Bomok-dong, Seogwipo-si, Jeju), in depth 21m; 10 spcimens (Seogwi-dong, Seogwipo-si, Jeju), in depth 18m.

Diagnosis. Parietes conical, surface pinkish red or white without any stripe; radii broad. Scutum triangular, occludent margin straight, toothed, adductor muscle pit deep; tergum with distinct growth ridge, articular ridge distinct, articular furrow deep (Fig. 74). Maxilla with well developed spines on all margins; labrum with 3 teeth on each crest; mandible with 5 teeth, second tooth bidentated; maxillule slightly notched (Fig. 75).

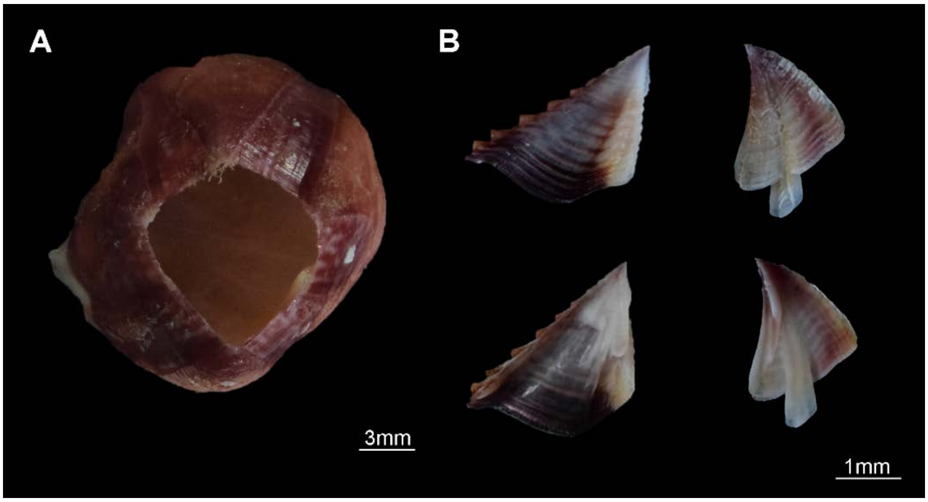

Fig. 74. *Megabalanus rosa* (Pilsbry, 1916). A, Pariests, top view; B, External and internal view of scutum and tergum.

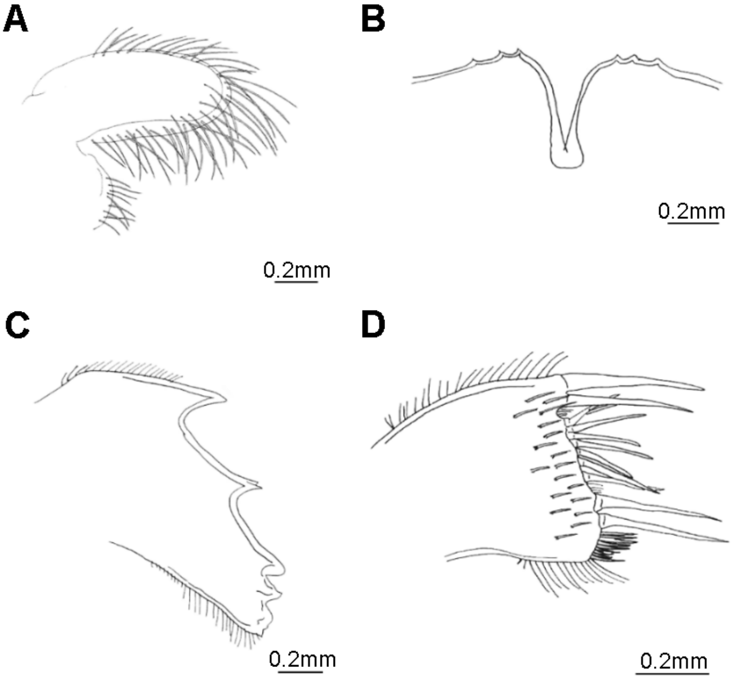

Fig. 75. Mouth parts of *Megabalanus rosa* (Pilsbry, 1916). A,Maxilla; B, Labrum; C, Mandible; D, Maxillule.

Distribution. China, Japan, Taiwan, the East Sea and Korea (Fig. 76).

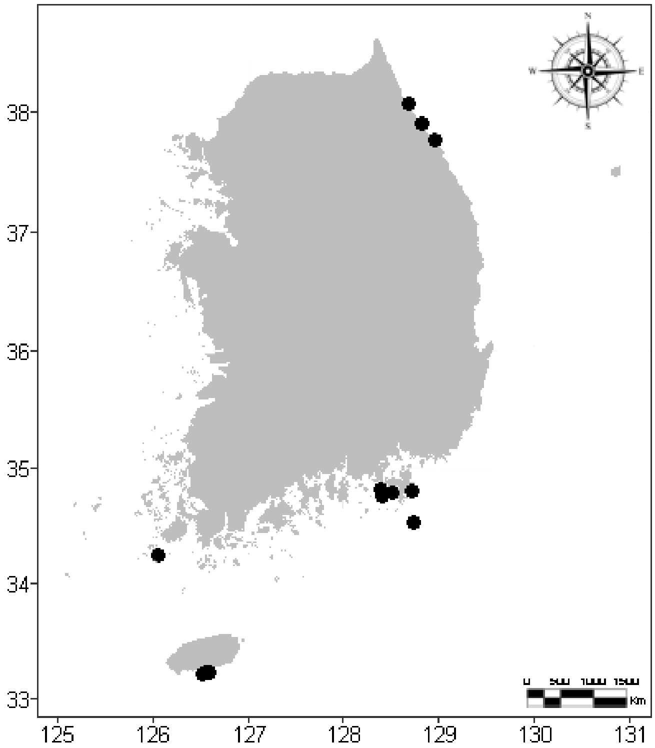

Fig. 76. Distribution of *Megabalanus rosa* (Pilsbry, 1916) in Korea.

Remarks. *Megabalanus rosa* is one of the most numerous acorn barnacles in Korea. The shell of the species is pinkish-red and sometimes white. The morphology of operculum can be used to identify this species in that the orifice is greater than 1/2 basal diameter. *M. rosa* has been found in clear warm-waters usually attaching to molluscan shells, on port structures and fish nets. Largest specimen has 47mm in basal diameter and 29mm in height.

***Megabalanus volcano* (Pilsbry, 1916)**

Balanus (Megabalanus) tintinnabulum volcano Pilsbry, 1916:60, pl. 11, fig. 2-2e.— Nilsson-Cantell, 1938:34.—Utinomi, 1970:350, pl. 18, fig. 6.

Megabalanus volcano.—Newman & Ross, 1976:69.—Yamaguchi, 1977:187, pl. 26, figs. 1-10, 15.—Foster, 1980:210.—Kim & Kim, 1980:179, pl. 8, figs. 1-7.

Previous records in Korea. Gyeongsangbuk-do; Gyeongsangnam-do; Jeollanam-do; Jeju-do (Kim, 1998).

Materials Examined. 3 specimens (Irun-myeon, Geoje), in depths between 10-20m; 8 specimens (Bomok-dong, Seogwipo-si, Jeju), in depth 21m; 10 spcimens (Seogwi-dong, Seogwipo-si, Jeju), in depth 18m.

Diagnosis. Parietes conical, large; radii broad. Scutum triangular, white, occludent margin straight, adductor muscle pit deep; tergum flat, outer surface with distinct growth ridge; articular furrow shallow; spur long (Fig. 77). Maxilla elongated; labrum notched, with 2-3 teeth on each crest; mandible with 5 teeth, second tooth bidentated; maxillule notched with some spines (Fig. 78).

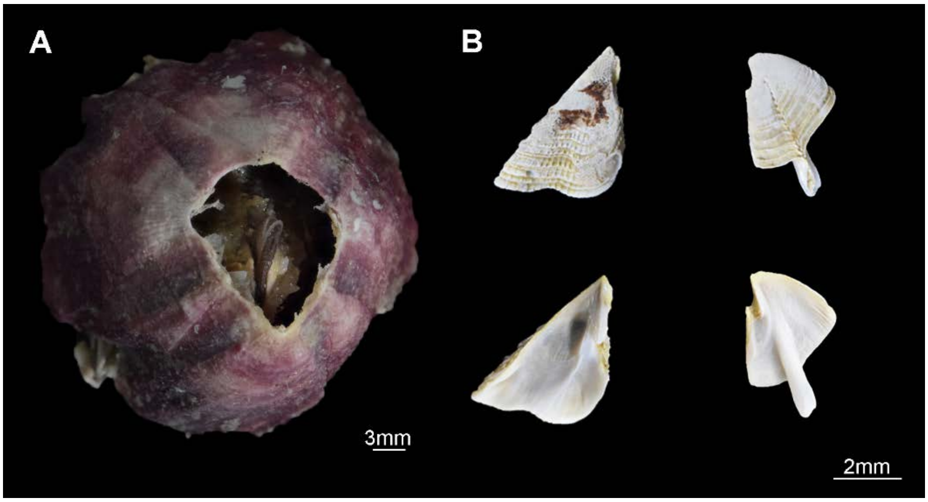

Fig. 77. *Megabalanus volcano* (Pilsbry, 1916). A, Pariests, top view; B, External and internal view of scutum and tergum.

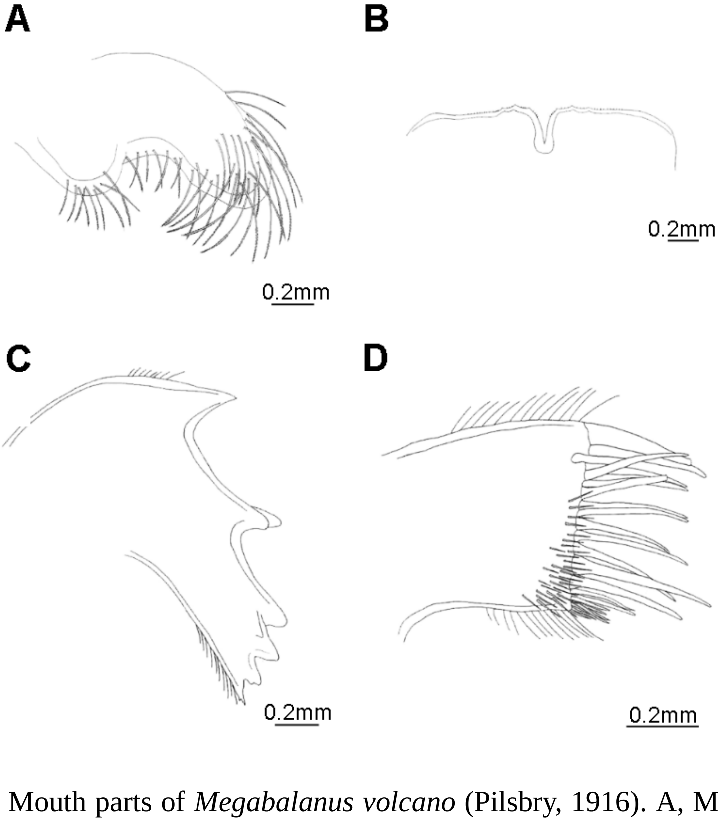

Fig. 78. Mouth parts of *Megabalanus volcano* (Pilsbry, 1916). A, Maxilla; B, Labrum; C, Mandible; D, Maxillule.

Distribution. China, Japan, Indian Ocean, Pacific Ocean, the East Sea and Korea (Fig. 79).

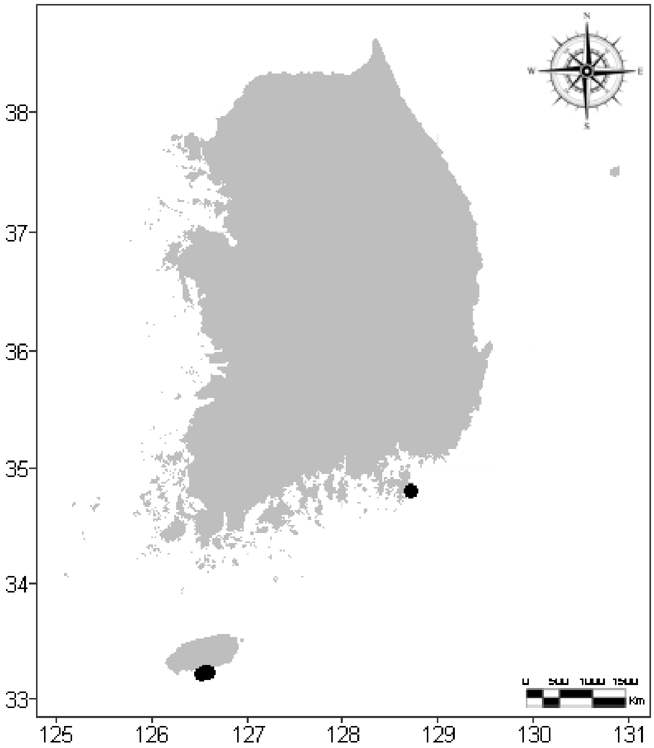

Fig. 79. Distribution of *Megabalanus volcano* (Pilsbry, 1916) in Korea.

Remarks. *Megabalanus volcano* is the largest surf-loving subtidal barnacle in Korea and is rather a pelagic form. This species is closely related to *M. rosa*. Both species are found on buyos together, but the shape of scutum is definitely different: the scutum of *M. volcano* has a strong and wavy growth ridge and highly elevated articular ridge.

Genus *Perforatus* Pitombo, 2004

Perforatus perforatus **(Bruguière, 1789)**

Balanus perforates Darwin, 1854:231, pl. 4, fig. 3a-3c, pl. 5, fig. 1a-1d.—Pilsbry, 1907:120, fig. 33.—Kerckhof, 2002:98.

Perforatus perforatus.—Pitombo, 2004:265.

Previous records in Korea. Guryongpo, Pohang-si, Gyeongsangbukdo; Yangpo, Pohang-si, Gyeongsangbukdo; Gampo, Gyeongju-si, Gyeongsangbukdo (Kim & Hong, 2010).

Materials Examined. 8 specimens (Haeundae-gu, Busan); 10 specimens (Guryongpo-eup, Pohang); 21 specimens (Janghohang-gil, Geundeok-myeon, Sancheock-si); numerous specimens (Jumunjin fish market, Gangeung-si), on a gastropod shell; 23 specimens (Yangho-gil, Ganghyeon-myeon, Yangyang-gun); numerous specimens (Daejinhang fish market, Hyeonnae-myeon, Goseong-gun), on a gastropod shell.

Diagnosis. Parietes conical, dull purple or pinkish; radii white, narrow. Scutum triangular; occludent margin straight, articular ridge distinct; tergum with distinct growth lines, spur longer than wide. Mandible with 5 teeth excluding inferior angle; maxillule with slightly notched; labrum with slightly notched, with fine small teeth on each crest.

Description. Shell conical, about 10-20mm basal diameter; 6 plates, externally dull purple, surface with dense longitudinal ridges. Orifice smaller compare to basal diameter. Radii white, narrow, with transverse striae; summits horizontal. Inferior surface with longitudinal ridges, basal end denticulated. Parietal tubes with single row (Fig. 80).

Scutum triangular, pale purple, tergal articular margin straight. Apex curved outwardly. External surface of scutum distinct with strong growth ridges and horizontal striations. Occludent margin straight and inclined with fine teeth. Articular margin straight. Basal margin convex. Articular ridge distinct, articular furrow deep. Adductor ridge distinct, close to basal margin. Adductor muscle pit distinct, deep. Pit for lateral depressor muscle deep (Fig. 80).

Tergum triangular, scutal articular margin slightly concave. Outer surface with distinct growth lines, carinal margin convex. Articular furrow wide and shallow. Spur long and narrow, spur furrow deep, distinct. Crests for depressor muscle indistinct (Fig. 80).

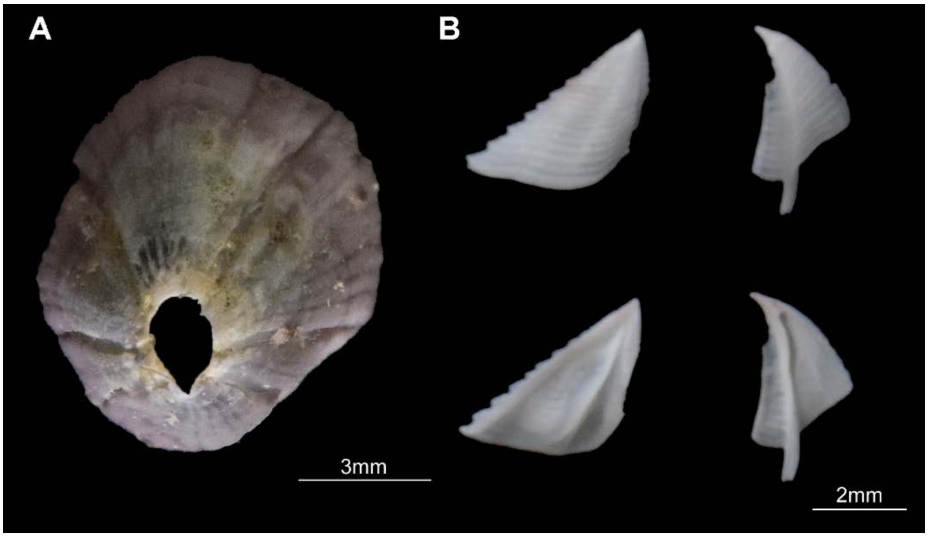

Fig. 80. *Perforatus perforatus* (Bruguière, 1789). A, Pariests, top view; B, External and internal view of scutum and tergum.

Cirrus I with unequal rami; anterior ramus long, with 24 segments; posterior ramus with 14 segments. Cirrus II with equal rami; anterior ramus and posterior ramus with 10 segments respectively. Cirrus III anterior ramus with 12 segments and 9 segments on posterior ramus, intermediate segments of cirrus III bearing sharp teeth. Cirri IV-VI long, slender, with subequal rami; cirrus IV anterior and posterior ramus with 18, 24 segments respectively; cirrus V with 22 and 25 respectively; cirrus VI with 24 and 25 respectively, intermediate anterior and posterior rami bearing 2-3 pairs of long serrulate setae (Fig. 81).

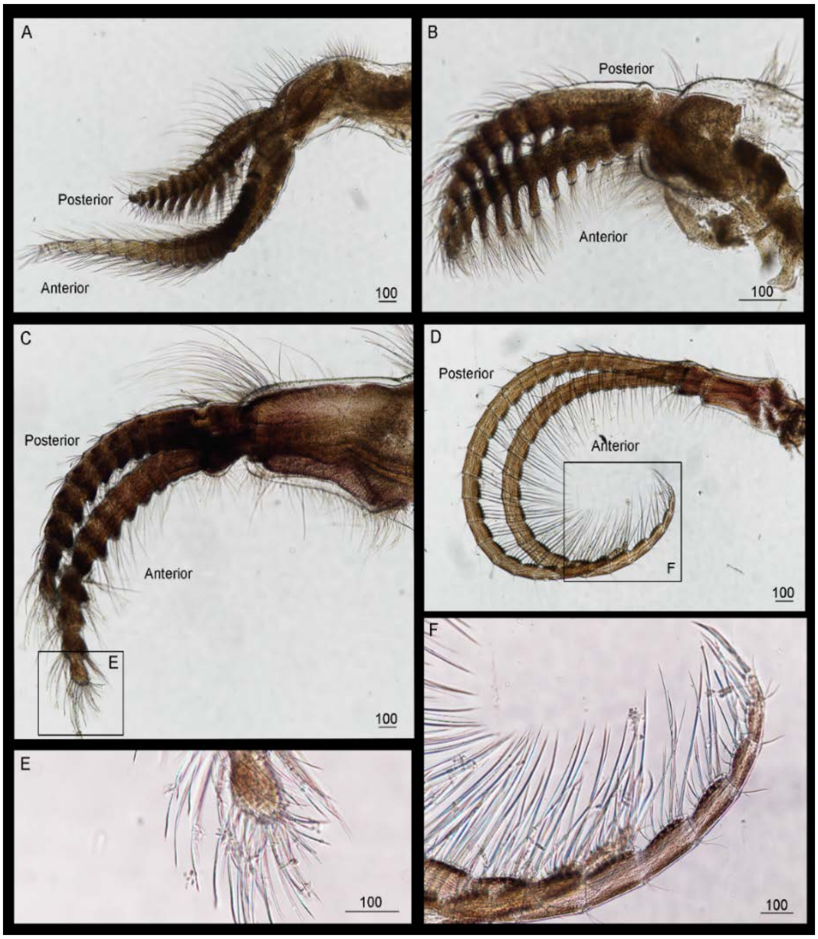

Fig. 81. Cirri of *Perforatus perforatus* (Bruguière, 1789). A, Cirrus I; B, Cirrus II; C, Cirrus III; D, Cirrus VI; E, Cirrus III with serrulate setae distally on anterior ramus; F, Cirrus VI with serrulate setae distally on both ramus. Scale bars in µm.

Maxilla lobed with dense serrulate setae on margin. Mandibular palp ovate, bearing short simple-type setae. Mandible with 5 teeth excluding inferior angle; second teeth bidentated; fourth tooth blunt; fifth tooth fused with inferior angle. Maxillule with slightly notch; upper and lower pair of spines well developed, with 8 spines between them; inferior angle with fine setae. Labrum with hairy fine small teeth on each crest (Fig. 82).

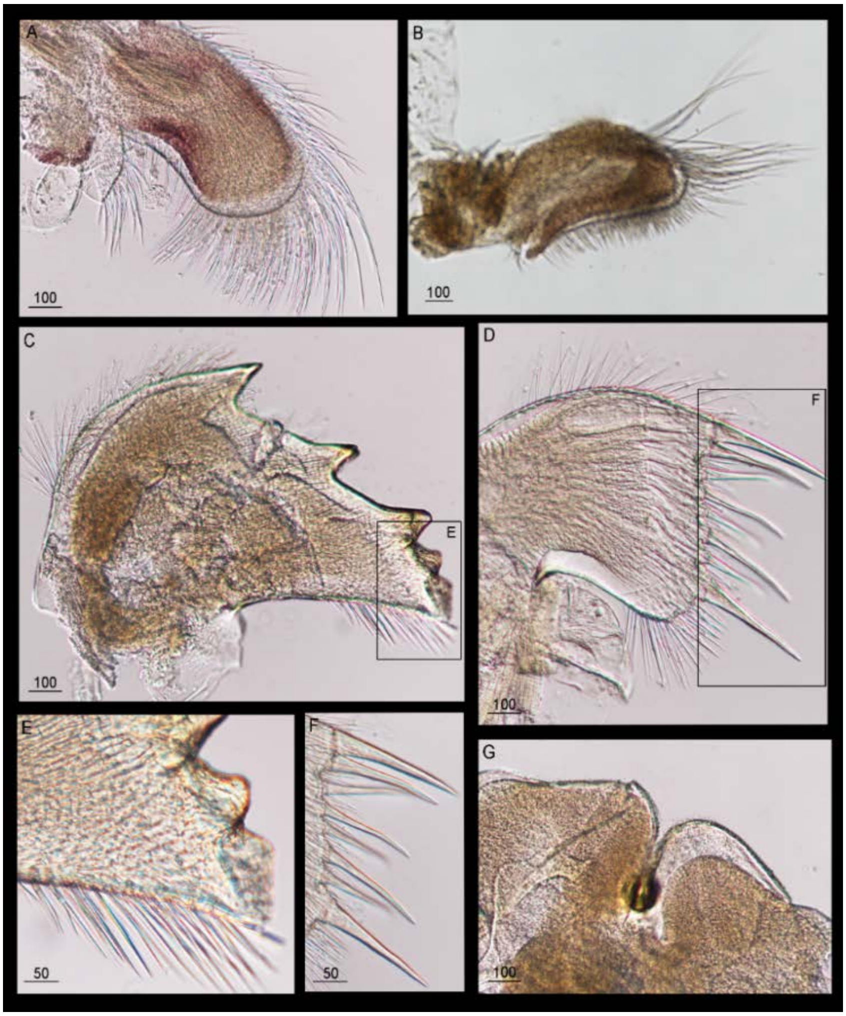

Fig. 82. Mouth parts of *Perforatus perforatus* (Bruguière, 1789). A, Maxilla; B, Mandibulatory palp; C, Mandible; D, Maxillule; E, Lower margin and inferior angle of mandible; F, Cutting edge of maxillule; G, Labrum. Scale bars in µm.

Distribution. Eastern Atlantic (common in the Mediterranean), southward to north-western Africa and Korea (Fig. 83).

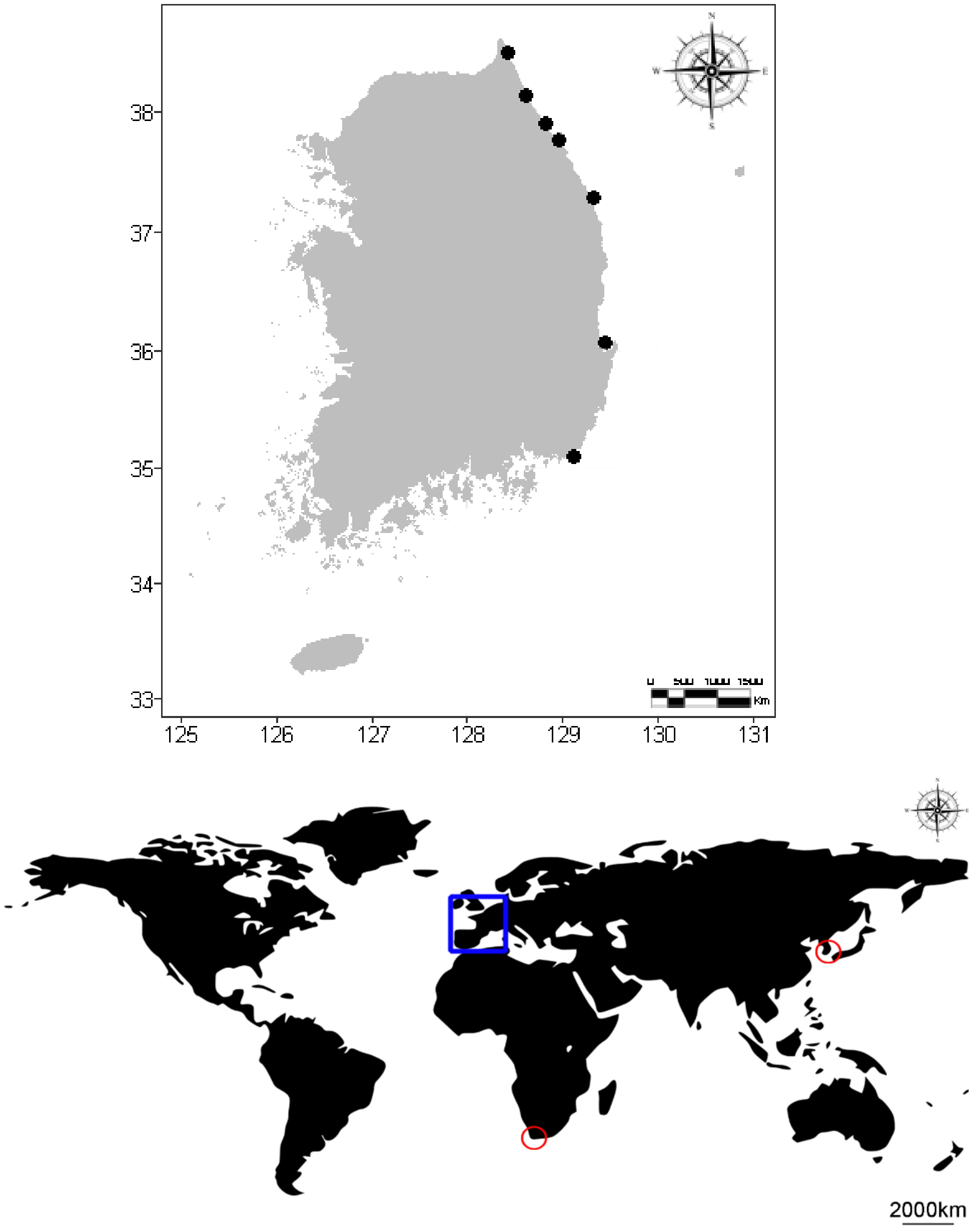

Fig. 83. Distribution of *Perforatus perforatus* (Bruguière, 1789). Legend: black circle = collected locality in Korea; red circle = distribution in world-wide; blue square = type locality.

Remarks. *Perforatus perforatus* is one of large barnacle which grows up to 3cm in diameter and height. This species is introduced barnacle in Korea. It has been found on the lower shore and in the neritic zone in warm temperate coasts of Korea and commonly occurs in the Mediterranean Sea along the eastern Atlantic coast. *P. perforates* can be found only in 3 ports of the southern coast of Korea until 2006 but has been started to expand their range with an increase in sea temperature and shipping ports. Now more than 5 sites of the southern and eastern coast of Korea were invaded by this species.

1.1.4 Discussion

Diversity of Shallow Water and Intertidal Barnacles in Korean Waters

From this study, 21 barnacle species were collected belonging to 14 genera. Among them, four species were found in either the intertidal zone or in shallow water (depth: 5–20m), five species were only found in shallow water. In addition, two coral-associated barnacles were collected, *Cantellius arcuatus* and *Cantellius* sp., of which the presence of these species in Korea has not been mentioned. These species were found in Jeju at depths between 5–20m. Prior to the present study, only two coral-associated barnacles were recorded from Korea, but their habitat was unclear as they were mostly caught by fishing nets thus far. The results of the present study increase the coral-associated barnacles to four species and identify the exact geographic names and host corals. Although, the Korean coral-associated barnacles are expected to remain smaller than those of Taiwan (36 species in 11 genera; Chan *et al*., 2013b), additional species will probably be discovered in Korea when benthic habitats are samples more intensively.

The taxonomic study of Korean barnacle species was conducted based on morphological characters (mainly for the shell and opercular plates). However, some intertidal barnacles have morphological variations affected by environmental differences. A high abundance of oysters can influence the recruitment of *T. japonica* and variation in the morphology of tergum and scutum (Figs. 21, 25). Under conditions of crowding, *C. challengeri* exhibits phenotypic plasticity in shell form and growth rate (Figs. 15, 18). Additionally, the barnacles *Tetraclitella chinensis* and *T. multicostata* are considered morphotypes of *T. chinensis* with same geographical distribution and under divergent selection pressure (Fig. 19).

Further study including additional sampling and examination will be needed for species which have different distributions and morphological variations. This can help to evaluate taxonomic status and explore the evolutionary basis of differences in morphology and geographical distributions.

Factors Affecting the Presence or Absence of Introduced Barnacles

At several sites surveyed in this study, *Perforatus perforatus* was absent in Korea Marine National Park areas. One of the reasons might be that they were primarily concentrated along the eastern coastal areas where some of the important international commercial shipping ports such as Busan, Ulsan and Donghae are located (Choi *et al*., 2013). Another might be that the distribution of *P. perforatus* is affected by the sea temperature of recipient waters. The average sea surface temperature between 2017 and 2018 around ports in Korea, where the population of this species is established, reached 25°C in the summer and 10°C in the winter. The salinity in the eastern coast is also higher than the southern and western coasts, but the chlorophyll *a* concentration is lower. Additionally, *P. perforatus* has been extending further north with climate changes in environmental conditions (Herbert *et al*., 2003). These findings suggest that the presence of could expand further northwards along the eastern coast of Korea.

For the remaining species of introduced barnacles, distribution varied among the sampling locations. *A. amphitrite* is a dominant fouling organism worldwide and is well established in the brackish waters of southern and western coasts in Korea, especially in ports attached on the bottom of ships and manmade structures. Also, there was an overlapping distribution between *A.*

amphitrite and *F. albicostatus*. This overlapping distribution and absence in the eastern coast may be due to the intolerance of high salinity rather than low sea temperature of this species. Generally, the appearance of *A. eburneus* is similar to *A. improvisus* and both species became successful cosmopolitan invaders. However, when comparing the absence or presence patterns in Korean waters, *A. eburneus* was absent in the eastern coast. The absence of this species is most likely not restricted by low salinity but rather by low winter temperature. Conversely, *A. improvisus* is present in the eastern coast and also occurs in brackish-water seas and estuaries in some sites, suggesting that its presence or absence in different sites is related to environmental effects of seawater temperature and salinity.

Under the effects of global warming, introduced species with a wide distribution and fluctuations in recruitment should be monitored. It may be useful to predict global climate change.

Biogeography of Barnacle Species on Korean Waters

In the present study, the composition of barnacles in Korean waters is related to the three different marine ecosystems. The geographical distribution range of barnacles is similar between the Yellow Sea Ecosystem and the Kuroshio. It can be attributed to four different driving forces: the Kuroshio main stream, northeast Asian Monsoon, tides, and buoyancy created by solar radiation and freshwater input. The Kuroshio intrudes northeastward, carrying heat and salt with variations. In the summer, the coastal currents transport the volume of freshwater to the Kuroshio region, and the sea surface water is heated by absorption of solar radiation. Under the mixing of fresh coastal waters and saline Kuroshio waters in the Yellow and East China Seas affecting the Kuroshio Ecosystem, the planktonic barnacle larvae can probably disperse between two ecosystems and cause overlapping of species composition. But the abundance patterns of shallow water and intertidal barnacles differed in these two ecosystems. One of the most common sponge-inhabiting barnacles in Korea, *Euacasta dofleini*, is present where the warm current approaches. This species had higher abundance in southern locations of Korea but its abundance decreased or were absent when approaching the eastern part of the Yellow Sea. It may be related to the YSWC seasonal circulation patterns. The YSWC is a seasonal compensation current, which occurs mainly in the winter, weakens quickly in the spring, and disappears in the summer and autumn (Guo and Hu, 2002). The distribution pattern of the intertidal barnacle, *Fistulobalanus kondakovi*, changed from the Yellow Sea coast to the south coast. It decreased in abundance in the Yellow Sea coast and was absent in diluted sea water. This pattern may be related to salinity. The salinity in the Yellow Sea Ecosystem is lower than the Kuroshio Ecosystem due to freshwater discharge from Changjiang river. The acorn barnacle, *Tetraclita japonica*, is a warm-water species typically attached to exposed rocks from the mid-to-low littoral zone in the Kuroshio Ecosystem and expands its distribution range into southern locations, but their abundance is low. This is probably affected by the increase in seawater temperature by global warming. Barnacle species composition in the Eastern coast Ecosystem is clearly different from other ecosystems. *Hesperibalanus hesperius hesperius* is only one present in this ecosystem and, conversely, *Capitulum mitella*, *T. japonica*, *E. dofleini*, *Fistulobalanus albicostatus*, *F. kondakovi*, and *A. amphitrite* are absent. *H. h. hesperius* is distributed on the eastern coast of Korea as a cold-water species, suggesting this is affected by sea temperature and cold current. However, *Balanus rostratus*, also known as a cold-water species, showed range expansion from the eastern coast and Yellow Sea coast to the southern coast. The individuals living along the southern coast are generally small and found in sponges. Also, the abundance of barnacles is rare in the Yellow Sea coast, which is subjected to dilution in the summer due to freshwater discharge. The expansion may be more affected by salinity than sea temperature.

In Korea waters, biogeographic patterns of some marine groups including copepods, decapods, algae, and mollusks have been well studied. Distributions of some copepods and decapods are affected by the sea surface temperature and three different marine ecosystems (Kim, 2004; Rho *et al*., 2005). Also, the distributional differences in endemic algaes support the idea that the East Sea had important sites as refugia during the Last Glacial Maximum (Kim *et al*., 2018). However, despite cold-water currents and different geographical and climate zones in the eastern part of the Korean seas from the other two parts, cold-water species of marine bivalve mollusks co-occur with tropical-subtropical species along the eastern coast because of the high summer sea water temperatures there (Lutaenko *et al*., 2019). Likewise, one of the warm-water introduced barnacle species, *P. perforatus*, has been rapidly expanding its range with increasing temperatures. This species was not previously known from Yangyang (Choi *et al*., 2013) but presently lives further north, overlaying occurrences of *H. h. hesperius*. Additionally, *Semibalanus cariosus* (Pallas, 1788) and *Chthamalus dalli* Pilsbry, 1916, which were previously recorded as cold-water species in the eastern coast, were absent in the studied sites. Precise understanding of the relationship between their distribution of time and habitat, however, is unknown.

Regular monitoring of the abundance of warm-and cold-water species influenced by oceanographic currents, sea water temperature, and salinity differences among the three marine ecosystems is necessary to predict climate change for the next few decades.

1.2 Molecular Taxonomic Study of studied Barnacles

1.2.1 Introduction

The order Sessilia is one of the most important ecologically and economically diverse groups belonging to the subphylum Crustacea. Barnacles are discovered in various environments, such as intertidal, subtidal, deep-sea and brackish water zone as well as freshwater. They are abundant and successful groups of marine ecosystems as their high density and fouling species that cause problems for marine industries (Chan *et al*., 2009).

Barnacles have a biphasic life cycle, consisting of the planktonic larval phase and sessile adult stage. Their variable geographical distribution, abundance, and genetic structure are affected by larval dispersal. Depending on larval dispersal and settlement, adult barnacles display an extreme variation of morphology within a species and are affected by both physical and biological factors, resulting in variation in geographical distribution.

Previous studies on barnacles are generally conducted on the morphology of shell, opercular plates (scutum and tergum) and arthropodal characters, including setal types of cirri and Mouth parts in Korea. However, the effects of extreme developmental ‘phenotypic plasticity’ in barnacles have been continuously reported. Given their sessile suspension feeders, the ability to capture food and compete with mates is important that the length of cirri and penis can be modified according to different wave exposure (Marchinko & Palmer, 2003; Chan & Hung, 2005; Hoch, 2008, 2011). According to Marchinko (2003), transplantation of *Balanus glandula* from exposed to shaded shore sites induced an increase in cirral length. Also, plastic loss and gain of leg segments in barnacles appear to be reversible (Kaji & Palmer, 2017). The change of the density aggregation of barnacles can affect the abundance and ecology of other associated species. Under conditions of crowding and sparse populations, there are differences in the growth form of shell and fecundity (Wu, 1980; Wethey, 1984). Additionally, introduced barnacle taxonomy is unclear due to the presence of cryptic species and despite their worldwide distribution, little is known about the phylogeography of introduced species. Misidentification of cryptic species can cause dramatic impacts on conservation. Therefore, it is important to determine the identification of introduced species, especially taxonomically difficult and cryptogenic taxa.

Molecular identification using partial genes of mitochondrial cytochrome c oxidase subunit I (COI) and mitochondrial 12S ribosomal DNA (12S rDNA) is now widely used when identification based on barnacle morphology is inconclusive including identification of cryptic species (Chan *et al*., 2007a, b). Using one gene can be effective, but it can be insufficient when used for the phylogeny of morphotypes and closely related species.

Based on both morphological and molecular phylogenetic analysis, this study was conducted to discriminate the species and evaluate taxonomic status. A total of 21 species were used.

1.2.2 Materials and Methods

Sampling

Barnacle specimens examined in this chapter were sequenced for the DNA identification after morphological identification of species. A total of 21 species representing 14 genera were sampled, *Capitulum* (*C. mitella*), *Chthamalus* (*C. challengeri*), *Tetraclitella* (*T. chinensis*), *Tetraclita* (*T. japonica*), *Euacasta* (*E. dofleini*), *Striatobalanus* (*S. amaryllis*), *Cantellius* (*C. arcuatus* and *Cantellius* sp.), *Pyrgomina* (*P. oulastreae*), *Fistulobalabus* (*F. albicostatus* and *F. kondakovi*), *Amphibalanus* (*A. amphitrite, A. reticulatus, A. eburneus* and *A. improvisus*), *Balanus* (*B. rostratus* and *B. trigonus*), *Megabalanus* (*M. rosa* and *M. volcano*), *Hesperibalanus* (*H. h. hesperius*) and *Perforatus* (*P. perforatus*). All intertidal barnacles were collected during low tide and others were collected using hammer and chisel at 5–20m in depth by SCUBA diving. Additionally, one stalked barnacle, *Lepas anserifera* collected from Jeju, Korea, in August 2018 was included in the phylogenetic analysis. This stalked barnacle can be easily found on shores where the floating materials arrive, but this species is not studied in the biogeography section as it is difficult to identify the exact habitat (Table 3.).

Table 3. List and collection information of the Korea samples examined (^{P} Phenotypic plasticity in three intertidal species, ^{C} Cryptic diversity of introduced species)

Sample ID	Species name	Date	Collection locality
19YS1	*Capitulum mitella*	18.04.17.	Hyeoldo, Jindo
19YS2		18.06.25.	Seomanghang, Jindo
19YS3		18.10.29.	Seogwipo, Jeju
18YS11	*Chthamalus challengeri* ^{P}	17.06.28.	Chaeseokgang, Buan
18YS12		18.09.05.	Ammyeondo, Taean
18YS13		18.10.29.	Seogwipo, Jeju
18JJ1 18JJ2	*Tetraclitella chinensis* ^{P}	18.10.29.	Seogwipo, Jeju

18JJ3			
18YS21	*Striatobalanus amaryllis*	17.04.13.	Chaeseokgang, Buan
18YS22		18.06.25.	Seomanghang, Jindo
18YS31	*Tetraclita japonica* [P]	17.04.13.	Chaeseokgang, Buan
18YS32		18.07.25.	Seomanghang, Jindo
18YS33		18.10.29.	Seogwipo, Jeju
18YS34	*Euacasta dofleini*	17.09.24.	Cheongsando, wando
18YS35			
18YS36		18.03.26.	Seogwipo, Jeju
18JJ15	*Cantellius arcuatus*	18.03.27.	Seogwipo, Jeju
18JJ16			
18JJ17			
18JJ20	*Cantellius* sp.	18.03.26.	Seogwipo, Jeju
18JJ21			
18JJ22			
18JJ23	*Pyrgomina oulastreae*	18.03.20.	Haeundae, Busan
18JJ24			
18JJ25		18.03.27.	Seogwipo, Jeju
18YS51	*Fistulobalanus albicostatus*	17.06.28.	Chaeseokgang, Buan
18YS52		17.09.24.	Cheongsando, Wando
18YS53		18.03.20.	Haeundae, Busan
18YS54	*Fistulobalanus kondakovi*	17.05.11.	Sangju, Namhae
18YS55			
18YS56		17.06.28.	Chaeseokgang, Buan
17YS71	*Amphibalanus amphitrite*	17.04.13.	Chaeseokgang, Buan
17YS72		18.03.21.	Pungwhali, Tongyoung
17YS73		18.08.15.	Hahyo port, Jeju
17YS81	*Amphibalanus eburneus* [C]	18.03.21.	Pungwhali, Tongyoung
17YS82		18.03.22.	Irun-myeon, Geoje
17YS83			
17YS91	*Amphibalanus improvisus* [C]	17.04.13.	Chaeseokgang, Buan
17YS92		18.07.18.	
17YS93		18.06.21.	Jumunjin, Gangneung
19MCP1	*Amphibalanus reticulatus*	18.06.25.	Seomanghang, Jindo
19MCP2		18.09.05.	Ammyeondo, Taean
17YS51	*Balanus rostratus*	17.04.13.	Chaeseokgang, Buan
17YS52		18.06.20.	Susangil, Yangyang
17YS37	*Balanus trigonus*	18.03.20.	Haeundae, Busan
17YS38		18.06.25.	Seomanghang, Jindo
17YS39		18.08.20.	Janghohang, Samcheck
17YS21	*Megabalanus rosa*	17.03.01.	Seogwipo, Jeju
17YS22		17.04.14	Irunmyeon, Geoje
17YS23		18.06.20.	Susangil, Yangyang
17YS26	*Megabalanus volcano*	17.04.14.	Irunmyeon, Geoje
17YS27		18.02.28	Seogwipo, Jeju
17YS28			
19JMJ1	*Perforatus perforatus*	17.05.25.	Jangsaengpo, Ulsan
19JMJ2		18.06.21.	Jumunjin, Gangneung
19JMJ3		18.11.06.	Guryongpo, Pohang
19GNP1		17.06.27.	Daejinhang, Goseong

19GNP2 19GNP3	*Hesperibalanus hesperius hesperius*		
19JJ1 19JJ2 19JJ3	*Lepas anserifera*	18.08.15.	Hahyo port, Jeju

Dna Extraction, PCR Amplication and Molecular Analysis

Genomic DNA was extracted from soft tissues of each specimen using the QIAamp DNA Micro kit (QIAGEN, Germany). Partial sequences from the mitochondrial 12S rDNA and COI genes were amplified using polymerase chain reaction (PCR) with primers 12S-FM and 12S-R2 (Tsang *et al*., 2015) in addition to the universal primer sets. LCO1490 and HCO 2198 (Folmer et al., 1994). DNA sequences were proofread using MEGA7 (Kumar *et al*., 2016). All sequences were aligned using multiple alignments and a fast Fourier transform (MAFFT, Katoh *et al*., 2002). Alignments were also checked by the eye. Some sequences were treated with gaps due to missing data. All phylogenetic analysis was performed based on maximum likelihood (ML) analysis in RAxML 8.0.2 (Stamarakis, 2014) implemented on the Cyberinfrastructure for Phylogenetic Research (CIPRES) using GTRGAMMA model of nucleotide substitution and 1,000 bootstrap replicates. In the multigene analysis, alignments of two genes (12s rDNA and COI) were concatenated and partitioned by gene regions to resolve alternative phylogenies. For all analysis, *Lepas anserifera* Linnaeus, 1767 was selected as outgroups. These species have a cosmopolitan distribution and are found around the world in tropical and subtropical seas. A matrix of pairwise distances within and among the species was calculated in MEGA7 using Kimura’s 2-parameter model (K2P) (Kumar *et al*., 2016).

1.2.3 Results

Molecular identification using both mitochondrial 12S rDNA and COI gene sequences complimented after the morphology-based identification. After trimming and aligning the sequences, 442 bp of 12S rDNA and 612 bp of COI were respectively obtained from 58 and 61 specimens of collected barnacle species. Sequence similarity (K2P distance, Table 4.) and the phylogenetic analysis (Maximum Likelihood, Figs. 84, 85) confirmed the identification of specimens, which reveal significant geographic variation and cryptic species. The phylograms based on the two markers showed high similarities (Fig. 84A, B). The phylogeny of the concatenated data set was similar to the phylogenetic trees derived from individual genes (Fig. 85). Among the 63 barnacle specimens investigated, three specimens were excluded from further comparisons based on K2P distance in the multigene analysis due to missing sequences. From the phylogenetic tree, 22 species formed its own clade with high support values respectively.

In pairwise comparisons, the K2P distance among the sequences ranged from 0.1% to 33.9% (Table 4). The intraspecific divergence of phenotypic plasticity in three barnacles, *T. japonica* and *T. chinensis* were only 0.1% and *C. chthamalus* was 0.5%. This suggests the environmental differences to induce variations in the shell morphology and growth rate can be from microhabitat differences and explain the adaptive ability to successfully colonize different substrate levels with different spatial variability gradients. Also, among the introduced barnacles, *A. improvisus* and *A. eburneus* have similar morphology, leading to confusion about precisely which species were recorded. The combined datasets of 12S and COI sequences classified species successfully, showing the lineage *A. improvisus* as a sister group to the lineage of *A. eburneus* and the pairwise distance was 8.8% between two species. Further studies are needed to confirm the identity and geographical distribution of the widely distributed species.

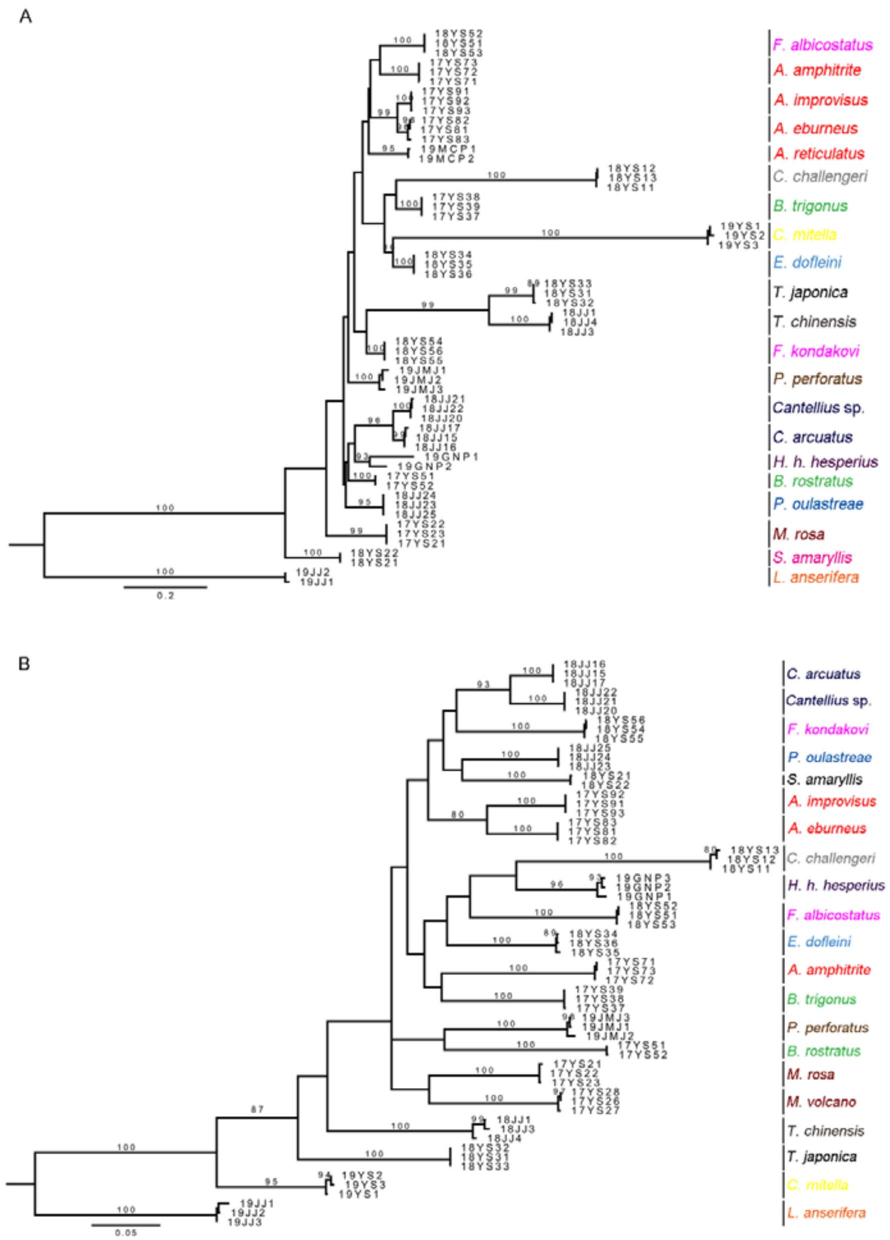

Fig. 84. Phylogenetic trees for barnacle species based on maximum likelihood (ML) analysis. A, 12S rDNA; B, cytochrome *c* oxidase subunit I (COI) sequences. Bootstrap scores of > 80% are presented at nodes. The scale bar indicates the number of nucleotide substitutions per site. The same genus was marked in the same color.

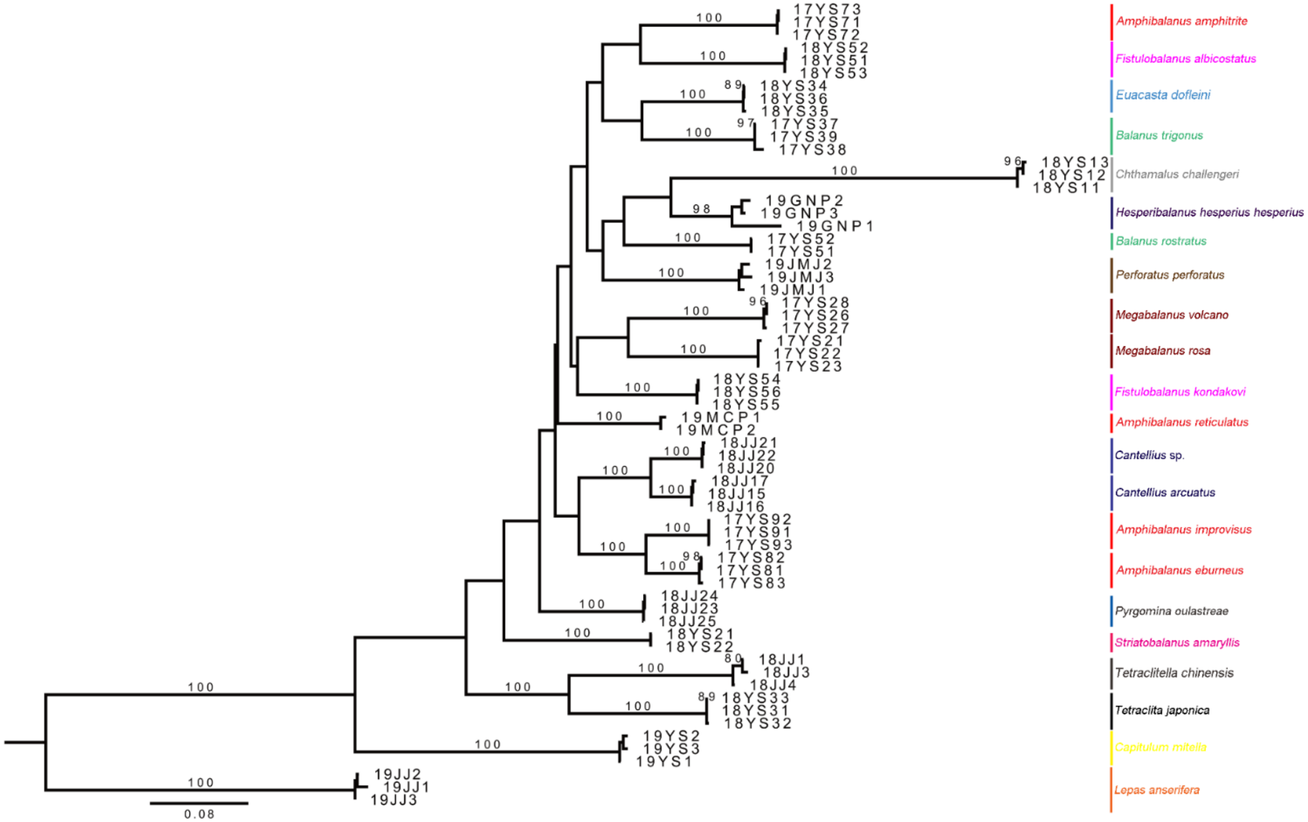

Fig. 85. The best scoring maximum likelihood (ML) tree based on concatenated 12S rDNA and cytochrome *c* oxidase subunit I (COI) datasets. Bootstrap scores of > 80% are presented at nodes. The scale bar indicates the number of nucleotide substitutions per site. The same genus was marked in the same color.

Table 4. Mean K2P distance for the concatenated molecular datasets for 12S rDNA + COI genes between and within the studied species. Used symbols:N/A - not available

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1. *Capitulum mitella*	0.008																					
2. *Chthamalus challengeri*	0.305	0.005																				
3. *Tetraclitella chinensis*	0.270	0.271	0.010																			
4. *Tetraclita japonica*	0.268	0.275	0.190	0.001																		
5. *Striatobalanus amaryllis*	0.259	0.244	0.225	0.224	0.001																	
6. *Hesperibalanus hesperius hesperius*	0.265	0.213	0.260	0.251	0.202	0.025																
7. *Euacasta dofleini*	0.265	0.238	0.238	0.239	0.199	0.182	0.003															
8. *Cantellius arcuatus*	0.270	0.223	0.222	0.228	0.176	0.180	0.160	0.003														
9. *Cantellius* sp. nov.	0.274	0.221	0.221	0.235	0.181	0.182	0.166	0.071	0.002													
10. *Pyrgomina oulastreae*	0.264	0.220	0.216	0.218	0.161	0.165	0.162	0.145	0.145	0.002												
11. *Fistulobalanus albicostatus*	0.268	0.230	0.240	0.252	0.208	0.185	0.181	0.174	0.180	0.171	0.001											
12. *Fistulobalanus kondakovi*	0.264	0.221	0.218	0.224	0.180	0.177	0.155	0.156	0.156	0.152	0.154	0.001										
13. *Amphibalanus reticulatus*	0.308	0.265	0.235	0.230	0.190	0.186	0.148	0.139	0.157	0.110	0.137	0.132	0.005									
14. *Amphibalanus amphitrite*	0.297	0.249	0.242	0.254	0.199	0.204	0.173	0.170	0.171	0.180	0.163	0.164	0.143	0.001								
15. *Amphibalanus eburneus*	0.276	0.235	0.243	0.233	0.181	0.194	0.159	0.144	0.145	0.161	0.186	0.154	0.134	0.175	0.004							
16. *Amphibalanus improvisus*	0.291	0.243	0.244	0.222	0.181	0.199	0.164	0.149	0.145	0.153	0.174	0.152	0.138	0.166	0.088	0.001						
17. *Balanus trigonus*	0.290	0.230	0.236	0.245	0.192	0.188	0.143	0.168	0.179	0.174	0.191	0.167	0.170	0.181	0.164	0.167	0.006					
18. *Balanus rostratus*	0.265	0.252	0.253	0.250	0.215	0.169	0.184	0.173	0.180	0.162	0.199	0.175	0.141	0.195	0.190	0.198	0.183	0.002				
19. *Megabalanus rosa*	0.265	0.231	0.239	0.237	0.206	0.205	0.169	0.187	0.199	0.181	0.211	0.187	0.184	0.214	0.161	0.182	0.191	0.190	0.003			
20. *Megabalanus volcano*	0.211	0.254	0.218	0.211	0.183	0.206	0.208	0.189	0.210	0.196	0.208	0.180	N/A	0.210	0.195	0.178	0.214	0.234	0.173	0.003		
21.*Perforatus perforatus*	0.273	0.250	0.223	0.231	0.206	0.194	0.167	0.187	0.175	0.156	0.185	0.165	0.135	0.174	0.171	0.173	0.162	0.165	0.176	0.186	0.015	
22. *Lepas anserifera* (outgroup)	0.313	0.322	0.327	0.309	0.295	0.291	0.320	0.292	0.308	0.317	0.298	0.316	0.339	0.303	0.303	0.317	0.315	0.307	0.304	0.288	0.300	0.008

Chapter 2.

Biodiversity and Host Specificity of Coral-Associated Barnacles in Korea, with Descriptions

2.1 Diversity and host specificity in coral-associated barnacles in northern coral distribution limit of East China Sea

2.1.1 Introduction

Coral reef ecosystem supports a high diversity of scleractinian corals and their associated fauna. More than 56% of coral-associated fauna form obligate symbiotic relationships with their coral hosts (Stella *et al*., 2011), and these associated fauna are major contributors to the overall biodiversity of the coral system (Blackall *et al*., 2015). The diversity of corals and their associated fauna is particularly high in the Coral Triangle region, which is considered a marine biodiversity hotspots. The distribution of coral reefs is limited by water temperature because hermatypic corals cannot survive in an environment with winter temperatures below 14–18°C (Veron, 1986). At high latitudes, where the water temperature is approximately 14°C, corals living at the limit of their geographical distribution are mainly composed of encrusting forms and exhibit considerably reduced growth and reproduction. Consequently, these high-latitude corals do not form intense reefs, and are called marginal communities. Studying the basic ecology of corals and their associated fauna is particularly crucial for conserving marginal coral reefs because they are very sensitive to impending environmental changes (De Palmas *et al*., 2015). Species diversity of corals at high latitudes and in marginal communities has been studied in some locations (Denis *et al*., 2013; Sugihara *et al*., 2014). However, the diversity of coral-associated fauna and their host usage in marginal communities have received limited attention.

Coral-associated barnacles are among the common obligate symbionts of scleractinian corals, and most species are classified in the family Pyrgomatidae under the order Sessilia (Ross & Newman, 1973). The bases of coral-associated barnacles are cup shaped and embedded in the skeleton of their host corals. The external calcified shells are overgrowths by the coral tissues. Coral-associated barnacles are principally suspension feeders but ^{13}C stable isotope studies have shown that the organic matter produced by coral zooxanthellae contributes to some carbon in the barnacles (Achituv & Mizrahi, 1996; Achituv *et al*., 1997). In return, ammonium released from the coral-associated barnacles is absorbed by the zooxanthellae in the corals. Up to date, more than 70 species of coral-associated barnacles have been reported worldwide, with variable degrees of host specificity (Tsang *et al*., 2009, 2014; Chan *et al*., 2013a, b).

In the West Pacific region, studies on the species diversity of coral-associated barnacles have been focused on tropical and subtropical coral reefs, where coral diversity is extremely high (*e.g*., Hong Kong [Foster, 1982]; Taiwan [Chan *et al*., 2013a, b, 2014]; Philippines [Rosell, 1981]). More than 50 coral-associated barnacle species have been recorded in the tropical and subtropical waters of the West Pacific, including a considerable number of specialists and generalists with respect to their coral hosts (Ross & Newman, 1973). Coral-associated barnacles in high-latitude regions probably exhibit different assemblages or host ranges. Most studies on barnacles associated with high-latitude corals have been conducted on the Pacific coast of Japan, under the influence of the warm Kuroshio Current. In this region, 30 coral-associated barnacle species from 100 species of coral hosts have been recorded (Asami & Yamaguchi, 1997).

Jeju Island is located in the southwestern waters of Korea, in the East China Sea, and the hydrology is influenced by the warm Tsushima Current, a branch of the Kuroshio Current, as well as the Yellow Sea runoff. Because of the low seawater temperature in winter and the minor influence from the Kuroshio Current, the island's benthic communities are mainly dominated by macroalgae and soft corals. Only eight species of zooxanthellate scleractinian corals and a few species of nonzooxanthellate corals have been recorded on Jeju Island (Sugihara *et al.*, 2014, Kim, 1998). The waters near Jeju Island are considered one of the northern limits of coral distribution in the East China Sea (Sugihara *et al.*, 2014). However, the diversity and host range of coral-associated barnacles at the northern limit of coral distribution are relatively unknown compared with that of barnacles on high-latitude corals in the Pacific Ocean. Only two species of coral-associated barnacles have been reported thus far on Jeju Island (Kim, 1998). The objective of the present study was to examine the diversity of coral-associated barnacles and their host relationship on Jeju Island, Korea.

2.1.2 Materials and Methods

Study Sites and Timing

In total, nine sites were selected in the southern waters of Jeju Island in August 2016 to collect coral-associated barnacles (Fig. 86). Coral-associated barnacles were collected through scuba diving at depths of 5–20m. Before sampling the coral-associated barnacles, the entire piece of coral with the barnacles was photographed *in situ* for coral identification. Small pieces of coral with embedded barnacles (approximately 5 × 5cm) were collected using hammer and chisel at a 5–20m depth through scuba diving. All barnacles and host corals were preserved in 95% EtOH.

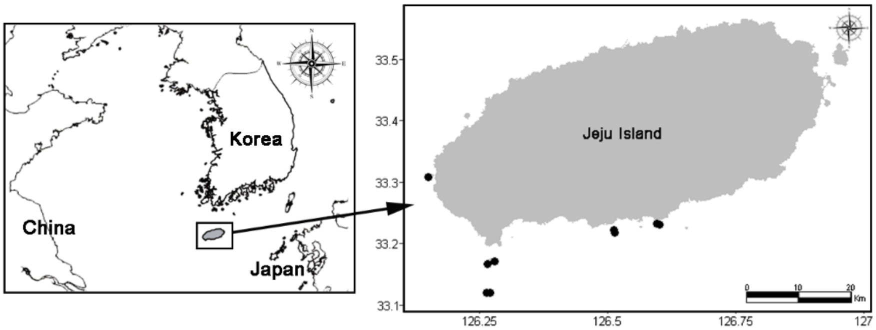

Fig. 86. Map of Jeju Island, Korea. Showing the collection sites of coral-associated barnacles used in this study.

Relative Coral Abundance

The coral diversity and abundance at the collection sites were quantified using the point transect techniques at Seop Seom (northeast [NE] and southeast waters) and Beom Seom, where coral abundance is relatively higher than that at other sites. At each site, 30m transects were established at 5–20m. Coral species in every 1m interval of the transect were photographed and identified. The percentage abundance of coral species at each site was calculated as the cumulative point abundance divided by the total point abundance (i.e. 30m = 30). Coral species were identified using the key and guides by Sugihara *et al*. (2014).

Abundance of Barnacles on Corals

For each barnacle specimen collected, the entire piece of coral with the barnacles was photographed *in situ* with a 9cm scale bar before collection. Number of coral-associated barnacles on each piece of coral hosts was measured from an equivalent 9cm x 9cm quadrat = 81cm^2 area inside each digital photograph. Variation in barnacle abundance on each coral host (number per 81cm^2 quadrat) was analysed using One-Way Analysis of Variance (ANOVA).

Morphological Examination

Barnacles were isolated from the host corals using forceps, and the morphological characteristics of shell parts (shells, scutum and tergum) and somatic bodies (six pairs of cirri, penis, and oral cone) were examined. Organic debris and coral tissue on the surface of the shells, scutum and tergum were removed using forceps and further cleaned ultrasonically (for 2–5 sec). The cleaned shells and opercular valves (scutum and tergum) were immersed in 1.5% bleach for approximately 5hours to completely digest the organic tissue, and the shells were then rinsed with slow-running purified water for 30 min and air-dried. The shells, scutum and tergum were gold coated and observed under SEM, following the methods of Chan *et al*. (2013b). The cirri, penis and oral cone were dissected from the somatic bodies and examined using a light microscope (Zeiss Scope A1, Zeiss, Germany) with high definition lenses (Zeiss Plan APO Chromat 40X/0.95 and ZEISS Plan APO Chromat 100x/1.4 oil), which allowed clear observation of setal types on the cirri and Mouth parts. The setal descriptions follow those of Chan *et al*. (2008c). The rostral–carinal basal diameter of the collected specimens was measured using a digital caliper (±0.1mm). All barnacle specimens were housed in the barnacle collection of the Coastal Ecology Laboratory of Academia Sinica, Taiwan and Laboratory of Systematics and Molecular Evolution in Seoul National University.

Molecular Analysis

Total genomic DNA was extracted from the soft tissue of barnacle specimens using the Qiagen QIAquick Tissue Kit (Chatsworth, CA, USA) following the manufacturer's instructions. Partial sequences of the mitochondrial genes 12S rDNA (12S) and cytochrome c oxidase subunit I (COI) were amplified using polymerase chain reaction with the primers 12S-FB and 12S-R2 (Tsang *et al*., 2009) and COI-F5 and COI-R4 (Chen *et al*., 2014) respectively. Mitochondrial markers including COI and 12S are useful for species delineations in coral-associated barnacles and a number of studies have used these two markers for new species descriptions (Achituv, 2009; Chan *et al*., 2013). There are large numbers of mitochondrial gene sequences from coral-associated barnacles available from the Genbank. The use of mitochondrial markers in the present study makes it possible to compare species diversity data from Jeju waters with other available mitochondrial sequences. The PCR solution contained 40ng of template DNA, 5μL of Taq DNA Polymerase Master Mix (1.5mM $MgCl_2$; Ampliqon, Denmark), 1μM of each primer, and ddH_2O for a total volume of 10μL. PCR was conducted under the following conditions: 2 min at 95°C for initial denaturation, 35 cycles of 30 sec at 95°C, 1 min at 48°C, 1 min at 72°C, and a final extension for 5 min at 72°C. The PCR products were then purified using a DNA gel purification kit (Tri-I Biotech, Taipei, Taiwan). Direct sequencing of the purified PCR products was performed using the ABI 3730XL Genetic Analyzer with BigDye terminator cycle sequencing reagents (Applied Biosystems, Foster City, CA, USA).

DNA sequences were proofread using MEGA v. 7 (Kumar *et al*., 2016) and aligned with the *Cantellius* sequences from GenBank through multiple alignment using MAFFT v. 6.717 (Katoh *et al*., 2002). Alignments were also examined visually and ambiguous positions were adjusted manually. A matrix of genetic distances within and among the species was generated using Kimura's two-parameter model in MEGA v. 7. The stability of clades was evaluated using bootstrap tests with 1,000 replications. A maximum likelihood (ML) test was conducted for concatenated datasets (mitochondrial 12S + COI). ML analysis was performed using RAxML-HPC2 on XSEDE (Stamatakis, 2014) through the online server Cyberinfrastructure for Phylogenetic Research (CIPRES) with the GTRGAMMA model of nucleotide substitution and 1,000 bootstrap replicates. For analysis, other *Cantellius* and pyrgomatid species available from the Genbank were used for comparisons and *Amphibalanus amphitrite* was selected as an outgroup. The use of *A. amphitrite* as an outgroup candidate is appropriate for molecular phylogenetic analysis of coral-associated barnacles because from a previous study on molecular phylogeny of coral-associated barnacles (Tsang *et al*., 2014), the coral-associated barnacle clade (pyrgomatid clade) is sister to balanid clade including *A. amphitrite*.

2.1.3 Results

Coral Abundance

The total coral abundance was 52% in northwest (NW) Seop Seom, 22% in NE Seop Seom, and approximately 10% in Beom Seom. Five species of corals were sampled, namely *Montipora millepora*, *Psammocora profundacella*, *P. albopicta*, *Oulastrea crispata* and *Alveopora japonica*. In NW Seop Seom, *M. millepora* had the highest relative abundance, with 26% coverage. *A. japonica* was more abundant in NE Seop Seom. *Psammocora* spp. and *O. crispata* were relatively less abundant among the sites studied (Fig. 87).

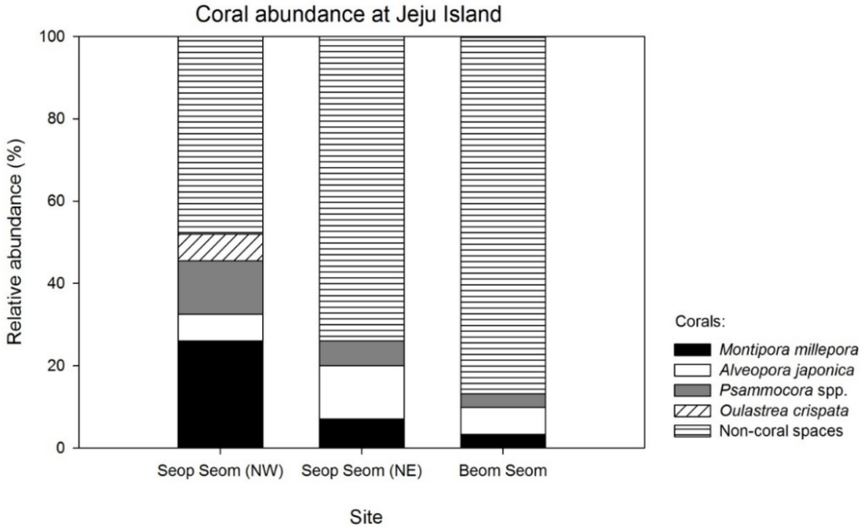

Fig. 87. Relative abundance of scleractinian corals in south and west waters of Seop Seom and Beom Seom off of Jeju waters from 30 metres transect surveys. *Psammocora* spp. include both *P. profundacella* and *P. albopicta*, which are difficult to identify *in situ* in the field without examining the columellae structure from the coral skeleton. Non-coral surfaces were colonized by soft corals, kelps and sponges.

Barnacle Diversity, Abundance and Host Usage

Among all the sites sampled, three species of barnacle covering two genera from two subfamilies were identified, namely the Pyrgomatinids *Cantellius arcuatus* and *Cantellius* sp. and the Megatrematinid *Pyrgomina oulastreae* (see section 2-2 for detailed taxonomic description of barnacle species). Among the eight sites studied, *C. arcuatus* was found exclusively on the coral *M. millepora*. *Cantellius* sp. was exclusively present on *A. japonica*. *P. oulastreae* was present on a number of coral hosts, such as *Psammocora* spp. (both *profudacella* and *albopicta*) and *Oulastrea crispata*, but it was absent from *Montipora* and *Alveopora* (Fig. 88).

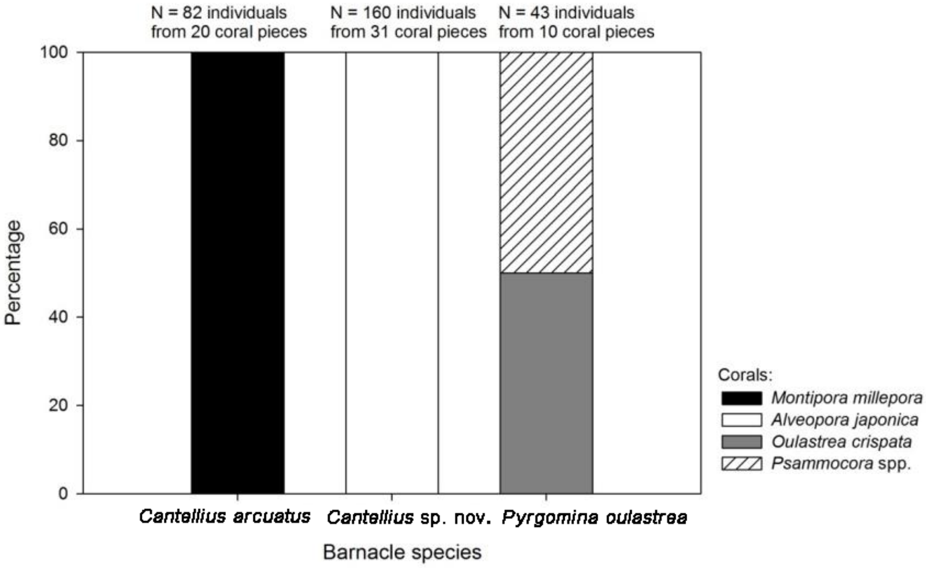

Fig. 88. Coral host usage by barnacles *Cantellius arcuatus, Cantellius* sp. and *Pyrgomina oulastreae* in Jeju Island. Note *C. arcuatus* and *Cantellius* sp. were 100% found on the coral *Montipora millepora* and *Alveopora japonica* respectively. *Pyrgomina oulastreae* are found on both *Psammocora* spp. and *Osulastrea crispata*. *Psammocora* spp. include both *P. profundacella* and *P. albopicta.*

Cantellius arcuatus has the highest abundance on its coral host *Montipora millepora*, reaching an average of 25 individuals per 81 cm^2 (Fig. 81). Compared to *C. arcuatus*, abundance of *Pyrgomina oulastreae* on *Psammocora* and *Oulastrea* corals are lower, reaching an average about 4.8 and 2.6 individuals per 81 cm^2 respectively (Fig. 81). *Cantellius* sp. has an average of 3.4 individuals per 81 cm^2. One-Way ANOVA showed that barnacle abundances on different corals were significant, $F_{(3,\ 57)} = 82.84$, $p < 0.05$. Pairwise SNK results showed that *Cantellius arcuatus* on the coral *M. millepora* has significantly higher abundance than *P. oulastreae* on *Psammocora* and *Oulastrea* corals and *Cantellius* sp. on *Alveopora* coral, whilst *P. oulastreae* and *Cantellius* sp. have similar abundances on their coral hosts (Fig. 89).

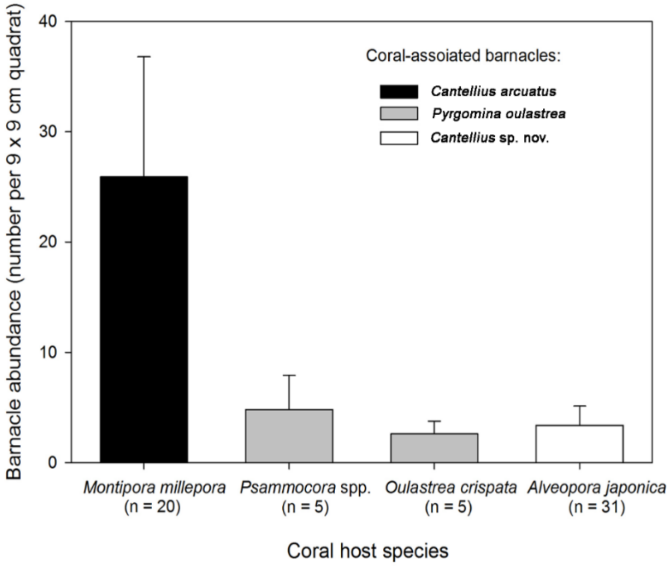

Fig. 89. Mean abundance (+1 standard deviation) of coral-associated barnacles *Cantellius arcuatus*, *Cantellius* sp. and *Pyrgomina oulastreae* on their coral hosts *Montipora millepora*, *Psammocora* spp., *Osulastrea crispata* and *Alveopora japonica*, respectively, in Jeju Island. *Psammocora* spp. include both *P. profundacella* and *P. albopicta.*

Molecular Analysis of Coral-Associated Barnacles

Phylogenetic trees from 12S and COI revealed similar patterns, except the species *Adna anglica* and *Pyrgomina oulastreaea* were not differentiated in the 12S marker (Figs. 90, 91). The multiple sequence alignment revealed that the K2P distance among the sequences ranged from 0.2% to 20.5% (Table 5). The intraspecific divergence of *C. arcuatus* was 0.4% (Table 5), and it was clustered in the same clade as the sequence of *Cantellius* sp. 2 (NCBI assession numbers:12S HG970552 and COI HG970494) and with *C. arcuatus* collected from Malaysia, Kochi in Japan, Taiwan and Papua New Guinea in the concatenated tree (12S + COI) (Fig. 92). From the concatenated tree, *Cantellius* sp. collected in the present study was clustered in its own clade, and it differed from *C. euspinulosum* collected in Taiwan (Fig. 92). Furthermore, their distant relationship was supported by the K2P distance, which was 9.1% (Table 5). *P. oulastreae* was clustered into its own clade, and located in another major clade containing *Adna* and *Ceratochoncha* (Fig. 92).

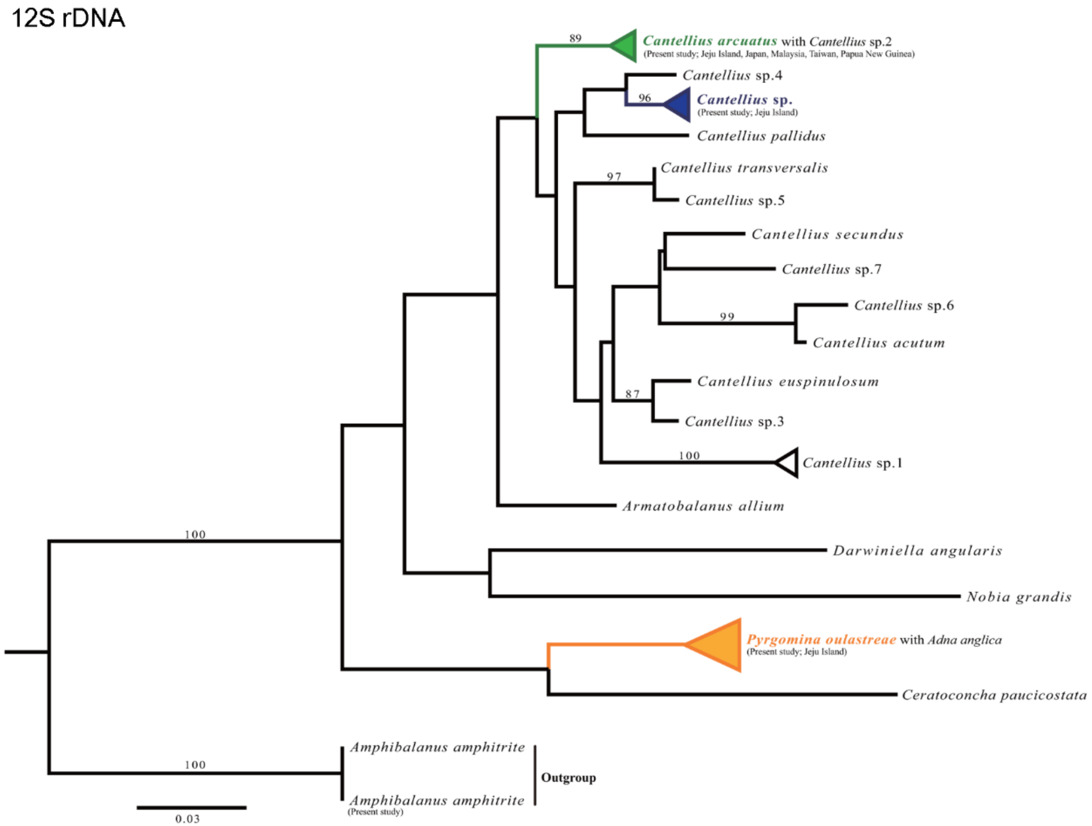

Fig. 90. Topology inferred individual molecular markers based on Maximum likelihood analysis of 12S, using *A. amphitrite* as outgroup. Bootstrap scores of >80 are presented at the nodes. The scale bar indicates the number of substitutions per site.

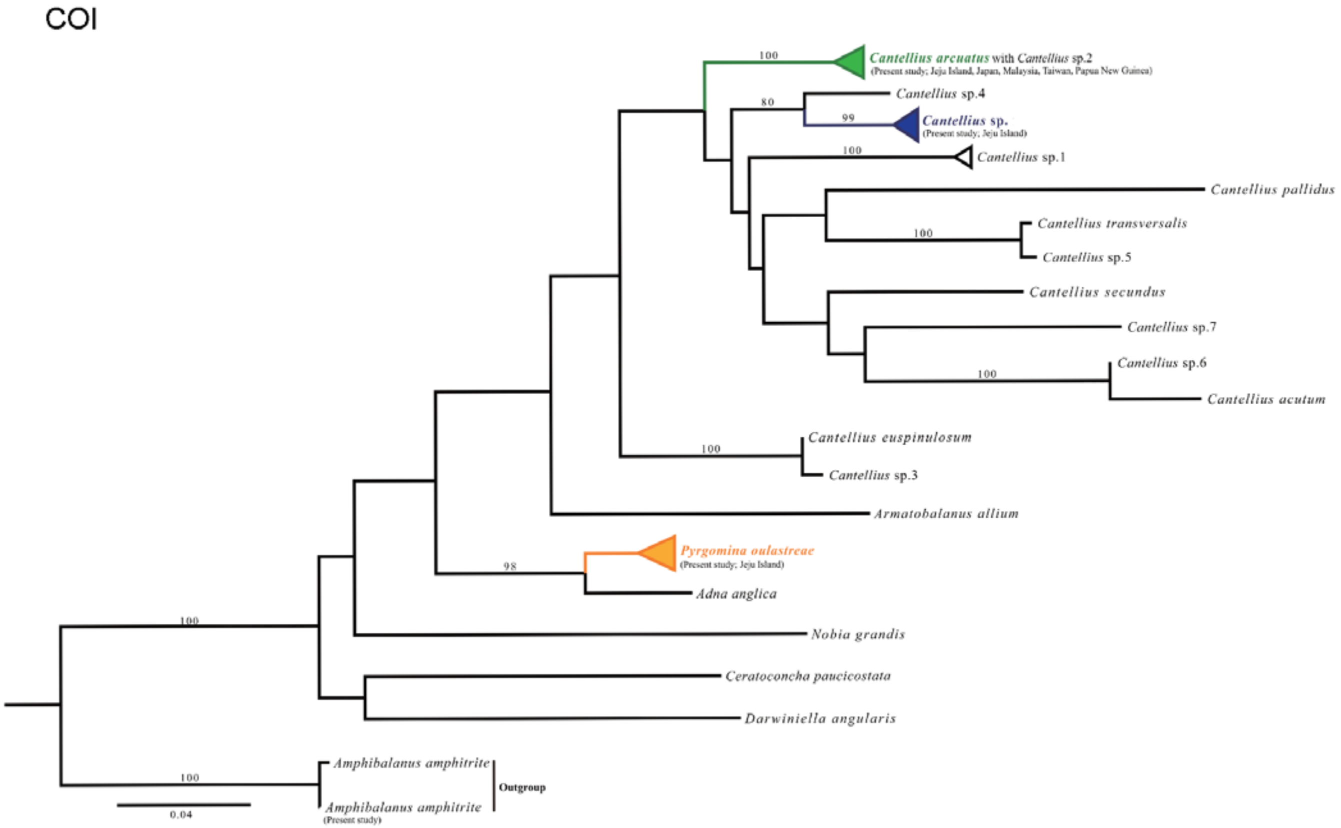

Fig. 91. Topology inferred individual molecular markers based on Maximum likelihood analysis of COI, using *A. amphitrite* as outgroup. Bootstrap scores of >80 are presented at the nodes. The scale bar indicates the number of substitutions per site.

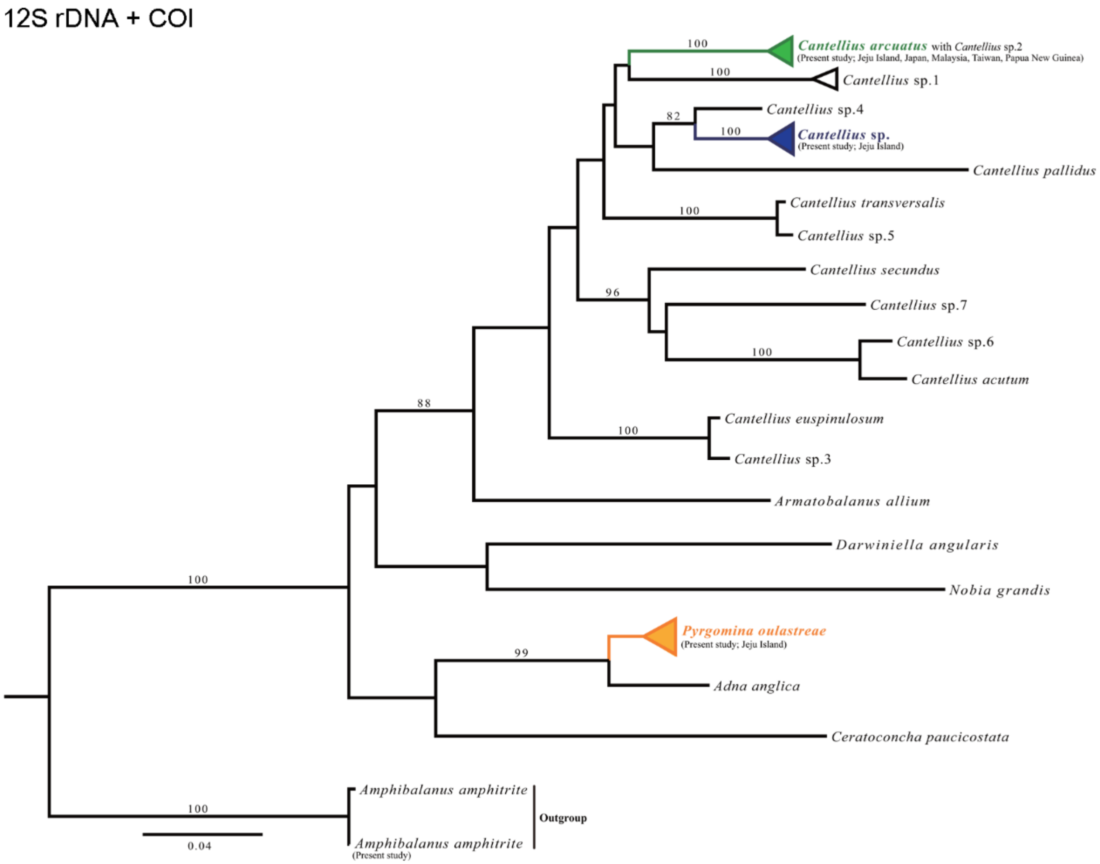

Fig. 92. Phylogenetic tree for coral-associated barnacles based on maximum likelihood analysis of the two mitochondrial gene datasets, using *A. amphitrite* as outgroup. Bootstrap scores > 80 are presented at the major nodes. The scale bar indicates the number of substitutions per site.

Table 5. Mean K2P distance for concatenated dataset between and within the studied species

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. *Cantellius acutum*	-																				
2. *Cantellius arcuatus*	0.088	0.004																			
3. *Cantellius* sp. (New species)	0.105	0.074	0.005																		
4. *Cantellius euspinulosum*	0.099	0.084	0.091	-																	
5. *Cantellius pallidus*	0.103	0.117	0.105	0.109	-																
6. *Cantellius* sp. 1	0.104	0.091	0.093	0.100	0.127	0.014															
7. *Cantellius* sp. 2	0.081	0.003	0.069	0.080	0.107	0.088	-														
8. *Cantellius* sp. 3	0.085	0.080	0.087	0.010	0.103	0.099	0.079	0.039													
9. *Cantellius* sp. 4	0.096	0.074	0.040	0.084	0.091	0.084	0.073	0.086	-												
10. *Cantellius* sp. 5	0.093	0.082	0.088	0.089	0.110	0.103	0.081	0.089	0.084	-											
11. *Cantellius* sp. 6	0.021	0.092	0.098	0.112	0.122	0.117	0.092	0.109	0.100	0.102	-										
12. *Cantellius* sp. 7	0.082	0.100	0.093	0.108	0.119	0.101	0.102	0.111	0.107	0.100	0.091	-									
13. *Cantellius secundus*	0.088	0.095	0.095	0.102	0.118	0.102	0.088	0.094	0.093	0.102	0.096	0.083	-								
14. *Cantellius transversalis*	0.097	0.082	0.093	0.093	0.107	0.101	0.080	0.089	0.082	0.008	0.103	0.097	0.105	-							
15. *Adna anglica*	0.130	0.143	0.137	0.132	0.144	0.129	0.142	0.136	0.141	0.146	0.160	0.148	0.140	0.146	-						
16. *Armatobalanus allium*	0.123	0.116	0.114	0.117	0.139	0.125	0.100	0.100	0.103	0.105	0.119	0.120	0.129	0.120	0.135	-					
17. *Ceratoconcha paucicostata*	0.148	0.140	0.156	0.158	0.149	0.142	0.138	0.164	0.149	0.158	0.172	0.154	0.155	0.156	0.134	0.151	-				
18. *Darwiniella angularis*	0.150	0.148	0.154	0.152	0.169	0.147	0.139	0.142	0.151	0.140	0.141	0.142	0.153	0.158	0.158	0.163	0.163	-			
19. *Pyrgomina oulastreae*	0.145	0.146	0.145	0.139	0.161	0.133	0.144	0.138	0.137	0.152	0.165	0.156	0.139	0.156	0.038	0.141	0.134	0.150	0.007		
20. *Nobia grandis*	0.166	0.171	0.168	0.175	0.172	0.166	0.153	0.165	0.155	0.159	0.166	0.155	0.172	0.175	0.152	0.191	0.161	0.158	0.165	0.006	
21. *Amphibalanus amphitrite* (outgroup)	0.179	0.169	0.166	0.178	0.205	0.171	0.161	0.174	0.166	0.170	0.184	0.176	0.187	0.178	0.165	0.166	0.171	0.170	0.164	0.191	0.002

2.1.4 Discussion

A total of 17 genera of coral-associated barnacles have been reported in West Pacific waters. In the present study, only three species of coral-associated barnacles—covering two genera and two subfamilies—were identified among five zooxanthellate coral species at Jeju Island. Apparently, the diversity of coral-associated barnacles is affected by interactions between the diversity of coral hosts, latitudinal gradients and oceanographic regimes. From reviewing the diversity of coral-associated barnacles along the latitudinal gradient from Honshu, Shikoku, Kyushu and Okinawa (Asami & Yamaguchi, 1997), Ogasawara Island (Ogawa, 1990) and Taiwan (Chan *et al.*, 2013a) and the number of coral species in these regions (Japan [Ministry of the Environment, Japan], Taiwan [Dai & Horng, 2009]), the diversity of coral-associated barnacle is influenced by both latitudes and coral diversity. At higher latitudes in, Boso, Japan, where there are 32 species of corals, only two species of coral-associated barnacles were present. In lower latitudes, the Izu and Shikoku regions—which have 80 and 52 coral species respectively—have 8-11 coral-associated barnacle species. Ogasawara Island has 230 corals species and contains 16 coral-associated barnacle species. The highest diversity of coral barnacles in the West Pacific is in Ishigaki, Iriomote Island and Taiwan, each of which has coral species number up to 300, 20-35 coral-associated barnacle species were sampled in these locations.

Oceanographic regimes can in addition affect the diversity of coral-associated barnacles. The Pacific coast of Honshu, Japan (*e.g.*, Wakayama, 33^{o}40′ N and Kochi 32^{o}40′ N) is at latitudes similar to those of the study region in Jeju Island (33^{o}10′ N). However, the high-latitude corals on the Pacific coast of Honshu are influenced by the main warm Kuroshio Current. Up to 70 species of corals (Denis *et al*., 2013) and 18 species of coral-associated barnacles (Asami & Yamaguchi, 1997) have been reported in this region. In Jeju Island, which receives much less influence from the Kuroshio Current, only three species of coral-associated barnacles were collected. In the Japan Sea off Honshu (Hyogo Peninsula, 35°44′ N and Shimane Peninsula, 35°43′ N), only one species, *P. oulastreae,* was found (Asami & Yamaguchi, 1997).

For the three species of coral-associated barnacles collected in the present study, the corals *M. millepora* and *A. japonica* were more common hosts than *Psammocora* and *Oulastrea*. This, and the finding that *C. arcuatus* has a higher abundance than the other two coral-associated barnacle species, suggest that *C. arcuatus* and *Cantellius* sp. are more abundant than *P. oulastreae* in Jeju waters. *C. arcuatus* and *Cantellius* sp. are specialists in Jeju waters, inhabiting only the corals *M. millepora* and *A. japonica*, respectively. *C. arcuatus* is a generalist near Taiwan, where it covers a wider range of coral hosts. For example, in Taiwan waters, *C. arcuatus* was recorded from corals such as *Montipora* spp. and *Porites* spp (Chan *et al*., 2013a, b). This suggests that the host specificity of coral-associated barnacles varies with the availability of coral hosts and latitude. *C. arcuatus* appears to be a specialist in Jeju waters due to less choice in coral hosts, but it can be a generalist in subtropical and tropical waters with higher coral diversity due to more choices in coral hosts.

C. euspinulosum was named by Broch (Broch, 1931), based on *Cresusia spinulosa* variety 1, described by Darwin (Darwin, 1854). Broch's specimens were found on madreporian corals, collected from Amboina and Jolo in Indonesian waters and Singapore. Since Broch, many researchers have reported *C. euspinulosum* from different locations in the Indo-Pacific. In the present study, DNA barcode sequences of *Cantellius* sp. did not match the sequences available from GenBank and from the author's collections of *Cantellius* specimens collected from Taiwan, Malaysia, Japan and Papua New

Guinea. In the molecular phylogenetic analysis, the DNA barcode sequences of *Cantellius* sp. were clustered in a different clade from that of the *C. euspinulosum* reported by Tsang *et al*. (2014) and Chan *et al*. (2013a, b), which mainly inhabits *Porites* corals in Taiwan. The rostral tooth in the scutum of *C. euspinulosum* was not obvious and the scutum had no adductor plate in the study by Chan *et al*. (2013a, b). By contrast, the rostral tooth was obvious and an adductor plate was present in *Cantellius* sp.. Results from the present study suggest that *Cantellius* sp. is a cryptic species complex or indicates a possibility of new species. Further studies should collect *C. euspinulosum* from the type locality and compare the genetic differences among populations from different geographical locations to ascertain the taxonomic status of *Cantellius* sp..

The morphology of *Cantellius* sp. is very similar to the illustration of *C. euspinulosum* from Palao provided by Hiro, 1936. According to the coral host ranges described by Hiro, 1936, *C. euspinulosum* in Palao was found only on the coral *Alveopora verriliana*. This suggests that *Cantellius* sp. is a specialist, found only on *Alveopora* corals.

P. oulastreae has a relatively wider host usage that includes *Psammocora* and *Oulastrea* corals. Utinomi (1962) also recorded a population of *P. oulastreae* that inhabits the coral *O. crispata* in Wakayama, Japan. In addition to the zooxanthellate coral hosts *Psammocora* and *Oulastrea*, Kim (1998) described a population of *P. oulastreae* from Busan and Jeju waters that inhabited nonzooxanthellate corals. *P. oulastreae* appears to be a cold-water species and is present at the extreme distribution limit of corals. *P. oulastreae* has been recorded from northern Honshu to Kyushu in Japan and at Jeju Island in the present study. According to the coral-associated barnacle survey by Asami and Yamaguchi (Asami & Yamaguchi, 1997), *P. oulastreae* is absent from Okinawa waters. Foster (1982) recorded *P. oulastreae* from Hong Kong that inhabited *O. crispata* and the nonzooxanthellate corals *Tubastrea* and

Dendrophyllia. However, Foster (1982) did not provide a detailed description of this species. The taxonomic status of *Pyrgomina* from Hong Kong will require further morphological and molecular analysis. Molecular analysis in the present study revealed that *P. oulastreae* is located in a major clade with *Adna* and *Megatrema*. This is additional evidence that Megatrematinae forms a monophyletic unit.

Coral-associated barnacles in marginal communities have much lower diversity than their subtropical and tropical counterparts. When host availability is limited and lacks much choice in coral hosts, the host usage of marginal coral-associated barnacles is highly specific compared with that of barnacles in subtropical and tropical reef systems that have multiple choices for coral hosts from higher coral diversity. Global climatic changes engender modifications or declines in the coral host assemblages in marginal coral communities. This can have a substantial effect on the diversity of coral-associated barnacles, considering that they have a narrow host range in the marginal coral region.

2.2 Faunal study of coral-associated barnacles in Korea

2.2.1 Introduction

Corals and their associated fauna are extremely diverse in tropical waters. The coral-associated barnacles of the sub-family Pyrgomatinae and Megatrematinae are obligatory symbionts of scleractinian corals in Korean waters. More than 70 nominal species of coral-associated barnacles are classified under the family Pyrgomatidae (Ross & Newman, 2002). However, only two coral-associated barnacles have been reported in Korean waters thus far: *Cantellius euspinulosum* (Broch, 1931) and *Pyrgomina oulastreae* (Utinomi, 1962). The present study was investigated on the three coral-associated barnacles of the corals *Monipora millepora*, *Alveopora japonica*, *Psammocora* spp. and *Oulastrea crispate* (Fig. 93). On the basis of morphological differences, two of coral-associated barnacles in the preset study are different from *Cantellius* species which present in Korea waters. These two species were published by the author (Chan *et al*., 2018), but were not given species names in Korean. In this part, detailed descriptions of coral-associated barnacles from Korean waters were provided.

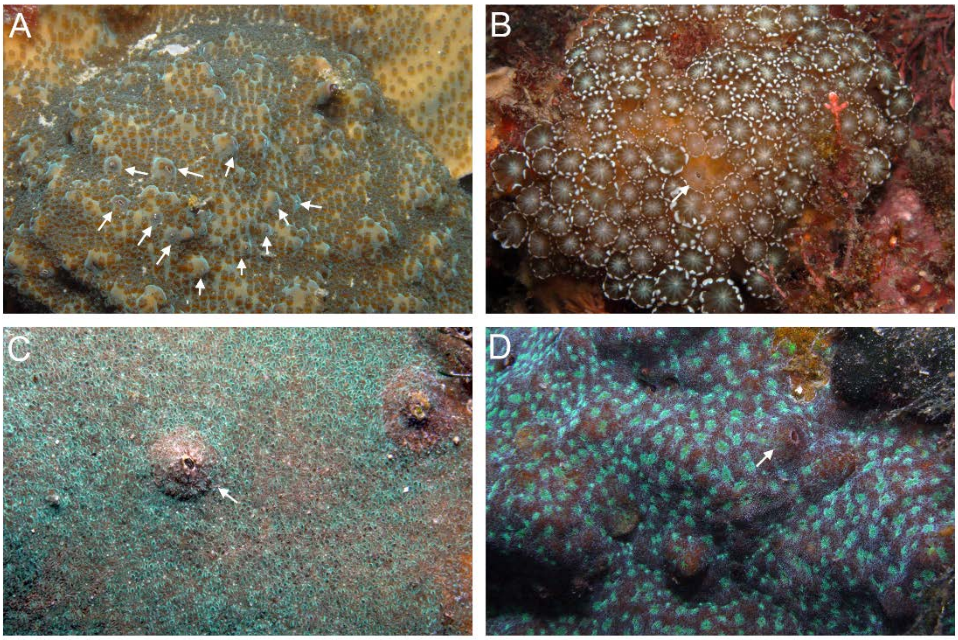

Fig. 93. In-situ underwater photos of coral associated barnacles in Jeju waters. A, Coral *Montipora millepora*, colonized by the barnacle *Cantellius arcuatus* (indicated by white arrows); B, Coral *Alveopora japonica* inhabited by a single individual of *Cantellius* sp., indicated by white arrow; C, *Psammocora* coral inhabited by the barnacle *Pyrgomina oulastreae*; D, Coral *Oulastrea crispata* inhabited by the barnacle *Pyrgomina oulastreae*. All coral-assiciated species are indicated by white arrows.

2.2.2 Materials and Methods

Sampling of coral-associated barnacles was conducted at nine sites of Jeju Island in Korea. Small pieces of coral with barnacles embedded were collected with hammers and chisels at depths of 5–20m by SCUBA diving. All specimens and host corals were preserved in 95% ethanol. Barnacles were dissected from the host corals using forceps and the morphological characters of shell parts (base, plates, scutum and, tergum) and somatic bodies (six pairs of cirri, penis and mouth) were examined. Shell parts were immersed 1.5% bleach for about five hours to digest the organic tissues and observed using the scanning electron microscopy (SEM). All six pairs of cirri, penis and Mouth parts were dissected from the somatic bodies and examined under a light microscope (Olympus BX60, Japan). The setal descriptions follow Chan *et al.* (2008c).

2.2.3 Systematic Accounts

Superfamily Balanoidea Leach, 1817 따개비상과

Family Pyrgomatidae Gray, 1825 산호따개비과

Subfamily Pyrgomatinae Gray, 1825 산호따개비아과

Genus *Cantellius* Ross and Newman, 1973 칸텔산호따개비속

1. *Cantellius arcuatus* Hiro, 1938

Creusia spinulosa forma *arcuata* Hiro, 1938:395, 403, fig. 3a-c, tab. II.—Kolosváry, 1947a:426-428; 1947b:364-367.—Utinomi, 1949a:69.

Cantellius arcuatum Ross & Newman, 1973:150, fig. 7d-e.—Newman & Ross, 1976:57.—Foster, 1980, tab. 5.

Cantellius arcuatus Galkin, 1986:1290.—Ogawa, 1992:app. tab.—Asami & Yamaguchi, 1997:14, figs. 1, 2.—Ogawa, 1998:12, fig. 11.—Chan, Chen & Achituv, 2013:12.

Materials examined. CEL-JJ-01, 211 specimens (BD 2.02 – 5.47 mm), 33°13.917' N 126°35.800' E, Seop Seom (NW), Jeju Island, Korea, 6 August 2016, on host coral *Montipora millepora*. CEL-JJ-02, 142 specimens (BD 1.29 – 7.18 mm), same data as CEL-JJ-01. CEL-JJ-13, 130 specimens (BD 2.53 – 8.05 mm), same data as CEL-JJ-01. CEL-JJ-14, 36 specimens (BD 3.01 – 5.98 mm), same data as CEL-JJ-01. CEL-JJ-15, 96 specimens (BD 2.16 – 7.59 mm), same data as CEL-JJ-01. CEL-JJ-16, 59 specimens (BD 2.43 – 8.00 mm), Seop Seom (NE), Jeju Island, Korea, 7 August 2016, on host coral *Montipora millepora*. CEL-JJ-17, 29 specimens (BD 3.46 – 5.65 mm), 33°13.839' N, 126°36.155' E, Seop Seom (SE), Jeju Island, Korea, 7 August

2016, on host coral *Montipora millepora*. CEL-JJ-18, 80 specimens (BD 2.46 – 8.53 mm), same data as CEL-JJ-16. CEL-JJ-19, 44 specimens (BD 2.34 – 4.34 mm), same data as CEL-JJ-16. CEL-JJ-20, 73 specimens (BD 1.93 – 5.87 mm), same data as CEL-JJ-16. CEL-JJ-23, 88 specimens (BD 1.76 – 7.02 mm), same data as CEL-JJ-17. CEL-JJ-25, 120 specimens (BD 2.436 – 9.70 mm), same data as CEL-JJ-17. CEL-JJ-28, 11 specimens (BD 2.11 – 6.16 mm), 33°07.214' N, 126°15.821' E, Marado (N), Jeju Island, Korea, 9 August 2016, on host coral *Montipora millepora*. CEL-JJ-33, 70 specimens (BD 2.80 – 3.80 mm), same data as CEL-JJ-16. CEL-JJ-34, 43 specimens (BD 2.82 – 6.97 mm), same data as CEL-JJ-17. CEL-JJ-35, 44 specimens (BD 3.62 – 8.79 mm), 33°13.115' N, 126°30.850' E, Beom Seom, Jeju Island, Korea, 10 August 2016, on host coral *Montipora millepora*. CEL-JJ-36, 14 specimens (BD 4.99 – 7.49 mm), Beom Seom, Jeju Island, Korea, 10 August 2016, on host coral *Montipora millepora*. CEL-JJ-38, 58 specimens (BD 3.89 – 6.73 mm), same data as CEL-JJ-36. CEL-JJ-41, 142 specimens (BD 1.52 – 5.96 mm), same data as CEL-JJ-36. CEL-JJ-43, 28 specimens (BD 2.72 – 6.65 mm), 33°13.345' N 126°30.753' E, Beom Seom (NW), Jeju Island, Korea, 11 August 2016, on host coral *Montipora millepora*.

Diagnosis. Shell composed of 4 separated plates. External surfaces of apex in scutum and tergum with honeycomb-like structure. Occludent margin of scutum straight, without a rostral tooth. Adductor plate absent in scutum. Tergum triangular, spur distinct, long and narrow. Medial furrow curved. Posterior side of segments on Cirri III with large spines.

Description. Shell ovate, white, 4-plated (rostrum, carina, and paired laterals). External surface covered by coral tissue. Base of shell with approximately 33 longitudinal septa radiating from rim of sheath to external surface of shell (8 in rostrum and 10 in carina, 8 in laterals, septa margin serrated. Orifice ovate, about 1/4 basal rostro-carinal diameter (Fig. 94).

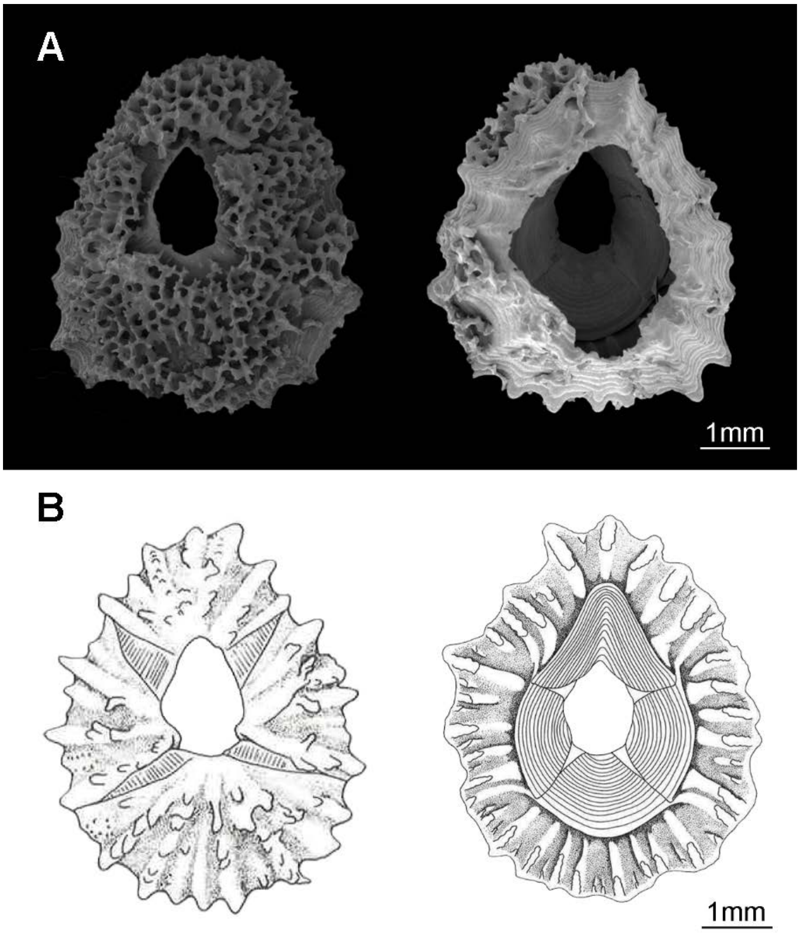

Fig. 94. *Cantellius arcuatus* Hiro, 1938. A, Scanning electrom microscopy of external and internal view of shell; B, Line drawing on the external and internal view of shell.

Scutum and tergum separated, white. Scutum triangular, width equal to height, occludent margin straight, without a rostral tooth, 12-14 teeth along occludent margin, tooth size increasing gradually from apex to base margin. Scutum apex with honeycomb-like pattern. External scutum surface with multiple horizontal striations. Internal view with an oval-shaped adductor muscle scar. Adductor plate absent. Basal margin of scutum with a notch near tergal margin. Tergum triangular. Spur distinct, long and narrow. Tergal apex curved toward scutal margin. External surface with a shallow medial furrow, curving from basal margin towards carinal margin, width of furrow increasing gradually from apex to base. External surface with horizontal striations, striations with row of small pores (Fig. 95).

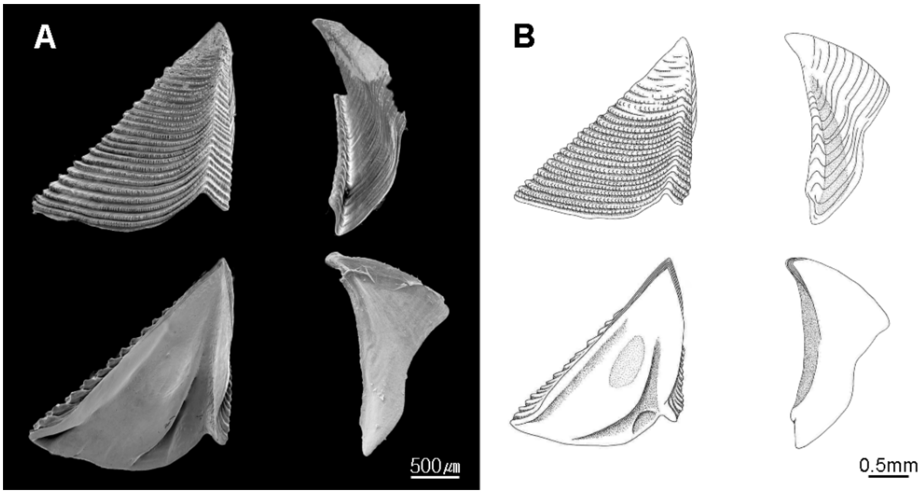

Fig. 95. Scutum and tergum of *Cantellius arcuatus* Hiro, 1938. A, Scanning electron microscopy of external and internal view of opercular plates; B, Line drawing on the external and internal view of opercular plates.

Cirrus I with unequal rami, anterior ramus long, slender, 13-segmented, posterior ramus 8-segmented, bearing serrulate setae. Cirrus II anterior ramus with 9-segments, slightly longer than posterior ramus (7-segmented), bearing serrulate setae (Fig. 96). Cirrus III anterior ramus 10-segmented, posterior ramus 8-segmented, bearing serrulate setae, with sharp teeth on base of each segment (Figs. 96, 97).

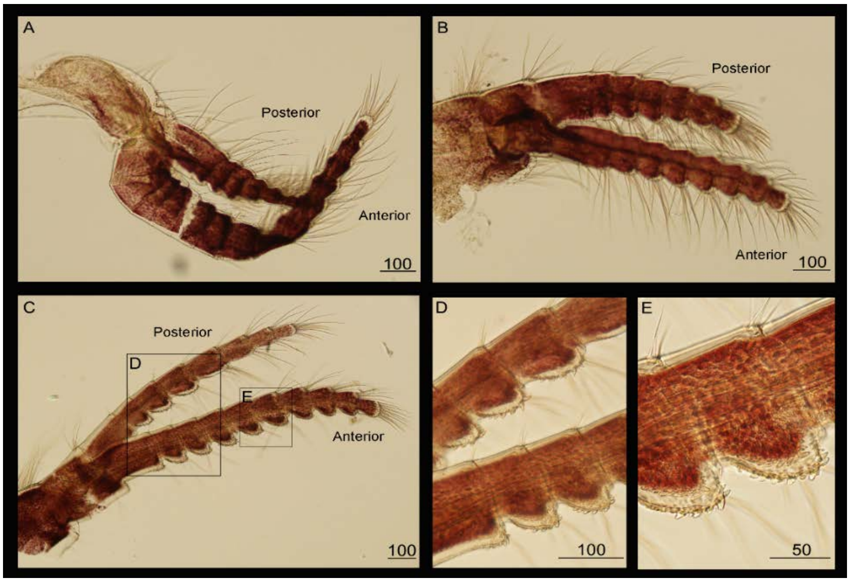

Fig. 96. Cirri I-III of *Cantellius arcuatus* Hiro, 1938. A, Cirrus I; B, Cirrus II; C, Cirrus III; D, Serrulate setae and teeth on both rami; E, Teeth on anterior ramus. Scale bars in µm.

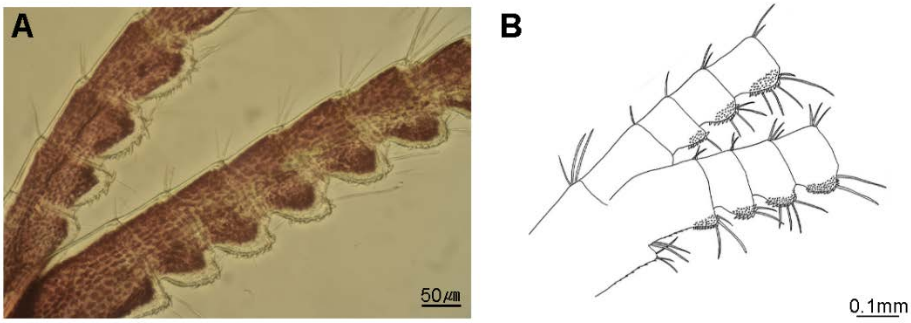

Fig. 97. Cirrus III of *Cantellius arcuatus* Hiro, 1938. A, Light microscopy on cirrus III, teeth on anerior ramus; B, Line drawing of teeth on cirrus III.

Cirri IV-VI very long, slender, rami sub-equal. Cirrus IV with anterior ramus 16-segmented, posterior ramus 18-segmented. Cirrus V (anterior 22-segmented, posterior 18-segmented), Cirrus VI (anterior 15-segmented, posterior 17-segmented). Each intermediate segment of ramus of Cirrus IV-VI with 2 pairs of long serrulate and 2 pairs simple setae (Fig. 98).

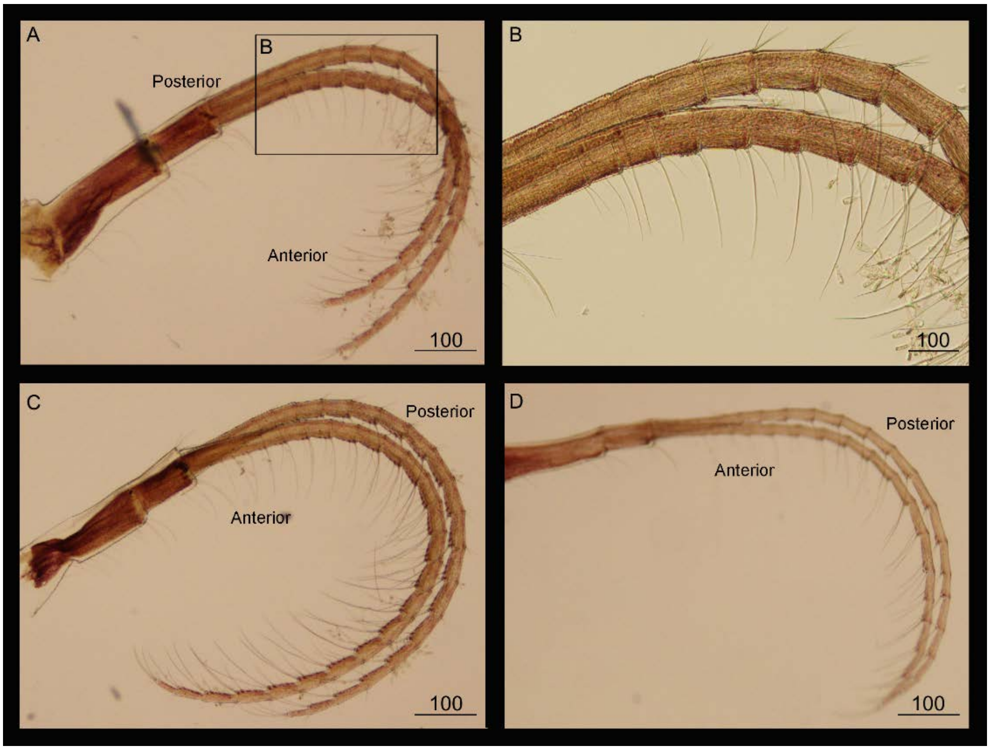

Fig. 98. Cirri IV-VI of *Cantellius arcuatus* Hiro, 1938. A, Cirrus IV; B, Intermediate segment with 2 pairs of serrulate setae on cirrus IV; C, Cirrus V; D, Cirrus VI. Scale bars in µm.

Penis length equal to length of Cirrus VI, annulated, with scattered short simple-type setae. Pedicel with a slightly sharp basidorsal point (Fig. 99).

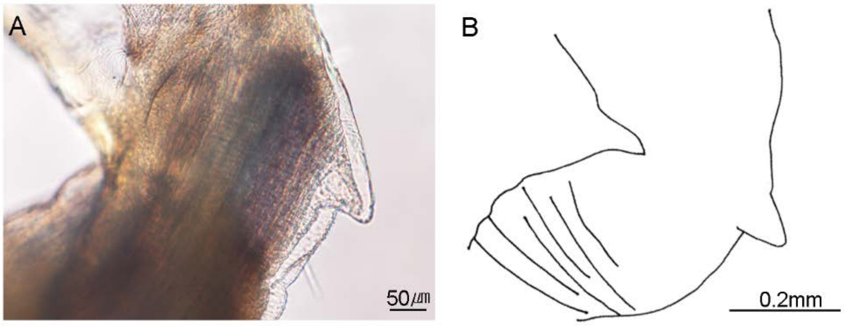

Fig. 99. Penis of *Cantellius arcuatus* Hiro, 1938. A, Light microscopy on penis; B, Line drawing of penis.

Maxilla ovate, with serrulate-type setae distally. Mandibular palp subtriangular, bearing serrulate setae distally and on interior margin. Mandible with 5 teeth, excluding inferior angle (3 specimens). Second to fourth teeth bidentate, the first 3 teeth occupied 3/4 length of cutting edge. Lower margin short, inferior angle blunt with simple-type setael. Maxillule cutting edge straight without notch, bearing row of 8-9 large setae. Region close to cutting edge with dense fine simple-type setae, anterior and posterior margins with long simple-type setae. Labrum bilobed, lobes separated by a V-shaped notch, 2-4 sharp teeth on each side of notch (Fig. 100).

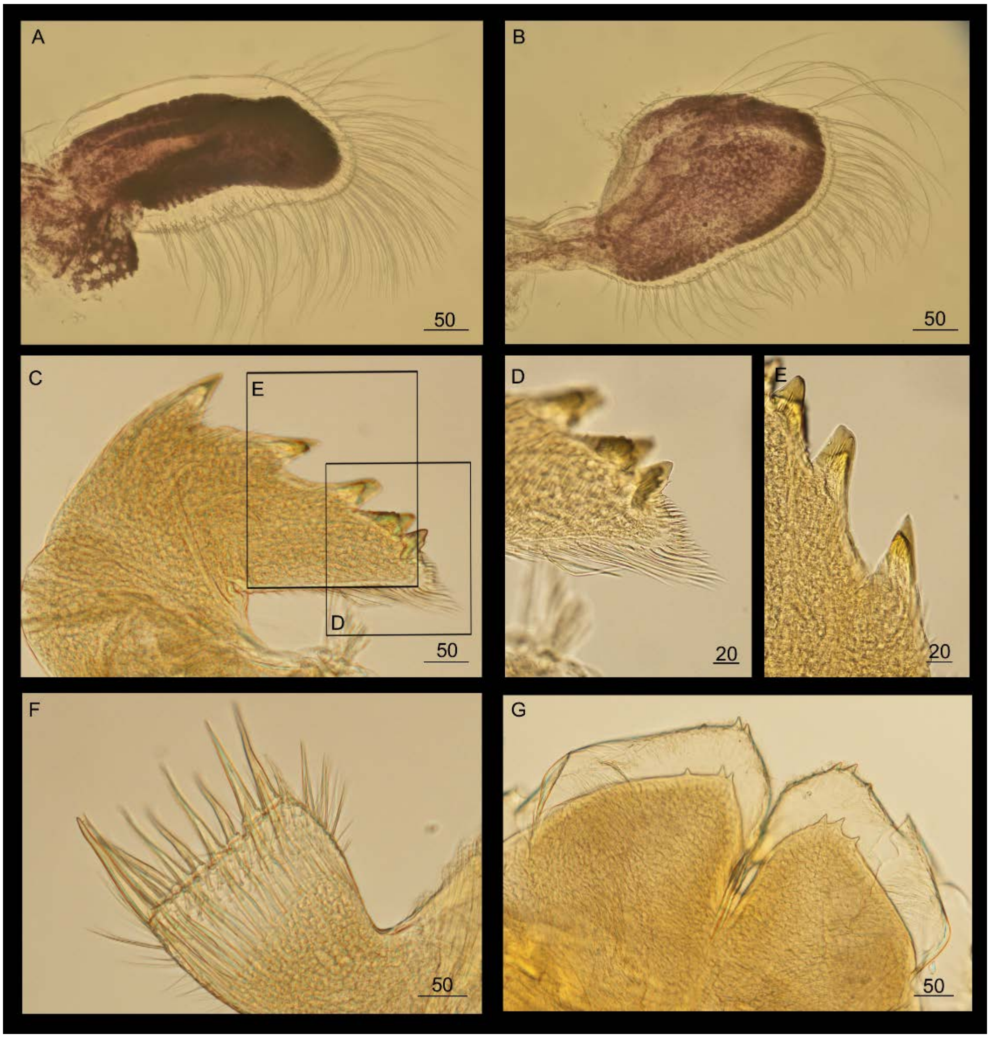

Fig. 100. Mouth parts of *Cantellius arcuatus* Hiro, 1938. A, Maxilla; B, Mandibulatory palp; C, Mandible; D, Inferior angle with simple-type setae; E, Bidentate second to fourth tooth; F, Maxillule; G, Labrum. Scale bars in μm.

Habitat. Jeju Island: recorded on host coral *Montipora millepora* exclusively (Fig. 101). Other regions: recorded on host coral includes *Acropora pruinosa* Brook, 1893, *Aropora* spp., *Coeloseris mayeri* Vaughan, 1918, *Montipora foliosa* Pallas, 1766, *M. prolifera* Brüggemann, 1879, *M.* spp., *Pavona crassa*

Dana, 1840, *P. lata* Dana, 1846, *Platygyra* sp., *Porites capricornis* Rehberg, 1891, *Porites* spp., *Psammocora contigua* Esper, 1797.

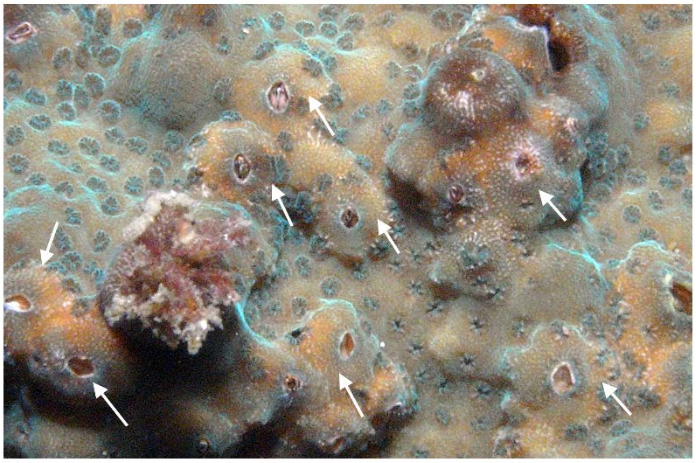

Fig. 101. Close up view of *Cantellius arcuatus*, on coral *Montipora millepora*, Jeju Island, Korea. For clarity, the barnacles were indicated by white arrows.

Distribution. Palau Island, Mauritius, Hong Kong, Japan, Taiwan, Papua New Guinea, Malaysia and Korea.

Remarks. *Cantellius arcuatus* Hiro, 1938 is the first report in the present study from Korean waters. The genus *Cantellius* have been recorded 26 species in the world. Of these, only two species have been reported in Korea from Jeju Island. This species is morphologically similar to *C. euspinulosum*, but can be distinguished by the absence of rostral tooth on the basal margin of the scutum. In *C. arcuatus*, there is a honeycomb-like pattern in the internal surface of the tergum apex. The present specimen agrees well with the original description.

2. ***Cantellius euspinulosum*** **(Broch, 1931)**

Pyrgoma (*Creusia*) *spinulosa* var. 1. Darwin, 1854:377-378, pl. 13, fig. 6a-d.

Creusia spinulosa var. VI. Gruvel, 1905:299, fig. 323.

Creusia spinulosa forma *euspinulosa*.—Broch, 1931:118.—Nilsson-Cantell, 1938:59, text fig. 20.—Hiro, 1938:393, fig. 1a-c.

Creusia spinulosa var. *eu-spinulosa*.—Hiro, 1935:48-50, fig. 1.

Cantellius euspinulosa.—Jones *et al*., 2000:273.—Achituv & Newman, 2002:392-393.

Cantellius euspinulosum.—Ross & Newman, 1973:150, fig. 7g-I.—Newman &Ross, 1976:57.—Anderson, 1992:289-292, figs. 7, 8.—Paulay & Ross, 2003:309.—Ogawa & Tachikawa, 2009:91, fig. 10.—Kim 1998:105, fig. 57.—Chan *et al*., 2013a:22, figs. 32-40.

Cantellius euspinulosus.—Poltarukha & Dautova, 2007:99, 101, fig 59.

Materials examined. No specimen.

Diagnosis. Shell ovate, pale pink. Base of shell with 23 longitudinal septa. Orifice round, about 2/5 length of rostro-carinal diameter. Scutum triangular, basal margin slightly concave with an oval-shaped lateral depressor muscle. Adductor ridge absent. Tergum triangular, width of basal margin equal to height. Spur blunt, short, close to basi -scutal angle. External surface of tergum with horizontal striations. Labrum with deep central notched and 1-3 teeth on each side. Mandible with 5 teeth, excluding inferior angle. Mandibulatory palp elongated. Maxilla with simple-type setae distally. Cirri I-II with unequal rami; anterior ramus longer than posterior ramus. Cirrus III with sharp teeth on the base of each segment. Cirri IV-VI long, slender, bearing serrulate setae.

Distribution. Indo-West Pacific, southern Japan and Korea.

Remarks. *Cantellius euspinulosum* closely resembles *C. arcuatus* Hiro, 1938 in having horizontal striations with a row of small pores of scutum and curved toward the scutal margin of the tergal apex. However, this species is easily distinguished by the presence of rostral tooth in scutum. Intraspecific variation in *C. euspinulosum* has been reported in the size of rostral tooth (Chan *et al*, 2013a).

This species has been recorded only from Taiwan, compared with other congeners which have a relatively broad distribution. Further sampling is required to better determine the distribution of *C. euspinulosum*.

3. *Cantellius* sp.

Type specimens. numerous specimens (Bomok-dong, Seogwipo-si, Jeju), in depths between 5-15m; numerous spcimens (Seogwi-dong, Seogwipo-si, Jeju), in depths between 5-15m; numerous specimens (Udo Island, Jeju), in depths between 5-15m.

Size (holotype). Basal diameter 6mm.

Diagnosis. Base of shell with 29 longitudinal septa, shell conical with 4 plates. Scutum triangular, with rostral tooth, width almost equal to height, occludent margin straigt with strong teeth; tergum flat, thin, spur blunt. Mandible with 5 teeth, fifth tooth fused with inferior angle; maxillule without notch; Labrum bilobed, 3 teeth on each crest. Serrulate setae present on cirrus I to III; cirrus IV to VI long, slender. Penis annulated, longer than cirrus VI.

Description. Shell conical and ovate, 4-plated (rostrum, carina, and paired laterals). External surface covered by coral tissue. Base of shell with approximately 29 longitudinal septa radiating from rim of sheath to external shell surface (8 in rostrum and carina, 6 and 7 in laterals, respectively), septa margin serrated. Orifice circular, about 2/5 length of rostro-carinal diameter (Fig. 102).

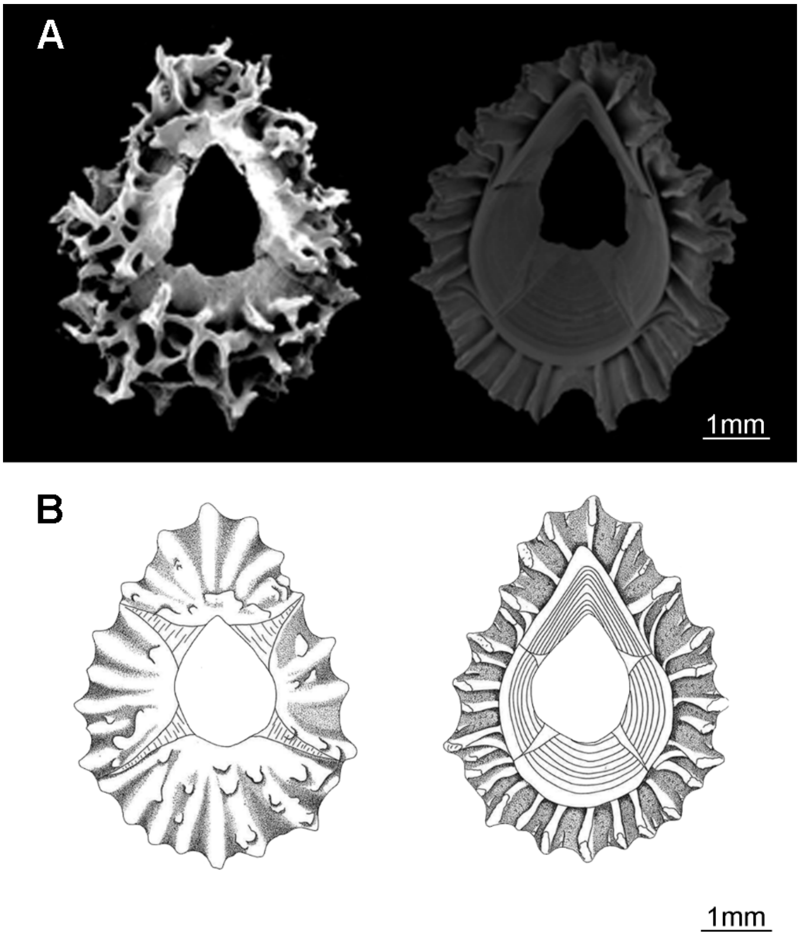

Fig. 102. *Cantellius* sp.. A, Scanning electrom microscopy of external and internal view of shell; B, Line drawing on the external and internal view of shell.

Scutum and tergum separated, basically white, with purple color in apex region. Scutum triangular, width approximately equal to height, occludent margin straight, rostral tooth and adductor plate present. External surface with horizontal striations, striations with row of small pores. Internal view with a deep depressor muscle crest, without an oval-shaped adductor muscle scar. Tergum triangular. Spur blunt, width of basal margin of tergum equal to height of tergum. External surface with a shallow medial furrow, extending from basal margin towards apex, width of furrow increasing gradually from apex to base. External surface with horizontal striations (Fig. 103).

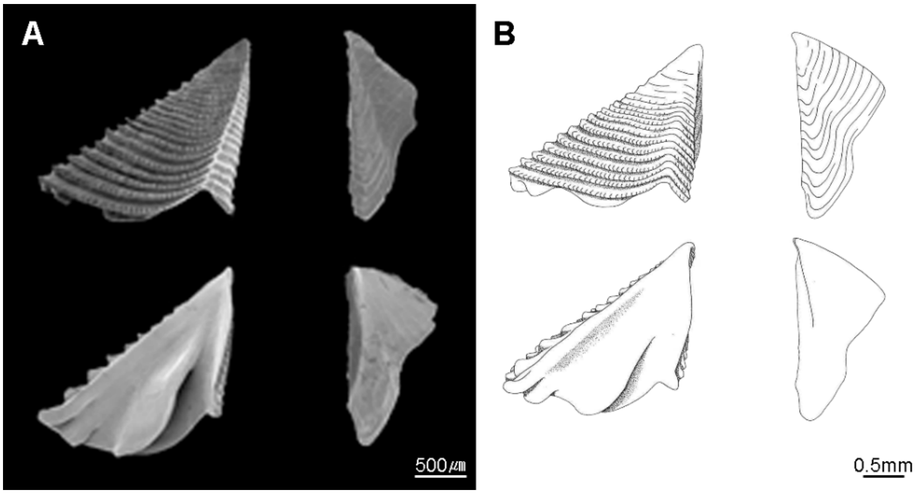

Fig. 103. Scutum and tergum of *Cantellius* sp.. A, Scanning electron microscopy of external and internal view of opercular plates; B, Line drawing on the external and internal view of opercular plates.

Cirrus I with unequal rami, anterior ramus long, slender, with 12-segments, posterior ramus 9-segmented, bearing serrulate setae. Cirrus II anterior ramus with 9-segments, slightly longer than posterior ramus (7-segmented), bearing serrulate setae. Cirrus III anterior ramus longer than posterior ramus, 12- and 9-segmented respectively, bearing serrulate setae, without small sharp teeth on base of each segment (Fig. 104).

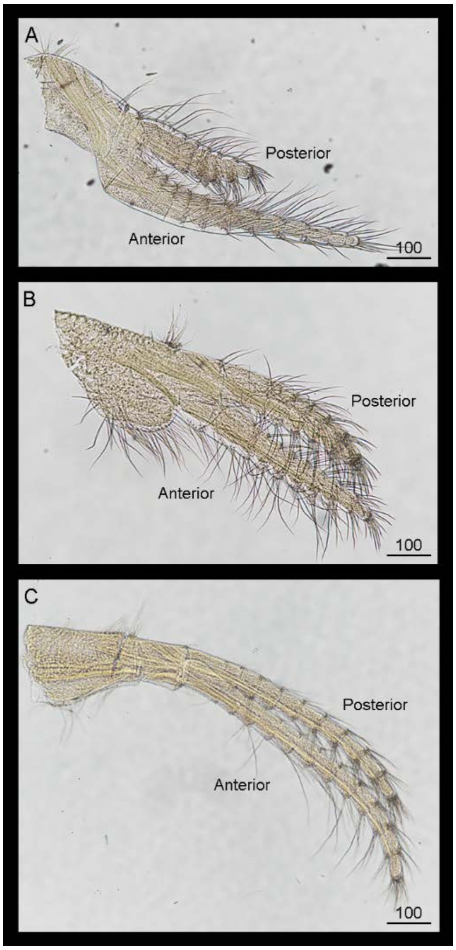

Fig. 104. Cirri I-III of *Cantellius* sp.. A, Cirrus I; B, Cirrus II; C, Cirrus III. Scale bars in µm.

Cirri IV-VI long, slender, rami similar in length, bearing serrulate setae. Cirrus IV with anterior ramus 30-segmented, posterior ramus 31-segmented, Cirrus V (anterior 30-segmented, posterior 31-segmented), Cirrus VI (anterior 32-segmented, posterior 31-segmented). Each intermediate segment of ramus of Cirrus IV-VI with 2-3 pairs of short simple setae (Fig. 105).

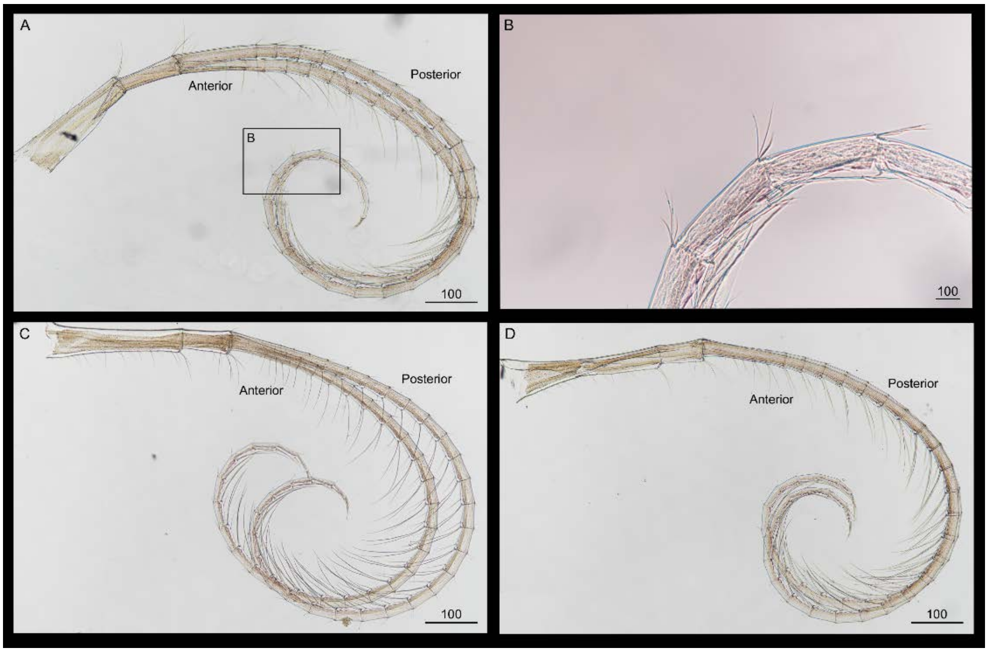

Fig. 105. Cirri IV-VI of *Cantellius* sp.. A, Cirrus IV; B, Intermediate segment with 2-3 pairs of serrulate setae on cirrus IV; C, Cirrus V; D, Cirrus VI. Scale bars in µm.

Penis annulated, with scattered short simple-type setae. Pedicel with blunt basidorsal point (Fig. 106).

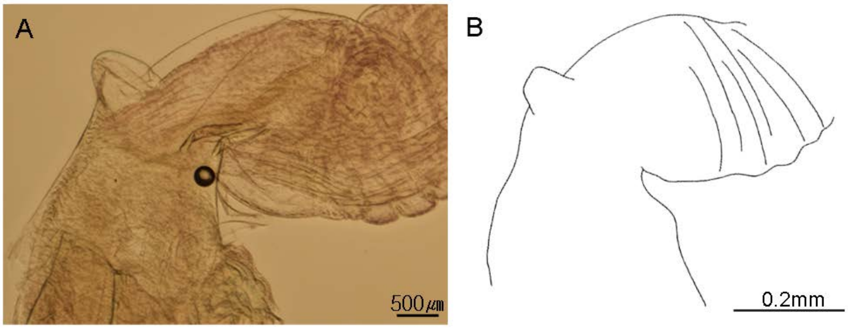

Fig. 106. Penis of *Cantellius* sp.. A, Light microscopy on penis; B, Line drawing of penis.

Maxilla ovate, with serrulate setae on margin. Mandibular palp elongated, bearing serrulate setae distally and on interior margin. Mandible with 5 teeth, excluding inferior angle. First 3 teeth occupied 4/5 length of cutting edge. Lateral surface, lower margin and cutting edge of mandible bearing simple-type setae. Lower margin short, inferior angle blunt with simple-type setae. Maxillule cutting edge straight without notch, bearing row of 9 large setae. Region close to cutting edge with dense simple-type setae, anterior and posterior margins with simple-type setae. Labrum bilobed, lobes separated by a V-shaped notch, 3 sharp teeth on each side of notch (Fig. 107).

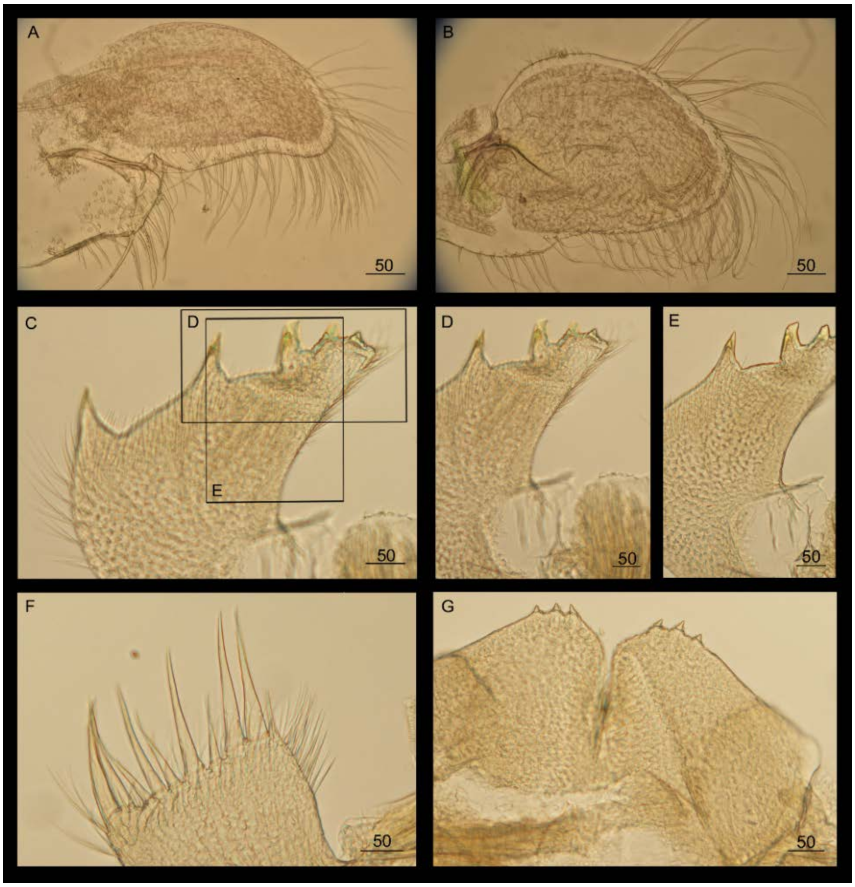

Fig. 107. Mouth parts of *Cantellius* sp.. A, Maxilla; B, Mandibulatory palp; C; Mandible; D, Inferior angle with simple-type setae; E, Bidentate second to fourth tooth; F, Maxillule; G, Labrum. Scale bars in µm.

Habitat. On host coral *Alveopora japonica* (Fig. 108)**.**

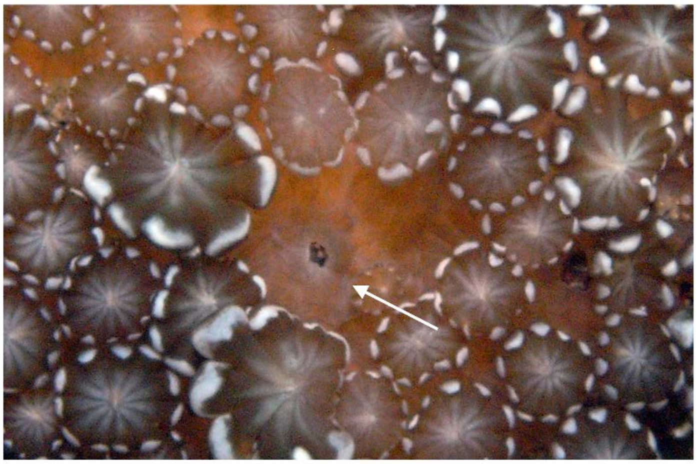

Fig. 108. Close up view of *Cantellius* sp., on coral *Alveopora japonica*, Jeju Island, Korea. For clarity, the barnacle was indicated by white arrow.

Distribution. At present only recorded in Jeju, Korea.

Remarks. This species is similar to *Cantellius euspinulosum* (Broch, 1931) in morphological characters of scutum and tergum: (1) the scutum with a rostral tooth, (2) basal margin with deep notch near the basi-tergal angle of scutum, (3) tergal apex curved towards scutal margin of tergum, and (4) the flat tergum with a wide and truncate spur. However it can be distinguished from *C. euspinulosum* by these characters: (1) the internal view of scutum has no oval-shaped adductor muscle scar, and (2) cirrus III has no sharp teeth on the base of each segment in the present study. Additionally, the rostral tooth of this present species is unapparent, which is differing from Hiro (1938) in which the specimens had an obvious rostral tooth. Comparing to Kim (1998), there is difference in the length of cirri: the posterior ramus is longer than anterior ramus in cirri I-III, but the present species have longer anterior ramus than posterior ramus. On the basis of these differences, this species is assigned to be a new one.

Subfamily Megatrematinae Holthuis, 1982 큰산호따개비아과

Genus *Pyrgomina* Baluk & Radwanski, 1967 큰산호따개비속

1. *Pyrgomina oulastreae* (Utinomi, 1962)

Pyrgoma oulastreae Utinomi, 1962:227, figs. 6-8.

Creusia spinulosa forma *quarta* Utinomi, 1949b:35.

Megatrema oulastreae.—Utinomi, 1967:229.—Kim, 1998:107, fig. 58.

Boscia oulastreae.—Ross & Newman, 1973:164.—Newman & Ross, 1976:59.—Foster, 1980:209.

Pyrgomina oulastreae.—Ross & Pitombo, 2002:61.

Materials examined. CEL-JJ-03, 14 specimens (BD 1.10 – 6.71 mm), 33°13.917' N 126°35.800' E, Seop Seom, Jeju Island, Korea, 6 August 2016, on host coral *Oulastrea crispata*. CEL-JJ-04, 5 specimens (BD 5.42 – 6.09 mm), 33°13.917' N 126°35.800' E, Seop Seom, Jeju Island, Korea, 6 August 2016, on host coral *Psammocora* sp. CEL-JJ-05, 9 specimens (BD 4.29 – 8.35 mm), same data as CEL-JJ-04. CEL-JJ-06, 43 specimens (BD 2.32 – 5.30 mm), same data as CEL-JJ-03. CEL-JJ-10, 10 specimens (BD 2.82 – 6.02 mm), same data as CEL-JJ-04. CEL-JJ-11, 107 specimens (BD 1.58 – 6.31 mm), same data as CEL-JJ-04. CEL-JJ-21, 6 specimens (BD 3.87 – 6.29 mm), Seop Seom (NE), Jeju Island, Korea, 7 August 2016, on host coral *Oulastrea crispata*. CEL-JJ-40, 11 specimens (BD 7.23 – 9.36 mm), 33°13.115' N, 126°30.850' E, Beom Seom, Jeju Island, Korea, 10 August 2016, on host coral *Psammocora* sp. CEL-JJ-42, 4 specimens (BD 2.15 – 6.23 mm), Beom Seom, Jeju Island, Korea, 10 August 2016, on host coral *Oulastrea crispata* CEL-JJ-44, 26 specimens (BD 2.38 – 5.36 mm), 33°13.345' N 126°30.753' E, Beom Seom, Jeju Island, Korea, 11 August 2016, on host coral *Oulastrea crispata*.

Diagnosis. Shell single plated, conical, solid, shell with 30-36 longitudinal ribs. Scutum and tergum separate and balanoid type. Internal side of scutum with well-developed lateral depressor muscle crests.

Description. Shell low conical, 2-plated (paired laterals and rostrum). External surface covered by coral tissue. Base of shell with approximately 35 longitudinal septa radiating from rim of sheath to external shell surface, septa margin serrated. From basal view, sheath with two lineation referred as pseudoalae[1]. Orifice circular, small, about 1/4 length of rostro-carinal diameter. Sheath long, with distinct growth lines. Basal margin of plates serrated (Fig. 109).

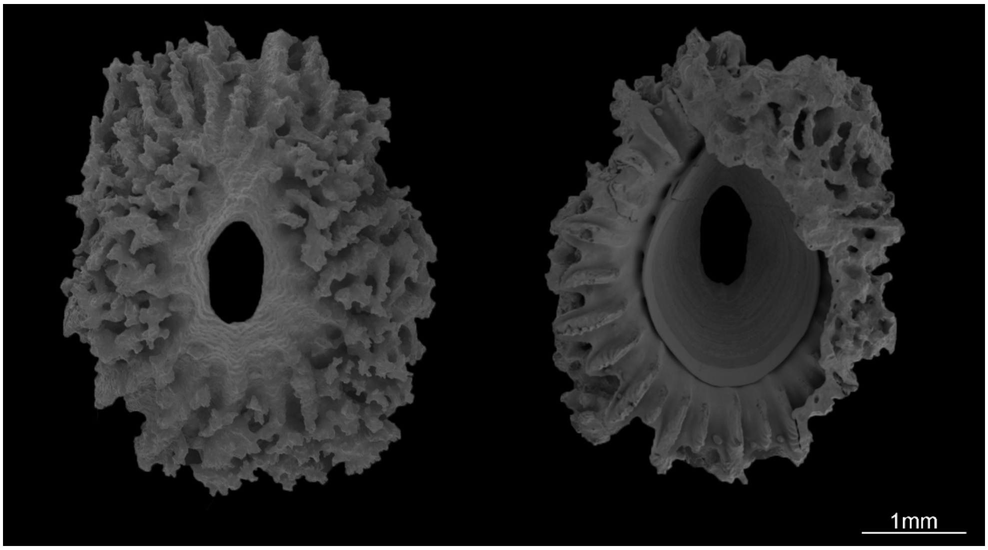

Fig. 109. *Pyrgomina oulastreae* (Utinomi, 1962). A,Scanning electrom microscopy of external and internal view of shell; B, Line drawing on the external and internal view of shell.

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[1] Pseudoalae is the position of the sheath where the junction of scutum and tergum attach on the basal margin of the sheath. This is the point of pivotal support of opercular plates during early ontogenic development.

Scutum and tergum balanoid and separated. Scutum triangular, wider than high and strongly convex ourwardly. Occludent margin straight with 11 teeth, rostral tooth and adductor plate absent. External surface with horizontal striations, minute granules along the growth lines. Internal view with an oval-shaped adductor and depressor muscle scar. Tergum triangular without distinct characters. Spur short and blunt, with rounded end. Basi-scutal angle present on scutal margin, at about 100^o. External surface with a medial furrow, extending from basal margin towards apex, width of furrow increasing gradually from apex to base. External surface with horizontal striations. Crests for depressor muscle absent (Fig. 110).

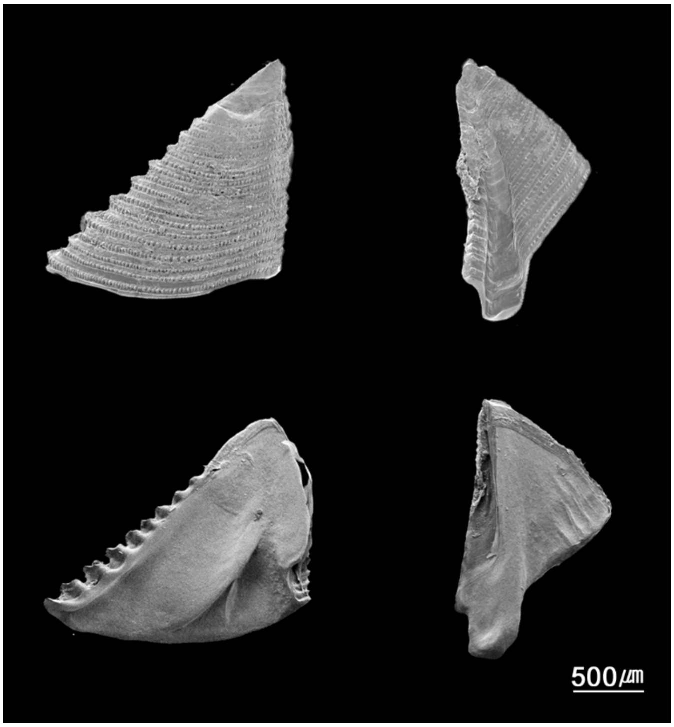

Fig. 110. Scutum and tergum of *Pyrgomina oulastreae* (Utinomi, 1962). Scanning electron microscopy of external and internal view of opercular plates.

Cirrus I with unequal rami, anterior ramus long, slender, with 13-segments, posterior ramus 6-segmented, bearing serrulate setae. Cirrus II anterior ramus with subequal rami, anterior ramus with 8 segments, posterior ramus 7-segmented, bearing serrulate setae. Cirrus III anterior ramus longer than posterior ramus, 8- and 6-segmented respectively, bearing 1-2 hooks and small teeth on both rami (Fig. 111).

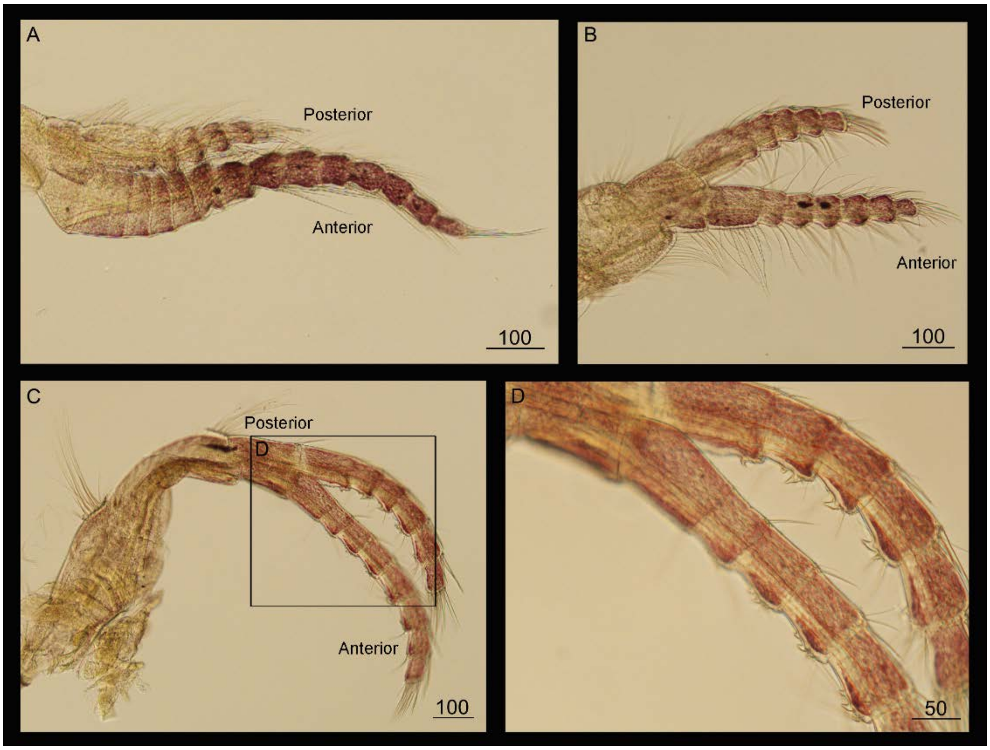

Fig. 111. Cirri I-III of *Pyrgomina oulastreae* (Utinomi, 1962). A, Cirrus I; B, Cirrus II; C, Cirrus III; D, 1-2 hooks and small teeth on both rami. Scale bars in μm.

Cirri IV-VI long, slender, rami similar in length, bearing serrulate setae. Cirrus IV with anterior ramus 14-segmented, posterior ramus 15-segmented, cirrus V (anterior 11-segmented, posterior 13-segmented) and cirrus VI with anterior ramus 18-segmented, posterior ramus 17-segmented. Each intermediate segment of ramus of cirri IV-VI with 1 pairs of long serrulate setae and 1 pairs of short simple setae (Fig. 112).

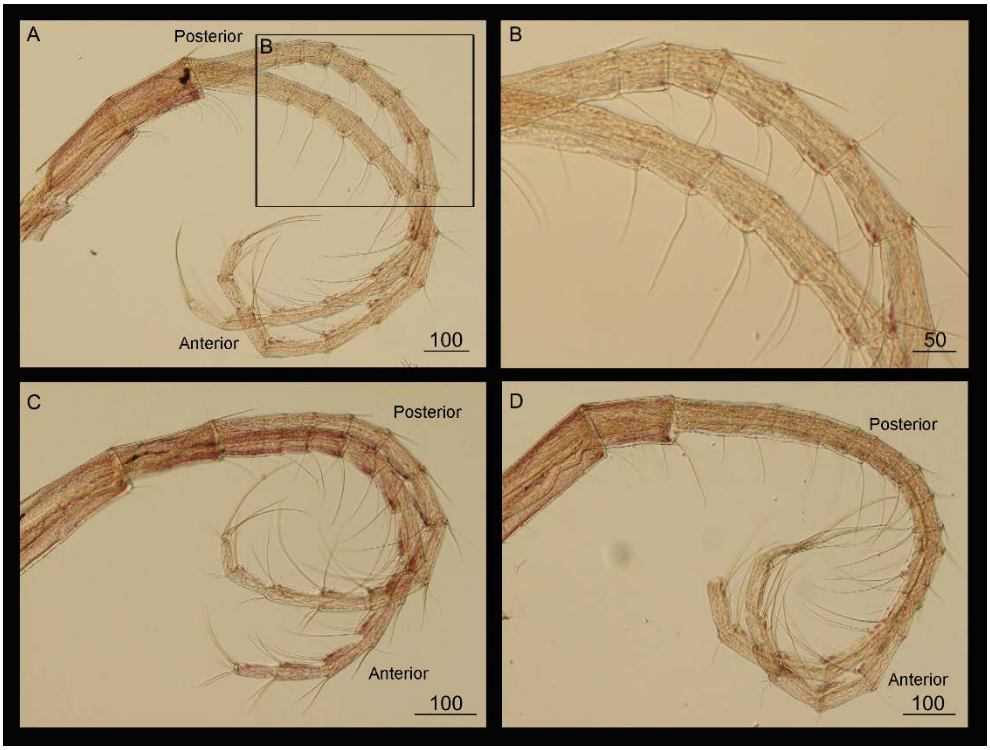

Fig. 112. Cirri IV-VI of *Pyrgomina oulastreae* (Utinomi, 1962). A, Cirrus IV; B, Intermediate segment with 1-2 pairs of serrulate setae on cirrus IV; C, Cirrus V; D, Cirrus VI. Scale bars in µm.

Penis long, with acute basidorsal point (Fig. 113).

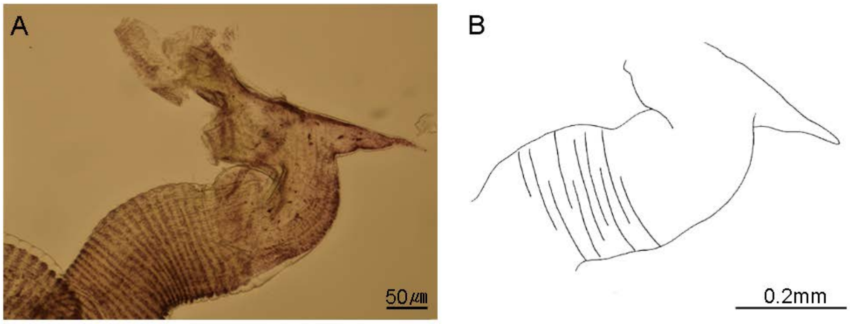

Fig. 113. Penis of *Pyrgomina oulastreae* (Utinomi, 1962). A, Light microscopy on penis; B, line drawing of penis.

Maxilla ovate, with serrulate setae on margin. Mandibular palp elongated, bearing serrulate setae distally and on interior margin. Mandible with 5 teeth, excluding inferior angle. Second and third teeth bidentate, first three teeth occupied 3/5 length of cutting edge. Lateral surface, lower margin and cutting edge of mandible bearing simple-type setae. Lower margin short, inferior angle blunt with simple-type setae. Maxillule cutting edge straight without notch, 2 large spines above notch and 3-4 setae between upper and lower pairs of spines. Anterior and posterior margins with simple-type setae. Labrum bilobed, lobes separated by a deeply V-shaped notch, 3 small teeth on each side of notch (Fig. 114).

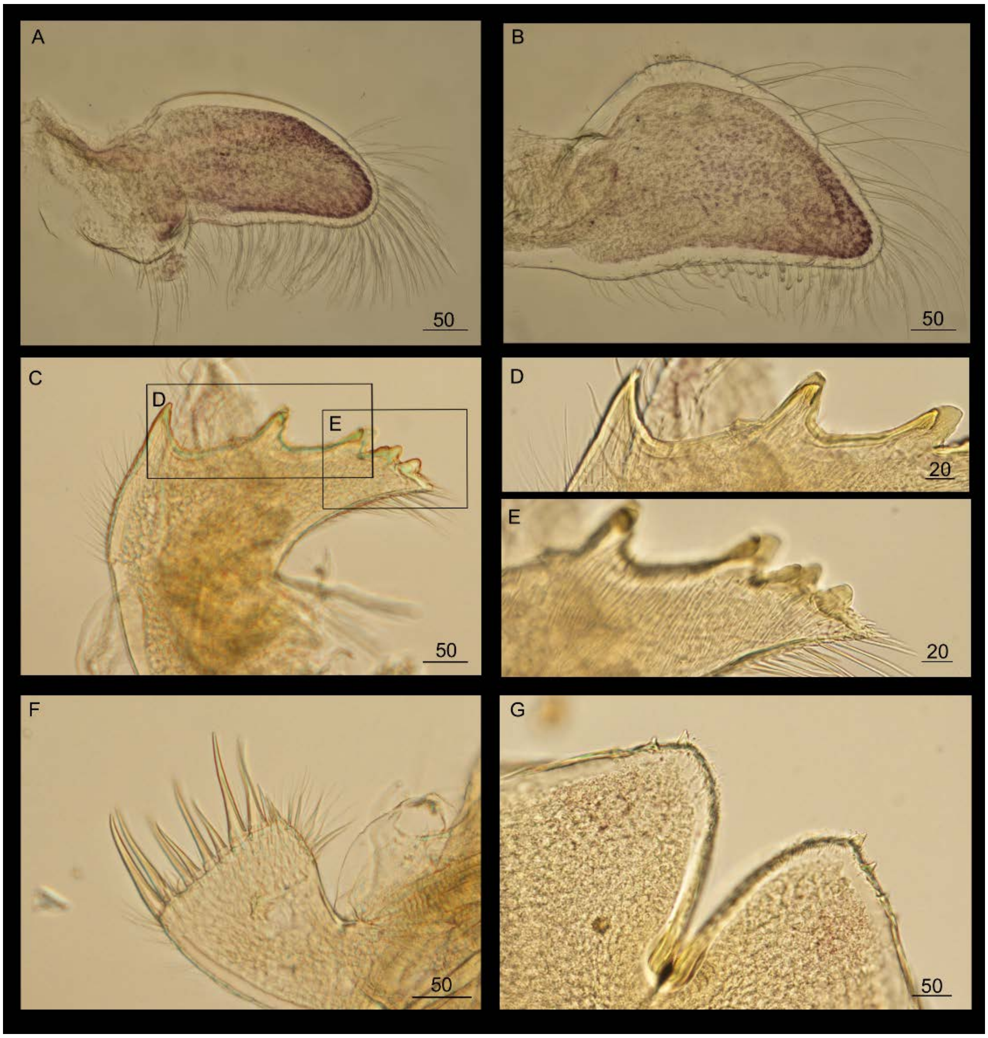

Fig. 114. Mouth parts of *Pyrgomina oulastreae* (Utinomi, 1962). A, Maxilla; B, Mandibulatory palp; C; Mandible; D, Bidentate second to third tooth; E, Inferior angle with simple-type setae; F, Maxillule; G, Labrum. Scale bars in µm.

Habitat. On host coral *Psammocora* spp., *Oulastrea crispata* and *Dichopsammia granulosa* (Fig. 115).

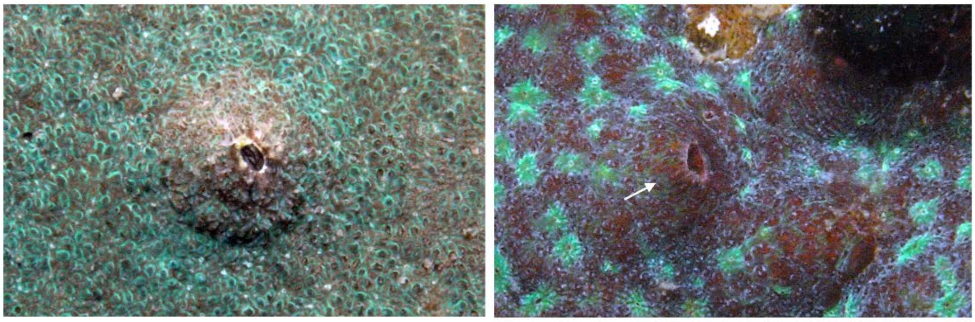

Fig. 115. Close up view of *Pyrgomina oulastreae* on two corals, *Psammocora* spp., and *Oulastrea crispata*. For clarity, the barnacle was indicated by white arrow.

Distribution. Japan and Korea.

Remarks. Ross and Newman (1973) revised the family Pyrgomatidae, in which this family is divided into three subfamilies including Pyrgomatinae (4 plate or united shells, separated or fused scutum and tergum), Ceratoconchinae (4 plate shells, separated scutum and tergum) and Bosciinae (fused shell and with separated balanoid shaped scutum and tergum). The subfamily Bosciinae composed of one genus *Boscia*. In Ross and Newman (1973), they concluded the name *Megatrema* is a synonym to *Boscia*. However, Holthuis (1982) found that the genus *Boscia* is pre-occupied. Holthuis explained *Megatrema* is the correct name to replace *Boscia*. Since Boscia is replaced, the subfamily name changed from Bosciinae to Megatrematinae. Ross and Pitombo (2002) conducted a revision in the subfamily Megatrematinae. In this revision, they place *Megatrema oulastreae* into the genus *Pyrgomina*.

The specimens examined generally agree well with the original description in the main characters. However, intraspecific variation in *P. oulastreae* has been reported in the basis of shell and presence of hooks in cirrus III and IV and notch of maxillule depending on the host corals (Kim, 1998). In the specimens, symbiotic on *Dichopsammia granulosa*, the basis is much deeper, the hooks are present on both rami of the cirri III and IV, and the notch of maxillule is distinct. In the present specimens from Jeju Island, symbiotic on two corals, *Psammocora* spp., and *Oulastrea crispata*, ths basis is shallow, the hooks are present only on rami of cirri III (Fig. 112C, D), and the notch of maxillule is absent (Fig. 114F).

The species of dendrophylliid corals *Oulastrea* and *Dichopsammia* are found in deep waters and all recorded *Pyrgoma* Leach, 1817 coral-associated species inhabit those corals. The distribution of dendrophylliid corals spans from the marginal coral community in temperate to the tropical region in the Pacific Ocean. However, species of *Pyrgoma* are absent from the Japan Sea as only *Pyrgomina oulastreae* has been recorded in dendrophylliid corals (Asami & Yamaguchi, 1997). Further sampling is required to better determine the distribution of dendrophylliid corals and *P. oulastreae* .

2.2.4 Discussion

In the present study, a total of four coral-associated barnacle species belonging to two genera in two families were identified using morphological analysis. Morphological analysis of coral-associated barnacles was based on the shell parts, including external shell plates and paired opercular plates (scutum and tergum).

The genus *Cantellius* is composed of 26 species in the world. Among them, *C. arcuatus* was reported in Korea and *Cantellius* sp. was considered to be unknown species, indicating a possibility of new species separated from the congeneric species. The species *C. arcuatus* has a similar shell type of *C. euspinulosum*, however, there are differences in opercular plates: *C. arcuatus* without a rostral tooth in the basal margin while *C. euspinulosum* has in scutum. The spur of tergum is distinct, long and narrow comparing to *C. euspinulosum*. The new species *Cantellius* sp. is also similar to *C. euspinulosum* by having distinct rostral tooth on scutum and the tergum illustrated Kim (1998). However, in the present study, the oval-shaped adductor muscle scars are unapparent, which is differing from previous records. Also, in the present study, the anterior ramus is longer than the posterior ramus in cirri I-III, which differs from Kim (1998) in having twice as long posterior ramus.

Not much is known about the genus *Pyrgomina*, only two species has been reported worldwide: *P. djanae* Ross & Pitombo, 2002 and *P. oulastreae* (Utinomi, 1962). The species *P. oulastreae* is known as a common coral-associated barnacle in Korea. In this study, the host corals *Psammocora* spp., *Oulastrea crispata* and *Dichopsammia granulosa* were collected at 5–20m depth. The species *Pyrgomina* has never been collected other coral species thus far.

Further studies are needed to find out more about the host specificity, distribution, and interactions between the coral-associated barnacles and corals.

Chapter 3.

Taxonomic Revision of Two Acorn Barnacles

3.1 The formation of lunule-like hollows in shells of the acorn barnacle *Tetraclitella chinensis*, with a reappraisal of the taxonomic status of *T. multicostata* (Cirripedia: Tetraclitidae)

3.1.1 Introduction

Members of the family Tetraclitidae Gruvel, 1903 are common barnacles in the intertidal zone. The four subfamilies of Tetraclitids (Tetraclitinae Gruvel, 1903, Tetraclitellinae Newman & Ross, 1976, Austrobalaninae Pilsbry, 1916, and Newmanellinae Ross & Perreault, 1999) differ in shell morphology and number of plates, which ranges from four to six. Most species of tetraclitids belong to the Tetraclitinae and Tetraclitellinae, which together comprise approximately 50 nominal species worldwide (Hiro, 1939b; Newman & Ross, 1976). Species of Tetraclitinae have conical shells with four multi-tubiferous wall plates that undergo monometric growth and are commonly found in wave-exposed areas. Shells of Tetraclitellinae also have four multi-tubiferous plates, but they are flattened as a result of diametrical growth (Tsang *et al*., 2015). *Tetraclitella chinensis* (Nilsson-Cantell, 1921) and *T. darwini* (Pilsbry, 1928) have been previously reported in Korea (Kim, 1998). *T. chinensis* has the uncommon and distinctive feature of six lunule-like hollows in the plates composing the shell wall:two hollows in the rostrum, two in the carina, and a single hollow in each of the lateral plates (Fig. 116A, B). Hiro (1939b) and Utinomi (1949a) described these hollows as ‘‘apertures’’ perforating the shell wall whereas Ross (1971) stated that the species has six ‘‘hollows’’ in the shell. Utinomi (1949b:36) mentioned that *T. chinensis* inhabits the undersides of stones or is affixed to other barnacles and shells and suggested that the barnacles were ‘‘apt to suffer death’’ when the stones were overturned.

Unlike *T. chinensis*, *T. multocostata* (Nilsson-Cantell, 1930a) has no hollos in its shell plates, but instead has multiple longitudinal ribs on the shell surface (Figs. 116C, D, 117). The multiple-loci phylogenetic tree (mitochondrial COI, 16S and 12S rRNA, and nuclear EF1, RPII, H3, and 18S rRNA) of Tetraclitidae published by Tsang *et al*. (2014) showed no strong genetic differentiation between *T. chinensis* and *T. multicostata,* which suggests that these two taxa are conspecific. To test this hypothesis, the natural abundances of *T. chinensis* and *T. multicostata* on Jeju Island, Korea were examined, where they are sympatric, and morphologies (opercular plate geometry, cirri, mouth 184arts and shell development) as well as the sequence divergences of two of the mitochondrial genes (12S rDNA and COI region) studied by Tsang *et al*. (2014) and one nuclear gene (ITS1), but by using many more specimens of each species from Korea, Taiwan and China. The nuclear gene (ITS1) has been proven to useful in species identification in tetraclitid barnacles (Chan *et al*., 2007c). This study describes the process of formation of the hollows in *T. chinensis* for the first time and compares this with the only other barnacle with similar hollows, *Chinochthamalus scutelliformis* (Darwin, 1854).

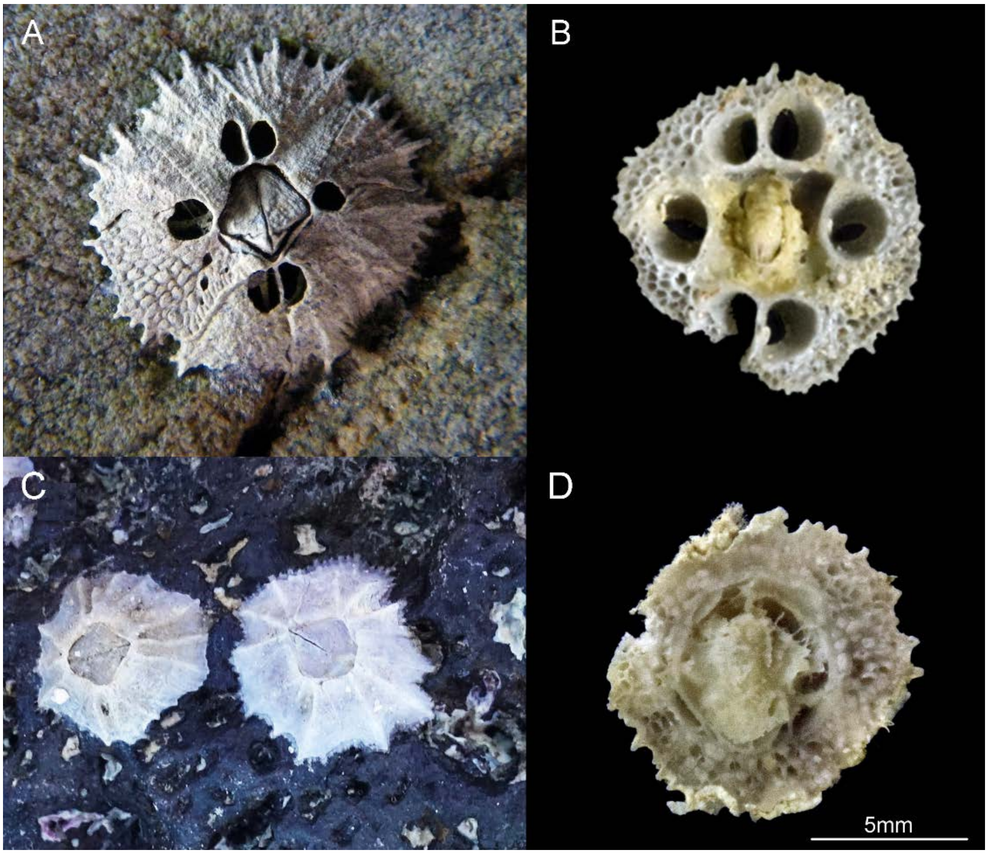

Fig. 116. *T. chinensis* (Nilsson-Cantell, 1921) and *T. multocostata* (Nilsson-Cantell, 1930). A, Top view of *T. chinensis* showing a shell composed of four plates with six hollows on the outer surface (two on the rostrum, two on the carina, and a single hollow on each lateral plates; B, Basal view of *T. chinensis* showing that the hollows are larger at the base than at the top; C, Top view of *T. multocostata,* showing the shells with longitudinal ribs; D, Basal view of *T. multocostata* showing a shell composed of four plates with no hollows. Scale bars in 5 mm.

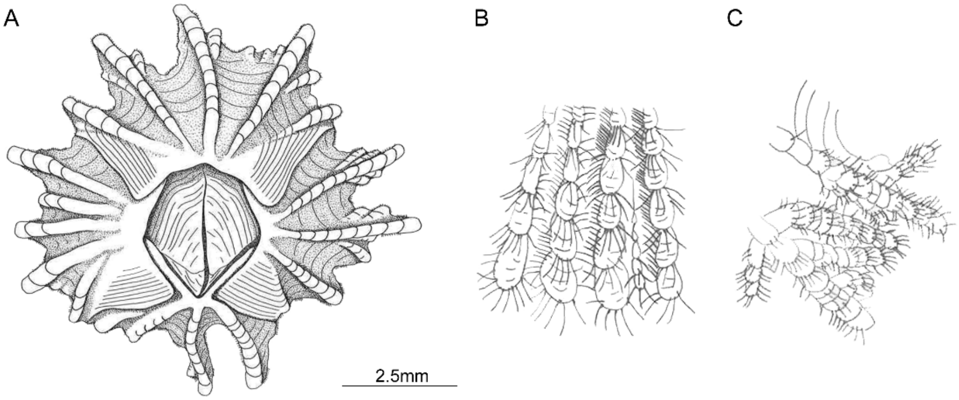

Fig. 117. Redrawing of shell of *T. multicostata*. A, Redeawing of *T. multicostata* from Utinomi (1962); B, Redrawing of shell of *T. multicostata* in Nilsson-Cantell (1930a); C, Redrawing of the main rib and accessory ribs on the shell of *T. multicostata* in Utinomi (1962).

3.1.2 Materials and Methods

Specimen Collection

Specimens of *T. chinensis* and *T. multicostata* were collected from low intertidal shores at Seogwipo, Jeju Island, Korea (33°13'48.0"N, 126°30'23.3"E) in March 2017. Additional samples of *T. chinensis* were collected from Jia-Ler-Shui, Kenting, Taiwan (21°35'35.9"N, 120°30'51.5"E) in July 2007 (Fig. 118), where it was found not only on the undersides of stones, but also on their upper surfaces. An additional sample of *T. multicostata* was collected on Hai Ling Island, China (21°34'22.54"N, 111°52'04.9"E) in May 2007 (Fig. 118). Also, two other congeners, *T. divisa* (Nilsson-Cantell, 1921) and *T. karandei* Ross, 1971, were collected from Kenting in July 2007 to compare molecular sequences. All specimens were preserved in 95% ethyl alcohol.

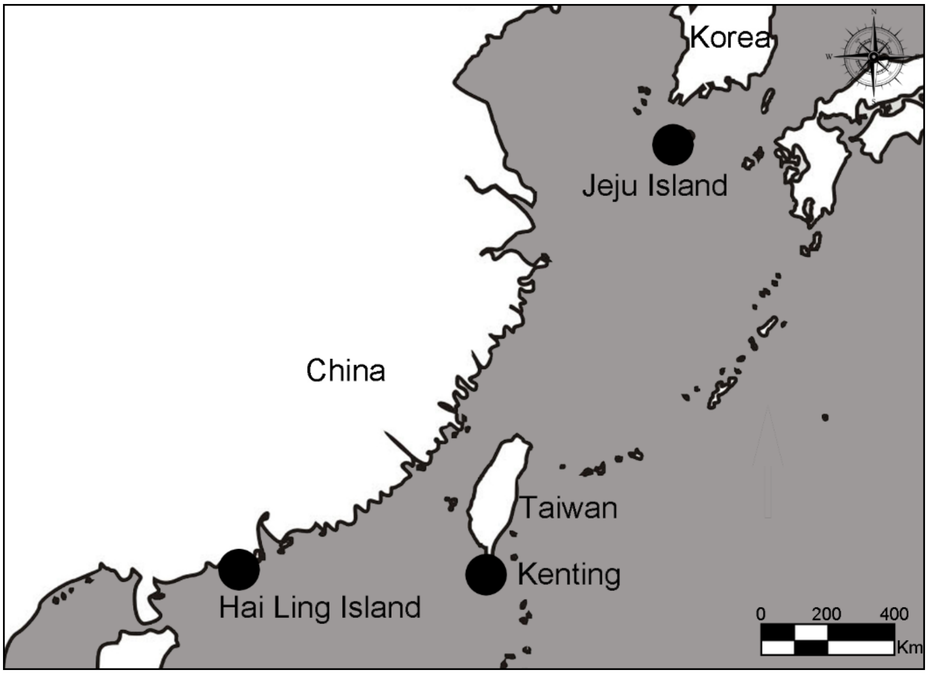

Fig. 118. Map of collecting sites in Korea, Taiwan and China.

Natural Abundance of *T. chinensis* and *T. multicostata*

First, randomly established forty 10 × 10cm quadrats along 30m stretches of shoreline at the low-mid tidal level (0.8–1.0m above chart datum, approximately at mean lower low tide level) in Seowipo, Jeju Island, where the two species are most abundant. Second, counted the number of barnacles present in digital photographs taken of each quadrat. Scanning electron microscopy (SEM) of shells and opercular plates and light microscopy of cirri, mouthparts, and penis was done. Shells, opercular plates, and somatic bodies of *T. chinensis* and *T. multicostata* from Taiwan, Korea, and China were dissected. Shells and opercular plates were immersed in 10% commercial bleach solution for 20 min, rinsed in distilled water three times, and air dried. The shells and opercular plates were palladium-coated prior to examination with a scanning electron microscope (FEI Quanta 2000; Thermo-Scientific, Waltham, MA, USA) following Chan *et al*. (2013b). The cirri, penis, and mouthparts of representative specimens were dissected and observed under light microscopes (Zeiss Axioscope Z1). The setal classification follows Chan *et al*. (2008c).

Examination of Shell Morphology and the Formation of Hollows

Samples collected from the Jeju Island quadrats by using hammer and chisel were preserved in 95% ethyl alcohol; the rostral-carinal basal diameter and the maximum shell width of each specimen of *Tetraclitella* were measured using digital calipers. The shapes and manner of formation of any hollows in the shell plates of specimens representing different size classes of *T. chinensis* and *T. multicostata* were examined, and also checked their patterns of ribs. To compare variation in the opercular plates (scutum and tergum) between the two species, the plates were resected from the shells of 10 individuals of each of *T. chinensis* and *T. multicostata* from Jeju Island and 10 individuals of *T. chinensis* from Kenting, and a digital photograph with a scale bar was taken of each set. Ten parameters of each scutum and tergum (seven lengths and three angles) were measured from the photographs using Image J (https://imagej.nih.gov/ij/) (Fig. 119A). Variations between these parameters in the two species were analyzed using multivariate analysis (PRIMER 6, Plymouth Routine in Multivariate Analysis, PRIMER-E, Plymouth, UK; Clarke, 1993). Data were square-root transformed prior to analysis and the Euclidean distance was used to calculate the similarity matrix. Non-metric Multidimensional Scaling (nMDS; Clarke, 1993) was used to generate two-dimensional plots of the opercular plates of *T. chinensis* and *T. multicostata* (Fig. 119B). Analysis of similarity (ANOSIM; Clarke, 1993) was used to test for differences in opercular plate parameters between the two species. Under the ANOSIM analysis, the degree of similarity between pairs can be indicated by R values in the Global Test, which range from 0 to 1, with 0 indicating the highest similarity and 1 the lowest similarity. Chan *et al*. (2007b, c) demonstrated the utility of this multivariate technique to discriminate between scutum and tergum parameters among tetraclitid species.

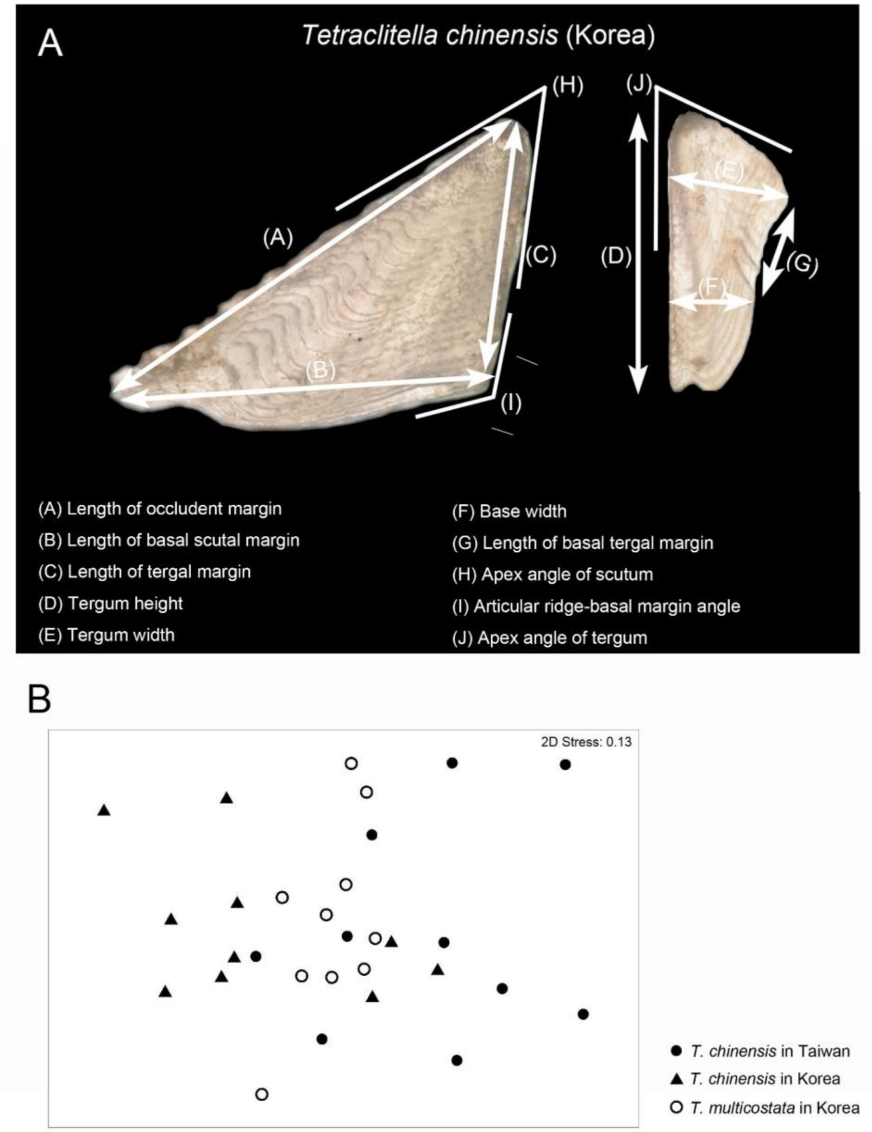

Fig. 119. Opercular plates of *T. multicostata* and nMDS patterns. A, Parameters (seven lengths, three angles) of the scutum and tergum for comparisons of opercular plate geometry between *T. chinensis* and *T. multicostata*; B, nMDS plot comparing opercular plate morphology between *T. chinensis* in Korea and Taiwan and *T. multicostata* in Korea.

Molecular Analysis

Genomic DNA was extracted from each specimen by using the commercial QIAamp Tissue Kit (QIAGEN, Hilden, Germany). Partial sequences from the mitochondrial 12S rDNA and COI genes were amplified using polymerase chain reaction (PCR) with primers 12S-FM and 12S R2 (Tsang *et al*., 2014) in addition to LCO1490 and HCO2198 (Folmer *et al*., 1994). The ITS region was amplified using primers SP-1-5’138 and SP-1-3’ (Chu *et al*., 2001). All sequences were proofread using MEGA ver. 7 (Kumar et al., 2016) and aligned with the *Tetraclitella* sequences from GenBank using Multiple Alignment and Fast Fourier Transform (MAFFT; Katoh *et al*., 2002). Alignments were also checked by eye, and ambiguous positions were adjusted manually. Some sequences in ITS1 were treated with gaps due to missing data. All phylogenetic analysis were performed based on maximum likelihood (ML) analysis in RAxML ver. 8 (Stamatakis, 2014) implemented on the Cyberinfrastructure for Phylogenetic Research (CIPRES; https://www.phylo.org/) using the GTRGAMMA model with 1,000 bootstrap replicates. The combined datasets of the three genes were concatenated to resolve alternative phylogenies. ML analysis was performed using for all analysis. Four *Tetraclita* species, *Chelonibia testudinaria* (Linnaeus, 1758), and *Amphibalanus amphitrite* (Darwin, 1854) were selected as outgroups because these species are phylogenetically close to the Tetraclitidae clade (Tsang *et al*., 2014). A matrix of genetic distances within and among the species was calculated in MEGA v. 7 using Kimura’s two-parameter model (Kumar *et al*., 2016).

3.1.3 Results

Natural Abundances of *T. chinensis* and *T. multicostata*

Tetraclitella chinensis and *T. multicostata* co-exist at the same tidal level on Jeju Island. The two species respectively reached a mean density of about 2.6 and 17.4 individuals per 10 × 10cm quadrat along the surveyed 30m of shoreline. Rock spaces were bare around individuals (Fig. 120). The mean abundance ratio of *T. chinensis* to *T. multicostata* in quadrats (N = 40) was 22.8:77.2.

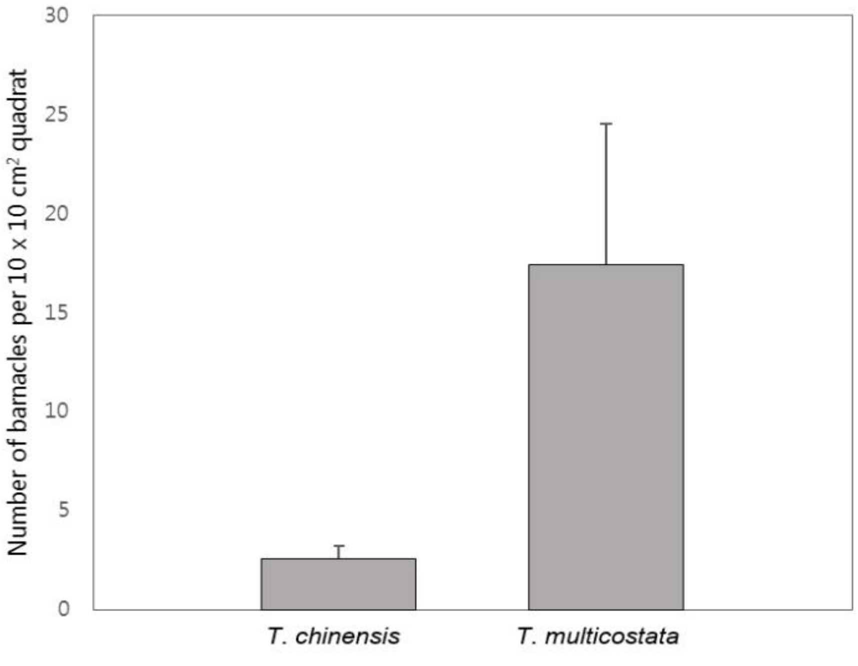

Fig. 120. Mean number (+1 standard error) of individuals of *T. chinensis* and *T. multicostata* per 10 × 10cm quadrat at Seogwipo, Jeju (N = 40).

Morphological Variation and Growth Pattern of *T. chinensis* and *T. multicostata*

Ordinations in the nMDS plots of scutum and tergum parameters of *T. chinensis* from Korea and Taiwan and *T. multicostata* from Korea clustered together but did not form distinct clades (Fig. 119B). The ANOSIM analysis also revealed no significant differences between *T. chinensis* and *T. multicostata* (Global R = 0.08, $P > 0.05$).

Development of Shell Hollows

The lunule-like shell hollows in *T. chinensis* are formed by the extension and fusion of the longitudinal ribs on the shell peri-meter. In the Jeju Island samples, the longitudinal ribs on the lateral plates started to fuse and form hollows when the shell diameter along the rostral-carinal axis reached 4–5 mm. Hollows started to form on the rostrum and carina when the shell diameter reached 5–6 mm (Fig. 121). In all, six hollows (two in the rostrum, two in the carina, and one in each lateral) were formed when the external ribs fused. Samples of *T. chinensis* from Kenting, Taiwan had fully formed hollows on the lateral plates at shell diameters of 4–5mm, whereas most of the individuals in the 5–6mm size class had fully formed hollows on all four shell plates (Fig. 121). Specimens of *T. multicostata* never had hollows or partial hollows in their shell plates, which were externally ornamented with multiple longitudinal ribs that did not anastomose. The process of development of hollows in intermediately hollowed individuals could not be observed due to their low abundance on the shore.

Fig. 121. Shell development patterns in *T. chinensis* and *T. multicostata*. Shell hollows formed on lateral plates in *T. chinensis* when the shell size reached 4–5mm in diameter; each plate in *T. multicostata*, however, had multiple longitudinal ribs and no hollows. Note that the scales are different among the different size classes. Scale bars in mm.

Molecular Phylogenetic Analysis

Each of the species sequenced was located in a separate lineage in trees based on the mitochondrial 12S rDNA and COI, except for *T. chinensis* and *T. multicostata*, which comprised a single lineage (Figs. 122, 123, 124A). Due to missing data and poor condition, 16 specimens of the total analysed were excluded from the nuclear ITS1 phylogenetic tree (Fig. 124B).

The phylogeny implied by the combined dataset (12S rDNA + COI + ITS1) (Fig. 125) was similar to the phylogenetic trees derived from individual genes (Figs. 122, 123, 124B), thereby supporting the conclusion that *T. chinensis* and *T. multicostata* constitute a single lineage with no clear separation between them. The lineage containing *T chinensis* + *T. multicostata* is sister to the lineage of *T. karandei*. These two lineages are then sister to *T. divisa*.

Overall, bootstrap values increased when the combined dataset was used. In pairwise comparisons, the K2P distance among the sequences ranged from 0.2% to 24.3% (Table 6). The intraspecific divergence of *T. chinensis* was 0.3% (Table 6). *T. chinensis* from Korea was clustered in the same lineage as *T. chinensis* from Taiwan and *T. multicostata* from Korea and China. The sequence divergence between *T. chinensis* and *T. multicostata* was only 0.9%. The interspecific K2P distance of other *Tetraclitella* species besides these two species ranged from 12.8% to 17.1% (Table 6).

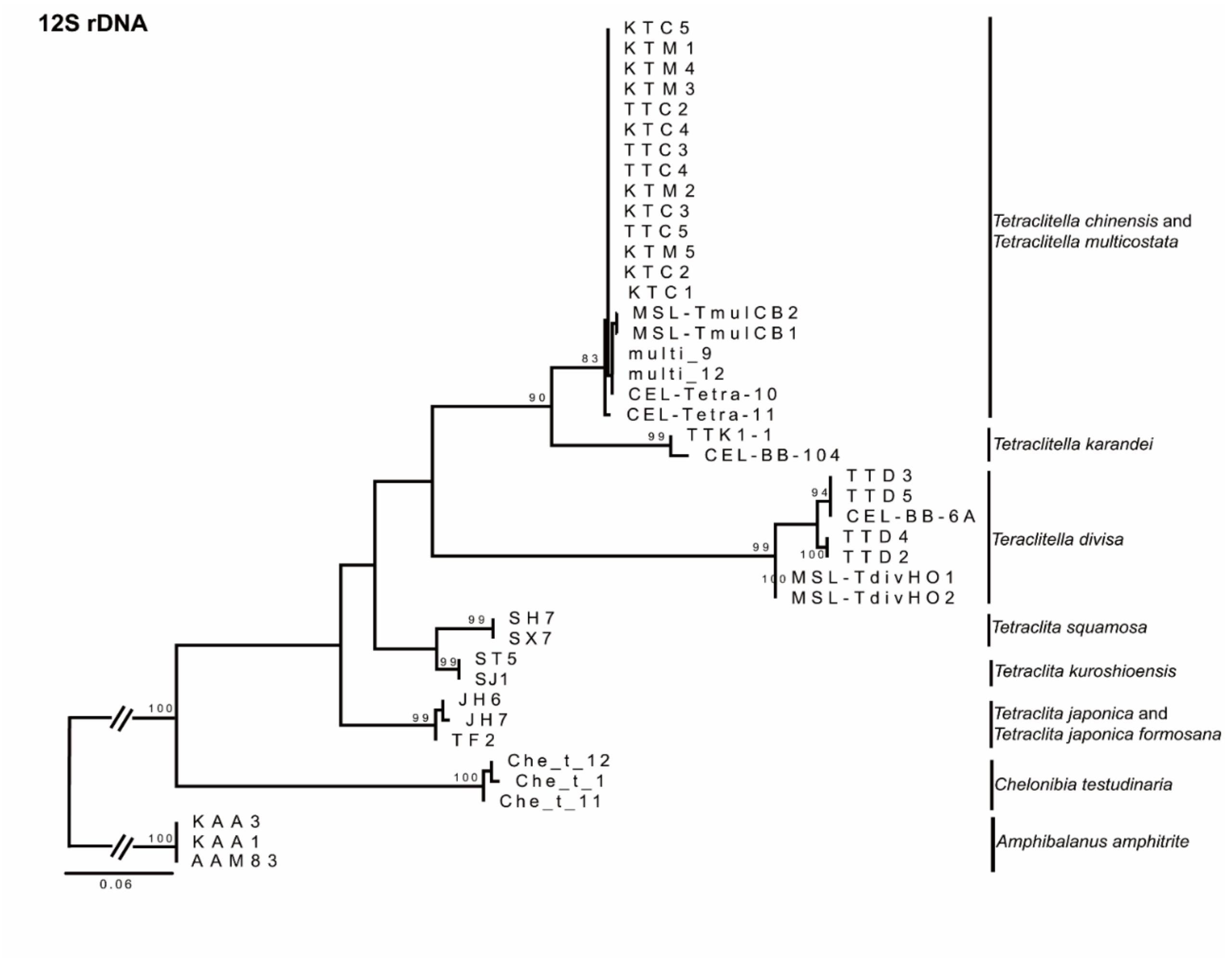

Fig. 122. Topology inferred individual molecular markers based on Maximum likelihood analysis of 12S rDNA.

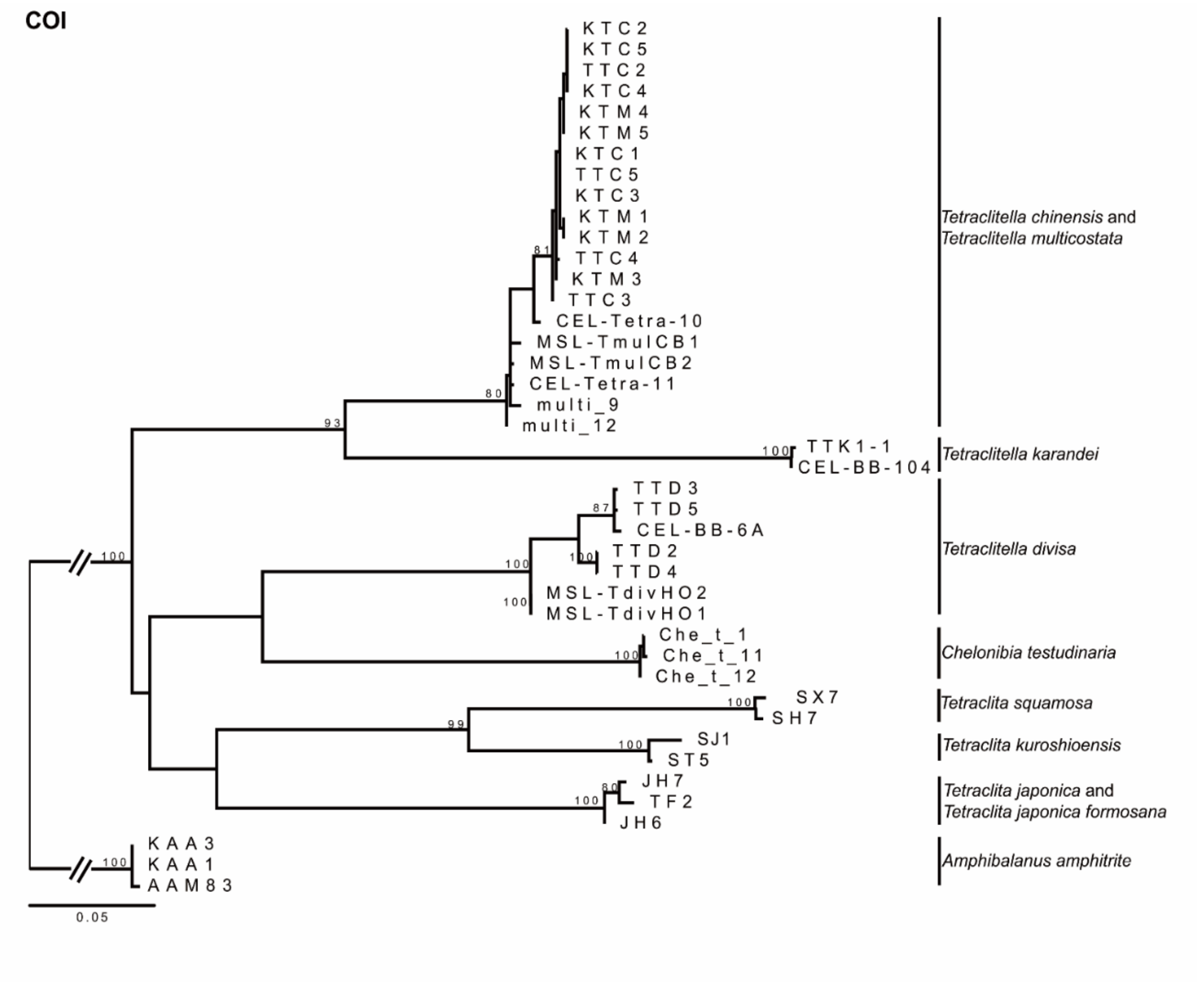

Fig. 123. Topology inferred individual molecular markers based on Maximum likelihood analysis of COI.

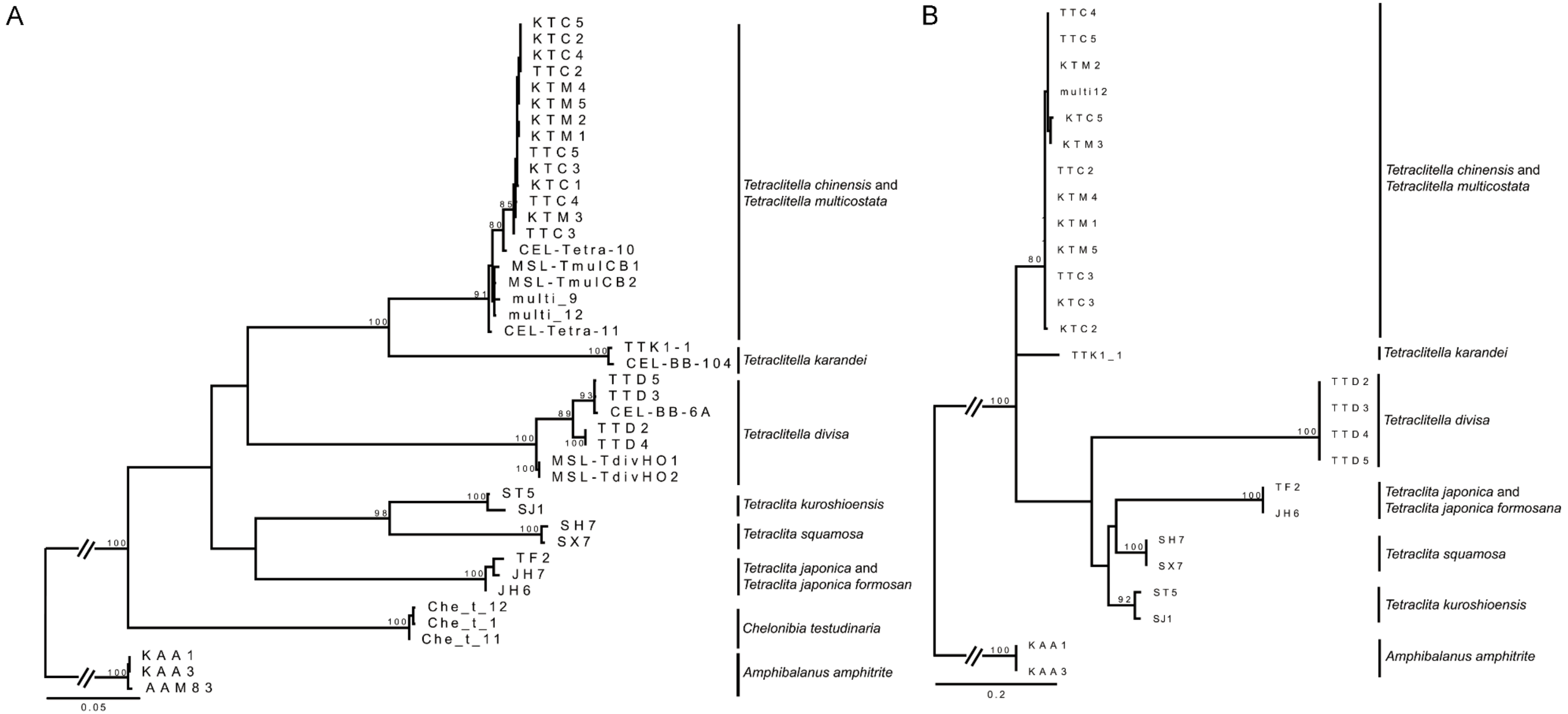

Fig. 124. Phylogenetic trees of *Tetraclitella* species, using four *Tetraclita* species, *Chelonibia testudinaria*, and *Amphibalanus amphitrite* as outgroups. A, Combined data sets of two mitochondrial genes (12S rDNA + COI); B, ITS1. Bootstrap scores of >80% are presented at the major nodes. The scale bar indicates the number of substitutions per site.

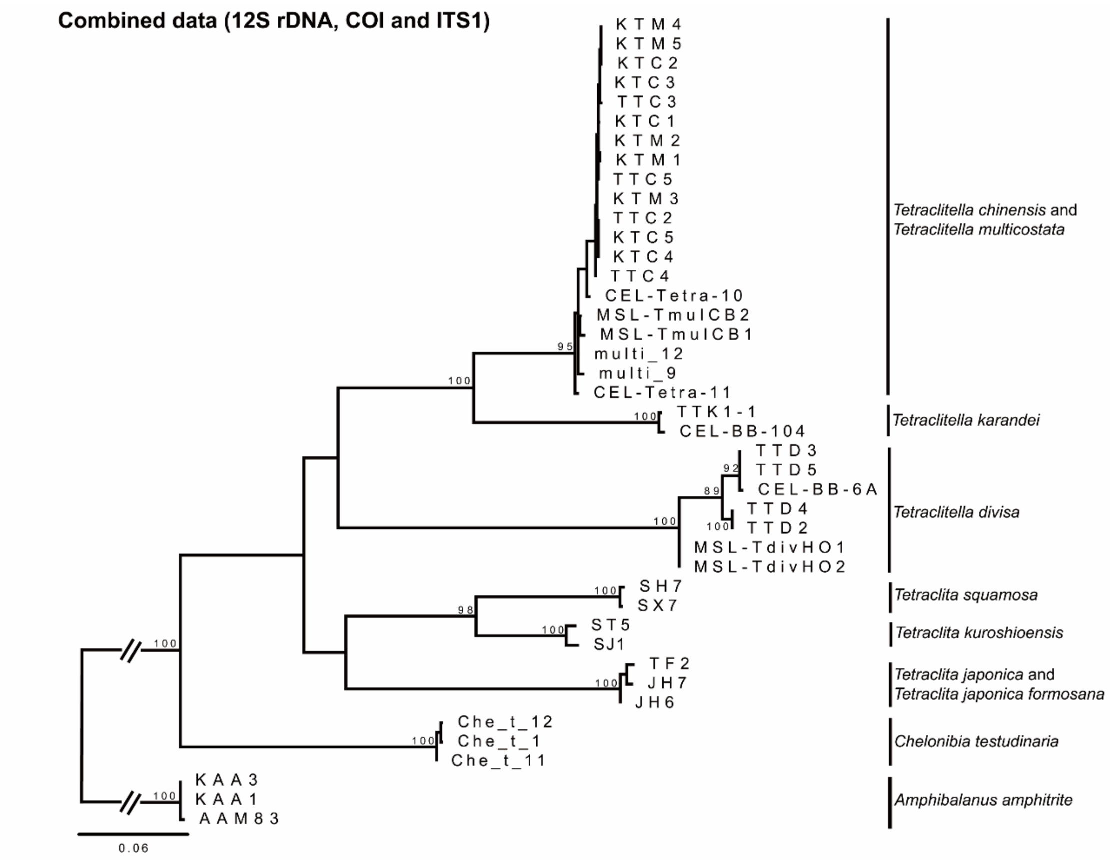

Fig. 125. Phylogenetic trees of *Tetraclitella* species based on maximum likelihood analysis of two mitochondrial genes and one nuclear gene (12S rDNA + COI + ITS1) datasets, using four *Tetraclita* species, *Chelonibia testudinaria*, and *Amphibalanus amphitrite* as outgroups. Bootstrap scores of >80% are presented at the major nodes. The scale bar indicates the number of substitutions per site.

Table 6. Mean K2P distance for the concatenated molecular dataset between and within the studied species

	1	2	3	4	5	6	7	8	9	10
1. *Tetraclitella chinensis*	0.003									
2. *Tetraclitella multicostata*	0.009	0.010								
3. *Tetraclitella karandei*	0.132	0.128	0.001							
4. *Tetraclitella divisa*	0.171	0.171	0.176	0.021						
5. *Tetraclita squamosa*	0.170	0.171	0.178	0.189	0.006					
6. *Tetraclita kuroshioensis*	0.154	0.154	0.171	0.168	0.107	0.012				
7. *Tetraclita japonica*	0.163	0.163	0.190	0.185	0.151	0.160	0.007			
8. *Tetraclita japonica formosana*	0.163	0.163	0.190	0.187	0.152	0.162	0.007	–		
9. *Chelonibia testudinaria*	0.201	0.202	0.200	0.176	0.202	0.177	0.197	0.199	0.003	
10. *Amphibalanus amphitrite*	0.211	0.213	0.243	0.204	0.223	0.218	0.219	0.218	0.227	0.002

Systematic Accounts

Superfamily Tetraclitoidea Gruvel, 1903

Family Tetraclitidae Gruvel, 1903

Subfamily Tetraclitellinae Newman & Ross, 1976

Genus *Tetraclitella* Hiro, 1939b

***Tetraclitella chinensis* (Nilsson-Cantell, 1921)**

Tetraclita purpurascens chinensis Nilsson-Cantell, 1921:59, fig. 81, pl. 3, fig. 12.—Hiro, 1939d:273, fig. 14.

Tetraclita purpurascens nipponensis Hiro, 1931:155, fig. 10, pl. 14, fig. 3-3d; 1937b:469.

Tetraclitella (*Tetraclitella*) *chinensis*.—Utinomi, 1949b:36; 1954:23; 1962:231.

Tetraclitella chinensis.—Utinomi, 1970:347.—Ross, 1971:217.—Rosell, 1975:96.—Newman & Ross, 1976:46.—Zevina & Tarasov, 1963:97, fig. 14.— Ren & Liu, 1979:347, pl. 3, figs. 5-9.—Chan *et al.*, 2009:205, fig. 175.

Tetraclita purpurascens var. *multicostata* Nilsson-Cantell, 1930a:18, fig. 5; 1930b:2.

Tetraclita multicostata.—Utinomi, 1962:231, figs. 9, 10.

Tetraclitella multicostata.— Ross, 1971:217.—Newman & Ross, 1976:47.—Ren & Liu, 1979:347, pl. 4, figs. 3-9.—Liu & Ren, 2007:335, fig. 150.—Chan *et al.*, 2009:211, fig. 181.

Tetraclitella multicostata digita Rosell, 1975:96

Materials examined. SNU-CRU-001. 10 specimens (*Tetraclitella chinensis*), Seogwipo, Jeju Island, Korea, March, 2017. SNU-CRU-002. 10 specimens (*Tetraclitella multicostata*), Seogwipo, Jeju Island, Korea, March, 2017. SNU-CRU-010, 10 specimens (*Tetraclitella chinensis*), Jia-Ler-Shui Kenting, Taiwan, July, 2007. CEL-Hai-Ling-001, 002. 2 specimens (*Tetraclitella* *multicostata*), Hailing Island, China, May, 2007.

Diagnosis. Shell with two major forms, hollowed and multicostate. Completely hollowed form with 6 hollows (each of carina and rostrum with 2 hollows, each of two laterals with a single hollow), shell surface with weak longitudinal ribs, radii smooth with horizontal striations. Intermediately hollowed form with less than 6 hollows, some plates without hollows having longitudinal ribs in surface. Multicostata form with longitudinal ribs on surface, often 4 major ribs on rostrum, 3 major ribs on carina, with accessory ribs extending from major ribs; radii smooth with horizontal striations, striations pronounced on uneroded specimens.

Descriptions. Shell flattened, composed of 4 plates (Fig. 116A-D). Outer surface of shell gray purple and with setae. Plates tubiferous. Base with honeycomb patterns of parietal tubes arranged in up to 2 or 3 layers. Basis weakly calcareous. Orifice quadrangular or pentagonal in shape. Two major morphological forms, hollowed and multicostate. Hollowed form with hollows in shell plates, either completely hollowed with 6 hollows (each of carina and rostrum with 2 hollows, each of 2 laterals with a single hollow) (Figs. 116A, 126A) or intermediately hollowed with fewer than 6 hollows (Fig. 127). Specimens with 5 hollows (1 in carina, 1 in each latera and 2 in rostrum; Fig. 127C), 4 hollows (Carina without hollow, 1 in each latera and 2 in rostrum; Fig. 127D), 3 hollows (1 in each latera and 1 in rostrum; Fig. 127E) and 1 hollow (only 1 in latera; Fig. 127A, B) encountered, as well as specimen with 3 hollows on rostrum, none on other plates (Fig. 127F). Plates without hollows in intermediately hollwed specimens with longitudinal ribs on surface.

Hollows oval-shaped, lunule-like. Circumference of hollows smaller on top of shell and bigger at base (Fig. 116A, B). Radii smooth with horizontal striations (Fig. 126A). Shell surface with longitudinal ribs. Ribs and shell surface with setae (Fig. 126B). Multicostata form without any hollows on shell (Fig. 116C, D). Shell surface with longitudinal ribs (Figs. 116C, 128). Ribs with horizontal striations. Four major longitudinal ribs on carina and 3 major longitudinal ribs on rostrum (Figs. 116C, 128). Secondary or accessory ribs developing from major ribs (Fig. 128A). Ribs and rest of plate surface armed with setae when observed under microscopes (Fig. 128B, C). Radii smooth with horizontal striations (Fig. 128A). In uneroded specimens (collected in Hai Ling Island), horizontal striations on radii pronounced (Fig. 128D, E, F).

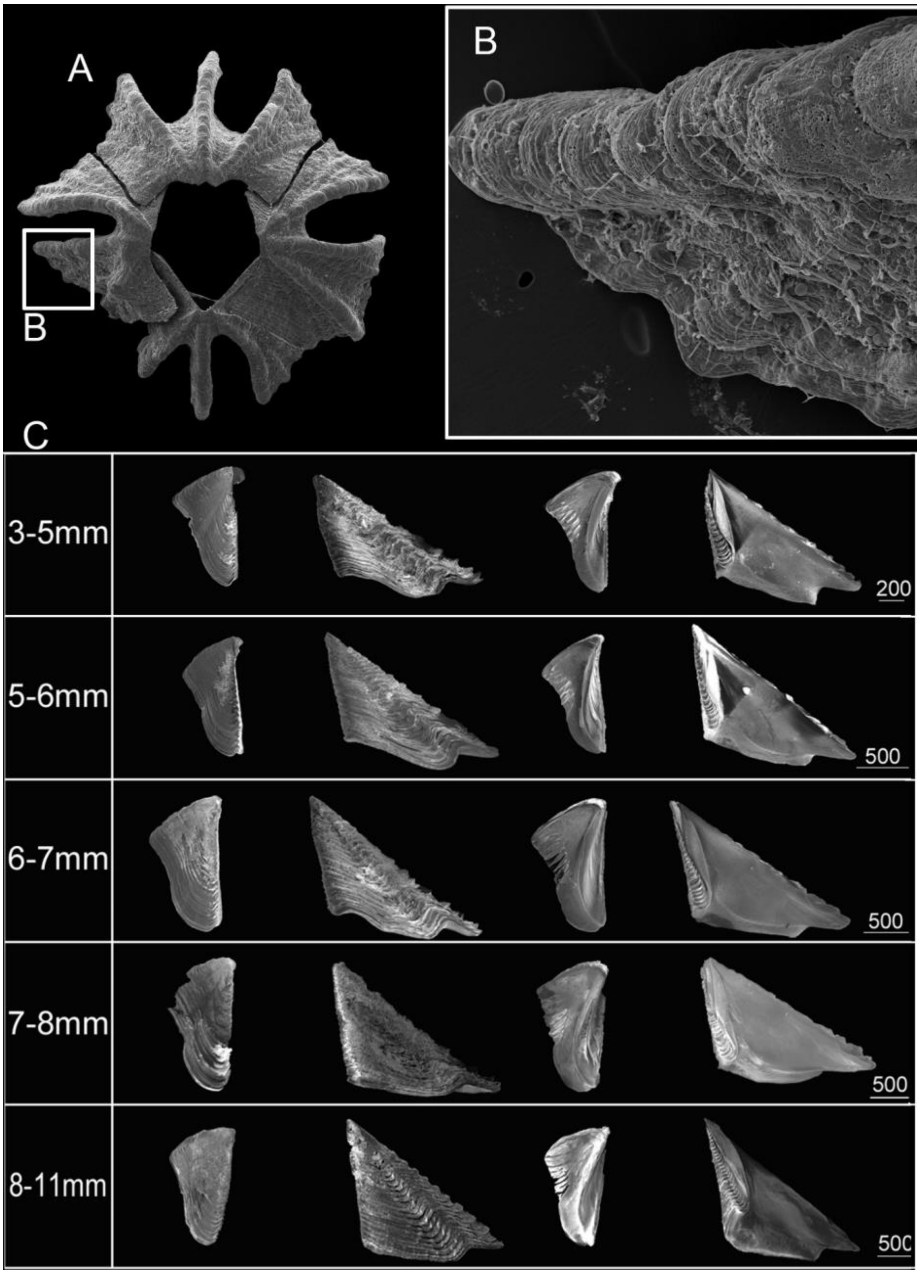

Fig. 126. Scanning Electron Microscopy on shells of *Tetraclitella chinensis* (Nilsson-Cantell, 1921). A, Hollow form; B, Maginified view of one of the rib extension at the shell rim, showing setae on shell surface; C, Scutum and tergum, showing the variation in shape among different size classes. Scale bars in μm.

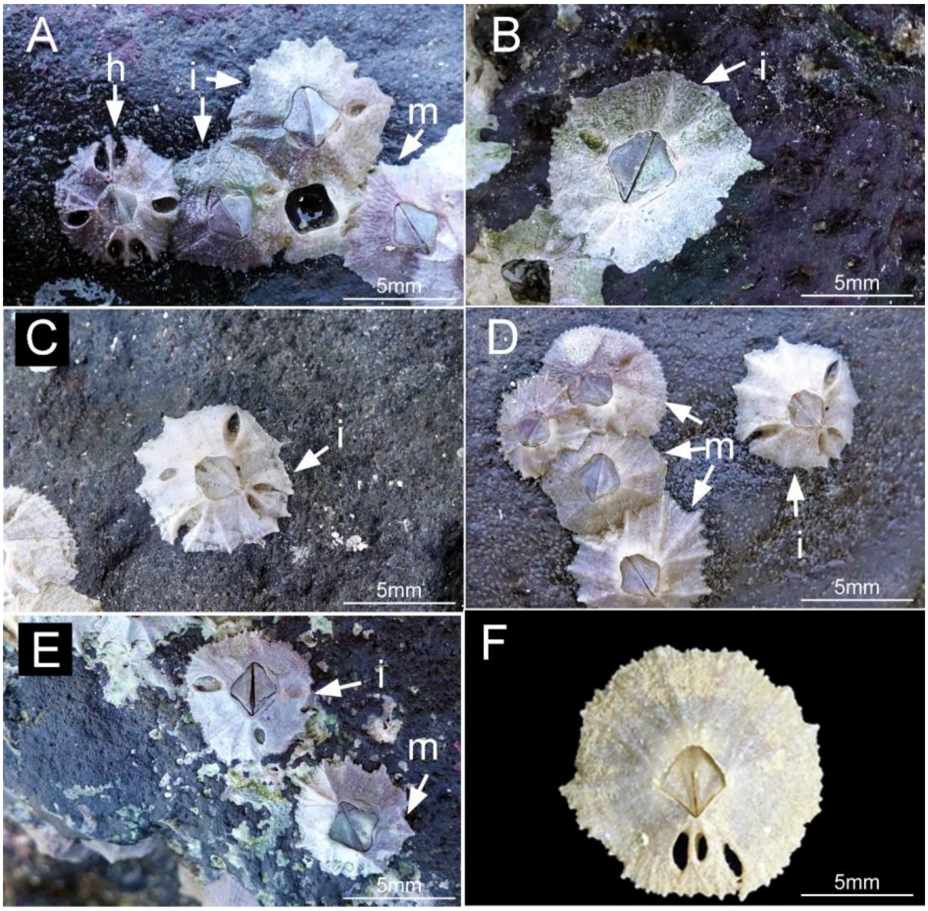

Fig. 127. *Tetraclitella chinensis* (Nilsson-Cantell, 1921). A, Presences of complete hollow form with six hollows (h), and intermediate hollow form with only one hollow and with shared character with multicostata form (i) and multicostata form; B, Intermediate hollow form with one hollow (i); C, Intermediate hollow form (i) with five follows, note the carina has one hollow; D, Intermediate hollow form (i) with four hollows (carina without hollows) and present together with multicostata form (m); E, Intermediate hollow form with three hollows (i), note carina has no hollow, rostrum has one hollow, present together with multicostata form (m); F, Iintermediate hollow form with three hollows on rostrum and all other plates are without hollows.

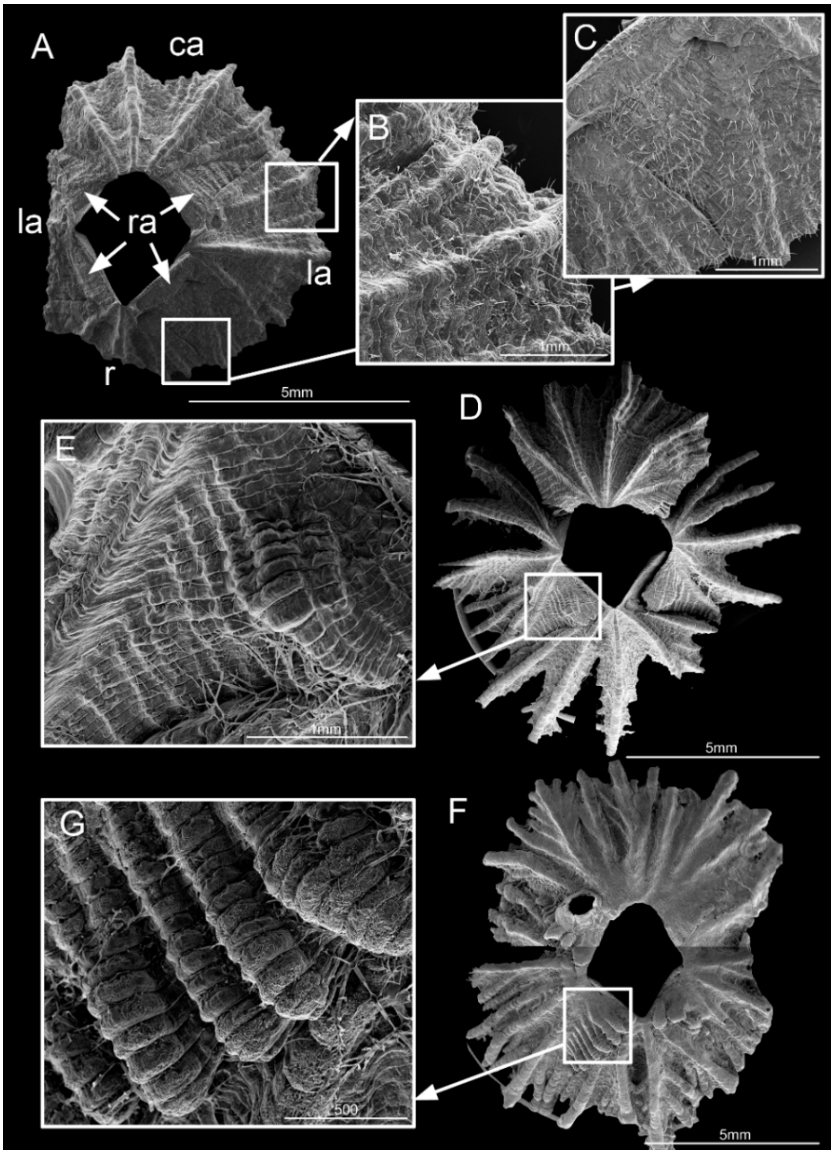

Fig. 128. Scanning Electron Microscope of shells of *Tetraclitella chinensis* (multicostate form). A, Shell from Jeju Korea, showing smooth radii (ra) with horizontal striations; B, C, Magnified shell surface showing setae on sjells; D, Small shell from Hai Ling Island, China; E, Showing the radii is pronounced and digitiform when it is not eroded; F, A larger specimen collected at Hai Ling Island, China; G, Showing the extension of accessory ribs and elevated radii. ca, carina; r, rostrum; la, lateral.

Scutum white, triangular, wider than high. Outer surface with distinct horizontal growth lines plus shallow or deep medial furrow (Figs. 126, 129, 130). Inner surface smooth. Occludent margin straight, slightly toothed near basal margin. Articular margin straight. Basal margin differing between hollowed form and multicostate form (Figs. 126, 129, 130), hollowed form with more pronounced notch in basal margin in small body sizes (Fig. 126C), multicostate form with less pronounced notch or no notch in basal margin (Fig. 129). Articular furrow deep, articular ridge highly elevated. Adductor muscle pit faint or absent. Basal margin with depressor muscle pits, with honeycomb pattern on surface (Figs. 126, 129, 130).

Tergum similar in both hollowed and multicostate forms. Tergum flat, higher than wide, shape variable (Figs. 126, 129, 130). Outer surface with distinct growth lines. Articular margin slightly convex or straight. Carinal margin straight. Articular furrow wide, shallow. Spur conspicuously short, wide, occupying nearly half of basal margin. Spur furrow absent. Crest for depressor muscle distinct (Figs. 126, 129, 130).

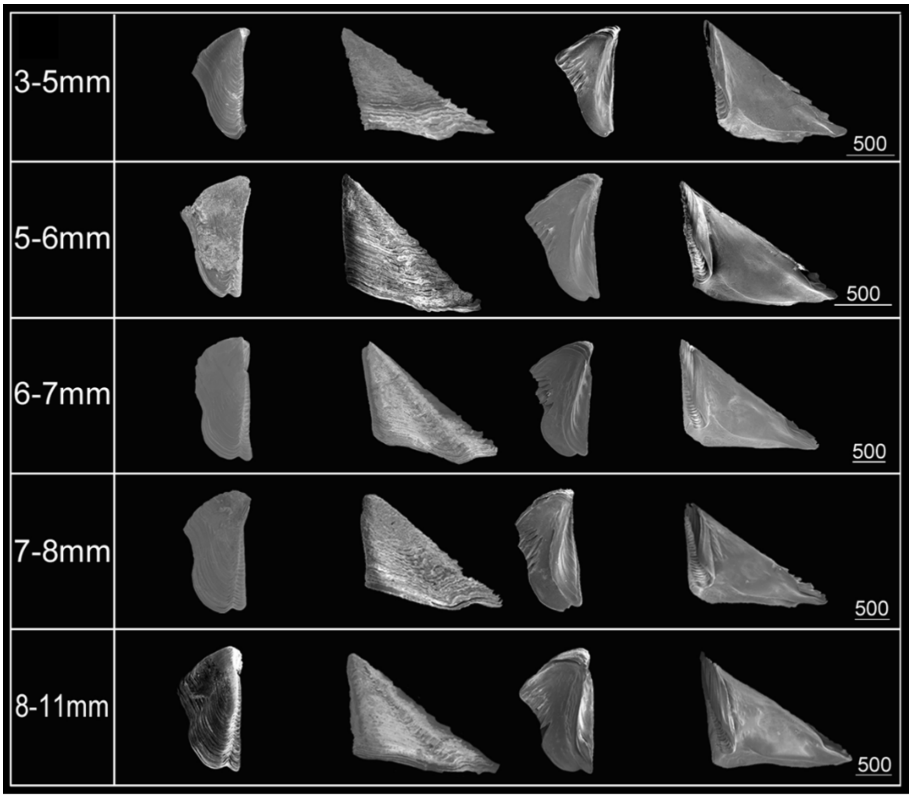

Fig. 129. Scanning Electron Microscopy on shells of scutum and tergum of *Tetraclitella chinensis* (multicostate form), showing the variation in shape among different size classes. Scale bars in µm.

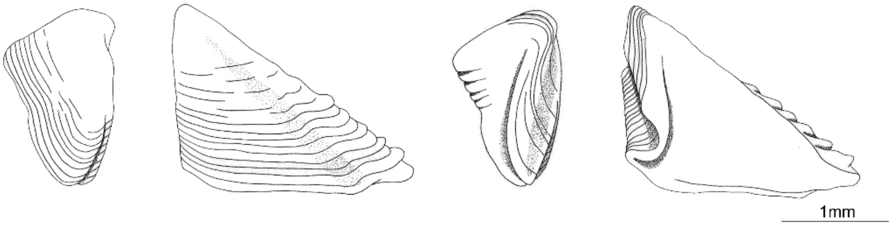

Fig. 130. *Tetraclitella chinensis* (multicostate form), line drawings of scutum and tergum.

Mouthparts similar in both forms. Maxilla small, bilobed with setae on margin of both lobes (Figs. 131A, 132A). Maxillule notched, with 2 large setae above notch, ~10 setae below notch (Figs. 131B, 132B). Mandible with 5 teeth excluding inferior angle; first tooth separated from rest; second, third teeth bidentate; fourth tooth blunt with fine teeth on cutting edge; fifth tooth close to inferior angle; inferior angle pointed with sharp setae (Figs. 131C, 132C, E, G). Mandibular palp elongated with serrulate setae on inferior margin (Figs. 131D, 132D). Labrum slightly notched with single teeth, simple setae on each side of cutting edge (Figs. 131E, 132F, H).

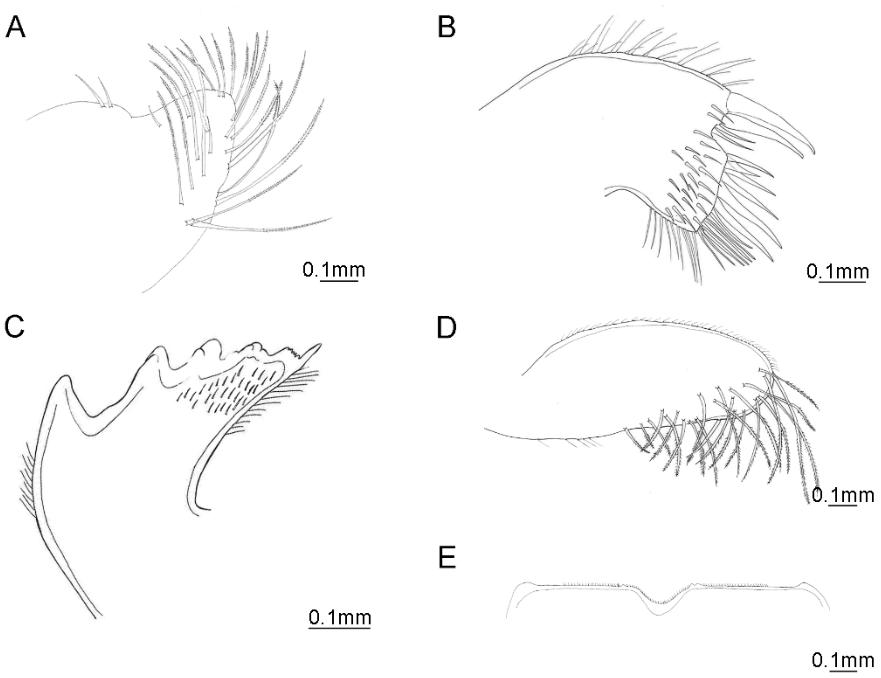

Fig. 131. *Tetraclitella chinensis* (hollowed form), line drawings of mouth parts. A, Maxilla; B, Maxillule; C, Mandible; D, Mandibulatory palp; E, labrum.

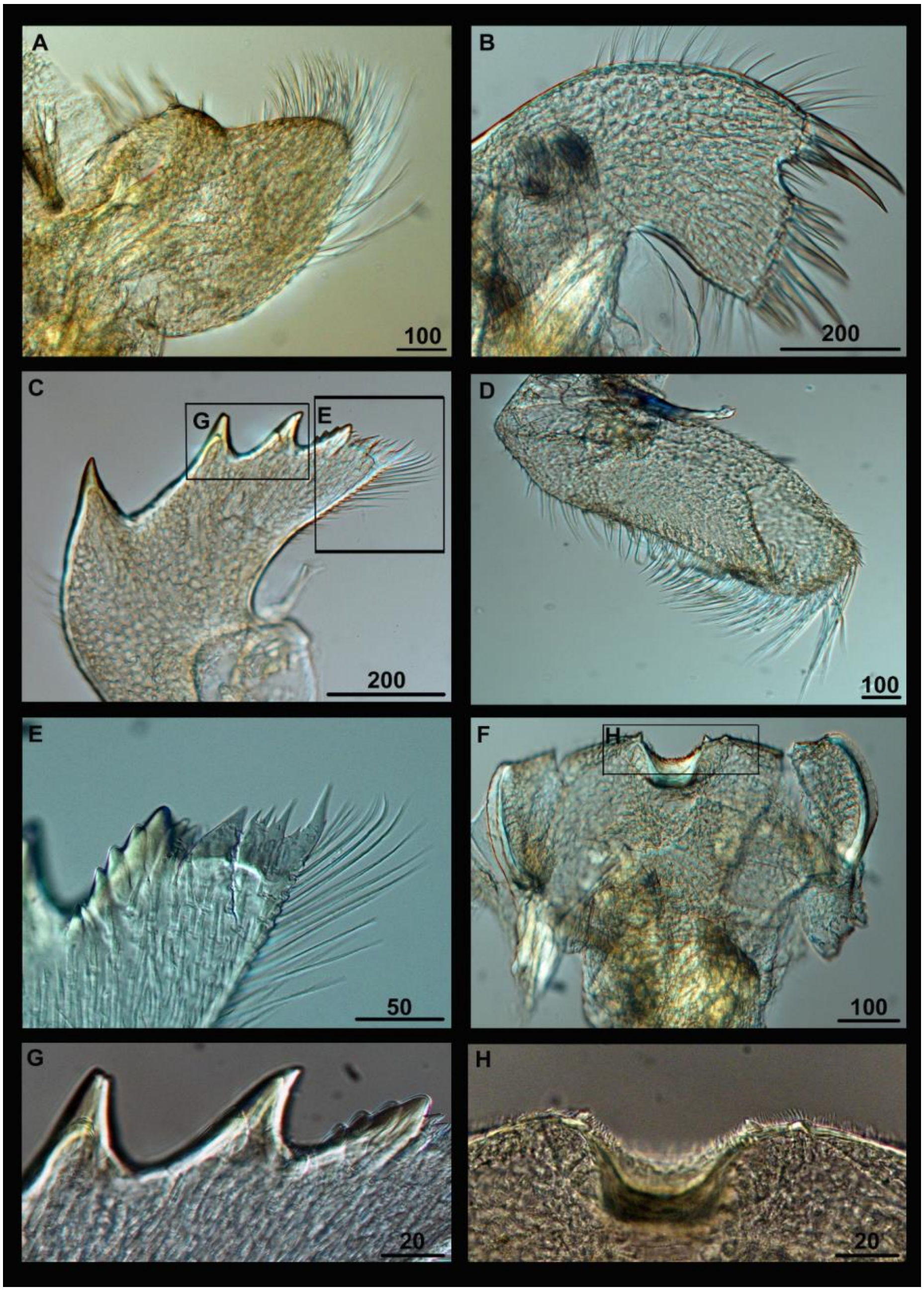

Fig. 132. *Tetraclitella chinensis* (hollowed form), light microscopy on mouth parts. A, Maxilla; B, Maxillule; C, Mandible; D, Mandibulatory palp; E, Inferior margin of mandible; F, labrum; G, Details of bidentate second and third teeth on mendible; H, small teeth on labrum. Scale bars in μm.

Cirral descriptions based on ranges of 4 specimens of each form. Cirrus I with unequal rami, anterior ramus (hollowed form: 10 to 11segments, multicostate form: 10–12segments) about 1.5 times longer than posterior ramus (hollowed form: 5 or 6segments, multicostate form: 6segments), both rami commonly with serrulate setae (Figs. 133A, 134A, B, C). Most distal segment of posterior ramus with bidentate setae in both forms (Fig. 134B, C). Cirrus II with subequal rami, anterior ramus (hollowed form: 7 or 8segments, multicostate form: 6 or 7segments), posterior ramus (both forms: 6 or 7segments) with serrulate, bidentate setae (Figs. 133B, 134D, E, F). Distal (hollowed form: 2, multicostate form: 2 or 3) segments of rami with bidentate setae (Fig. 134E, F). Cirrus III with subequal rami, anterior ramus (hollowed form: 7 or 8segments, multicostate form: 6 or 7segments), posterior ramus (hollowed, multicostate forms: 6 or 7segments) with serrulate, bidentate setae (hollowed form: 8 segments, multicostate form: 6segments) (Figs. 133C, 134G, H, I). Distal (hollowed form: 2, multicostate form: 2 or 3) segments of anterior ramus with bidentate setae while all segments in posterior ramus of both forms with bidentate setae (Fig. 134H, I) (segment counts in Table 7). Cirri IV-VI with anterior, posterior rami of similar length (segment counts in Table 7). Intermediate segments of cirri IV-VI with 4 pairs of setae (Figs. 133D, 135A-F).

Penis 1.5 times longer than cirrus VI, with scattered short, simple setae. Pedicel without basidorsal point (Fig. 135G, H, I).

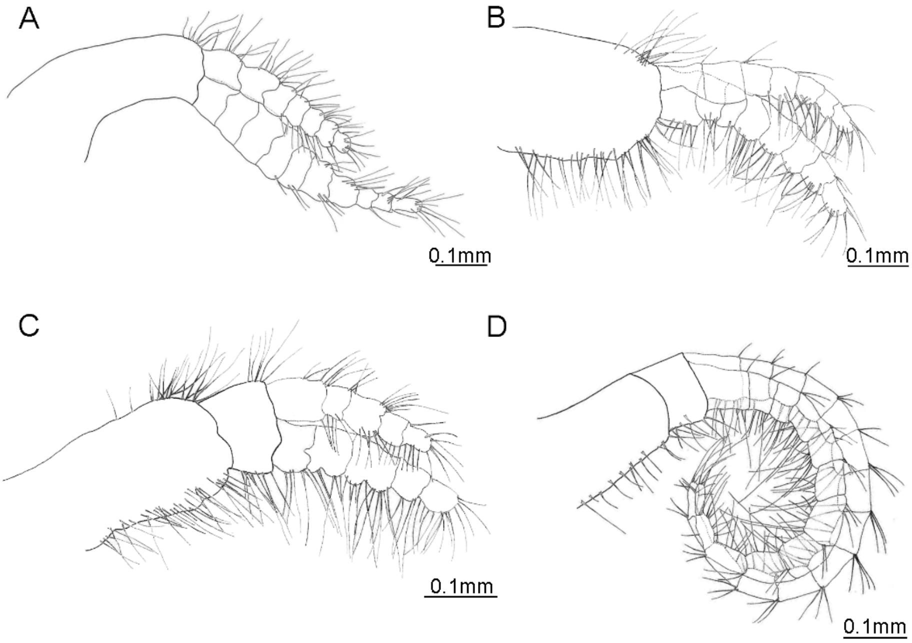

Fig. 133. *Tetraclitella chinensis* (hollowed form), line drawings of cirri I–IV. A, Cirrus I; B, Currus II; C, Cirrus III; D, Cirrus IV.

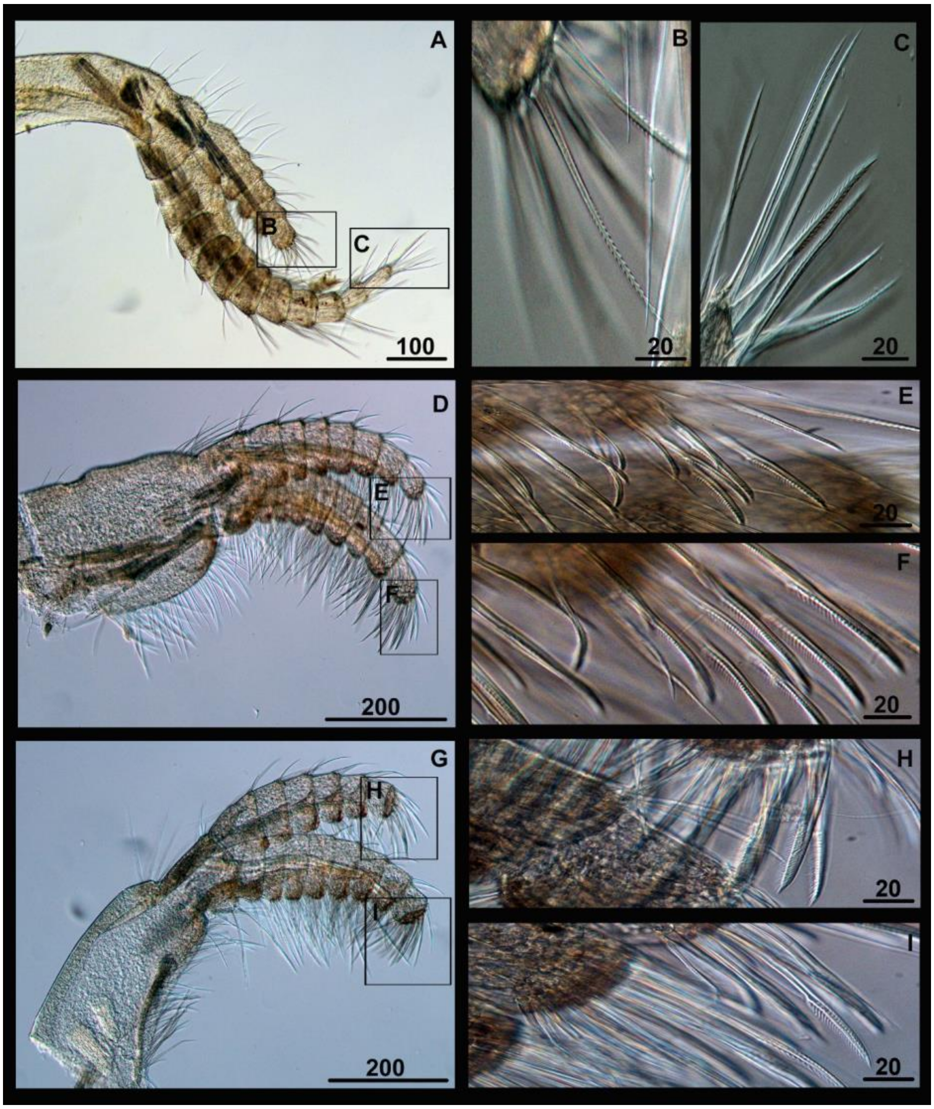

Fig. 134. *Tetraclitella chinensis* (hollowed form), light microscopy on cirri I-III. A, Cirrus I with unequal rami; B, Details of bidentate setae on apex of posterior ramus; C, Sserrulate setae; D, Cirrus II with subequal rami; E, Details of distal serrulate and bidentate setae on anterior ramus; F, Distal serrulate and bidentate setae on posterior ramus; G, Cirrus III with subequal rami; H, Details of distal serrulate and bidentate setae on anterior ramus; I, Distal serrulate and bidentate setae on posterior ramus. Scale bars in µm.

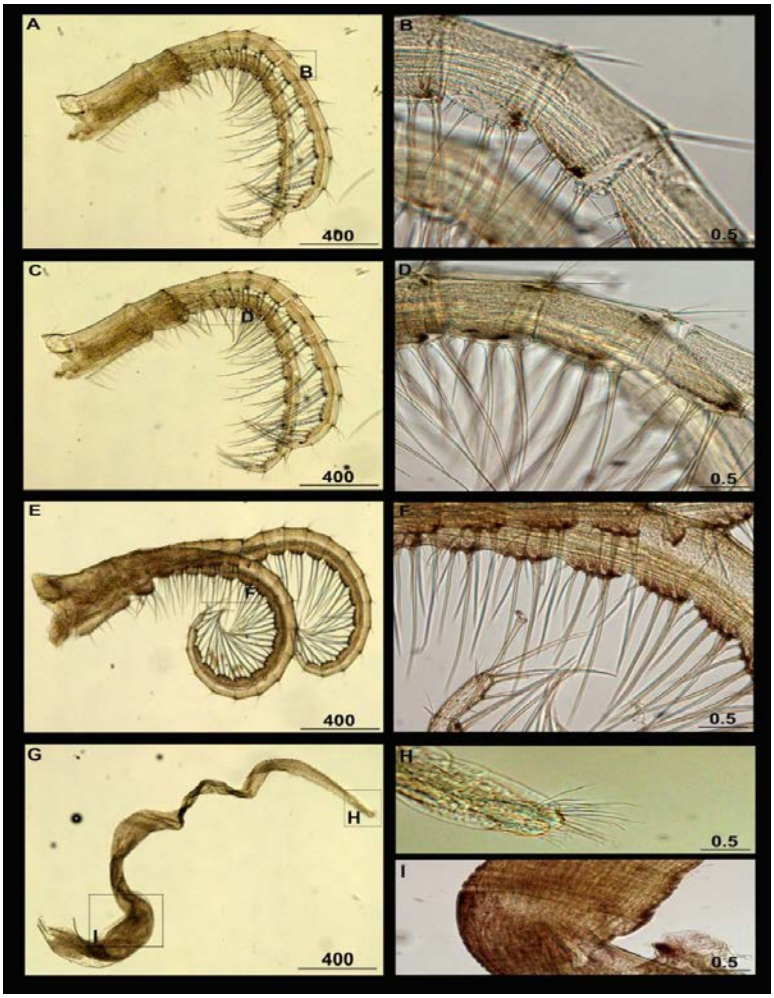

Fig. 135. *Tetraclitella chinensis* (hollowed form), light microscopy on cirri IV-VI and penis. A, Cirrus IV of *Tetraclitella chinensis* (hollowed form) showing subequal rami; B, Details of intermediate segment with four pairs of serrulate setae; C, Cirrus V showing subequal rami; D, Details of intermediate segment with four pairs of serrulate setae; E, Cirrus VI showing subequal rami; F, Details of intermediate segment with four pairs of serrulate setae; G, Penis; H, Tip of penis; I, Basidorsal point of penis. Scale bars in A, C, E, G:µm, B, D, F, H, I:mm.

Table 7. Cirral segment counts of *Tetraclitella chinensis*

	Hollowed form						Multicostate form					
	I		II		III		I		II		III	
No	Anterior	Posterior	Anterior	Posterior	Anterior	Posterior	Anterior	Posterior	Anterior	Posterior	Anterior	Posterior
1	10	6	7	6	7	6	10	6	6	6	6	6
2	10	5	7	6	7	6	11	6	7	7	7	7
3	11	6	8	7	8	7	12	6	7	6	7	7
	IV		V		VI		IV		V		VI	
No.	Anterior	Posterior	Anterior	Posterior	Anterior	Posterior	Anterior	Posterior	Anterior	Posterior	Anterior	Posterior
1	12	12	12	12	18	18	11	13	13	13	15	15
2	12	12	13	13	19	29	13	14	16	16	17	17
3	13	13	14	14	18	18	13	14	16	17	16	17

Distribution. Indo-West Pacific region.

Remarks. *Tetraclitella multicostata* was first identified as *Tetraclita purpurascens* var. *multicostata* by Nilsson-Cantell (1930a), who based it on one small, dried specimen from Jefbi, Misool Archipelago, Indonesia, and provided a brief description. According to Nilsson-Cantell (1930a, b), *T. multicostata* has a longitudinally ribbed shell and its radii have transverse ribs. The figure in Nilsson-Cantell (1930a) shows setae on the ribs. Utinomi (1962) provided a more detailed description of *T. multicostata* from Kagoshima, Japan and stated that there are four main ribs on the carina and three on the rostrum. Utinomi (1962) raised *T. multicostata* to the species level due to diagnostic morphological differences from *Tetraclitella purpurascens* (Wood, 1815). The morphology of the specimens of *T. multicostata* collected by us in Korea and China fits the descriptions of Nilsson-Cantell (1930a, b) and Utinomi (1962). The collected samples have ramified tubes and there are four major ribs on the carina and three major ribs on the rostrum. Accessory ribs develop from the major ribs (Fig. 117A, B, C). The samples represent *T. multicostata*, but the radii of the samples collected in Hai Ling Island, China are relatively less eroded, and the horizontal striations are more pronounced and expressed as digitiform riblets. Such features were also reported in the Philippine samples of Rosell (1975), who described them as a subspecies, *Tetraclita multicostata digita*. Rosell, 1975.

As in the study of Tsang *et al*. (2014), our molecular phylogenetic analysis, which included both mitochondrial and nuclear markers, showed no distinct genetic divergence between *T. chinensis* and *T. multicostata*. These results provide strong evidence that these two nominal species are conspecific and suggests that the observed shell-wall variation (or dimorphism) may have arisen in response to environmental or biological factors. Mitochondrial DNA, including the DNA barcoding region (COI), is considered useful and reliable in species delineation (Hubert & Hanner, 2015). Hickerson *et al.* (2006) nevertheless pointed out that DNA barcoding based on a single gene can often fail to discover new species, especially in recently isolated populations or reproductively isolated lineages. Three markers were used for species delineation, two mitochondrial DNA genes (COI and 12S) and one nuclear gene (ITS1). The nuclear marker ITS1 has been shown to be reliable in species delineation in tetraclitid barnacles (Chan *et al.*, 2007b). Both *T. chinensis* and *T. multicostata* are clustered in the same lineage in individual gene trees and a combined gene tree (Figs. 122, 123, 124, 125), whereas all other closely related species within the genus/family are separated into distinct lineages. Kimura K2P analysis indicates a range of sequence divergence between *T. chinensis* and *T. multicostata* of only 0.9%., which falls within the intra-specific range of sequence divergences in tetraclitid barnacles (Chan *et al.* 2007b, c). De Queiroz (1999, 2007) reviewed different species concepts and proposed a unified concept that considered species to represent separately evolving metapopulation lineage. According to de Queiroz (1999:50, fig. 3.1), lineages are “unbranched; that is, they follow a single path or line anytime an entity in the series has more than one direct descendant”. Our resulting lineage containing both *T. chinensis* and *T. multicostata* is unbrached, has *T. karandei* as its sister group, and both share a common ancestor. Despite the distinct morphological differences between *T. chinensis* and *T. multicostata*, individuals were found with characters of both species at Seogwipo in Jeju Island, Korea. These individuals have fewer than six hollows in the shell (because some shell plates lack hollows) and have prominent longitudinal ribs similar to the multicostate form. The mouthparts, penis, and cirri are not different between the two species. While Utinomi (1962) described the basal margin of the scutum as almost straight in *T. multicostata*, Hiro (1939b) described it as notched at the end of the margin in *T. chinensis*. Present specimens from Taiwan, Korea, and China, show that the presence of a notch is variable, with some being slightly notched, whereas others have a clearly more notched basal margin. Based on molecular and morphological investigations and the presence of intermediately hollowed forms, *T. chinensis* and *T. multicostata* are conspecific, with the name *T. chinensis* having priority.

Similar conspecific shell variation has been reported in *Chelonibia testudinaria* and *Chthamalus anisopoma* Pilsbry, 1916. *Chelonibia testudinaria* inhabits the carapace surface of sea turtles, and has pits or depressions at the shell plate junctions to house the dwarf males. *Chelonibia patula* (Ranzani, 1818) inhabits the surface of crabs and has a smooth shell surface without any pits. Its dwarf males are scattered randomly on the shell surface. The molecular divergence of the 12S, COI, and 16S gene and amplified fragment length polymorphism (AFLP) analysis has shown that these two species are conspecific and that such shell variations may be host-driven (Cheang *et al*., 2013). *Chthamalus anisopoma* inhabits upper-intertidal shores in the Gulf of California and appears to have two shell forms, a conical and a bent shell morph, where the shell is bent at a right angle with the orifice facing downwards. Sequence divergence in 12S and COI mt rDNA genes has shown that these two forms are conspecific and that such morphological variation is induced by the presence of predatory snails (Mokady *et al*., 2000).

Both hollowed and multicostate forms are sympatrically present together in Jeju Island. At Hailing Island, China only the multicostate form was found on the shores in contrast to hollowed forms in Kenting, Taiwan. Factors affecting the distribution of these two forms should receive further attention.

Key to Species of *Tetraclitella* s.s. Recognized by Ross and Perreault (1999)

1. Shells with hollows ..……………..……….. *T. chinensis* (hollowed form)

Shell without hollows ..…………………...…………..…………………2

2. Shell surface smooth ………………………*T. divisa* (Nilsson-Cantell, 1921)

Shell surface with longitudinal striations …………………………………. 3

3. Rostrum with 3 and carina with 4 main longitudinal ribs…………………

……………………………………………… *T. chinensis* (multicostate form)

Rostrum and carina with numerous fine longitudinal ribs …………………. 4

4. Radii with pronounced digitiform striations ……… *T. karandei* Ross, 1971

Radii smooth, without elevated projections …………………………………

……………………………………… *T. depressa* Foster & Anderson, 1986

3.1.4 Discussion

The presence of lunule-like hollows is uncommon in the shells of barnacles, and species of *Tetraclitella* can be easily distinguished by their shells, with *T. chinensis* having six distinctive hollows in its shell. Hiro (1939b) suggested that the hollows are parietal tubes of the shell plates, and Utinomi (1949b:36) noted that the "perforated state is very common in older specimens, though not found in small or younger ones." Present studies show more precisely that once the barnacle shell reaches a diameter of 4–5 mm, the longitudinal ribs fuse at the perimeter of the shell to form the hollows and that the hollows in the lateral plates form before those in the rostral and carinal plates. This pattern supports the hypothesis of Ross (1971) that, because the formation of these hollows extends to the outer margins of the barnacle shell, *T. chinensis* develops a broader base. Utinomi (1949b:36) noted that *T. chinensis* in Kyushu, Japan included specimens with "few or numerous prominent radial ridges," with the hollows were "very common" but evidently not universal in large specimens, so his samples may have included *T. multicostata*, although not dominant as in the studied sites.

Ross (1971) further hypothesized that the hollow-perforated shells of *T. chinensis* may somehow prevent individuals from being crushed as a result of overcrowding. The present studies, however, show that there are bare spaces around individuals. The hollow-perforated shell form may be an adaptation to reduce the effects of overcrowding. However, fully developed hollows retain water during low tides after the barnacles have been immersed. Those hollows could thus provide some protection from heat stress.

Among the sessile barnacles, only *T. chinensis* and *Chinochthamalus scutelliformis*, which are common on southeastern Asia shores, have hollows in their wall plates (Liu & Ren, 2007). *Chinochthamalus scutelliformis*, has six shell plates with four hollows in contrast to the four shell plates with six hollows of *T. chinensis*. Two of the hollows of hollowed form of *C. scutelliformis* are a bilateral pair formed at the junctions of the carinal lateral and rostral lateral plates, and the other two hollows are formed in the carina (Fig. 136). The former two hollows arise as gaps between the two other plates on each side of the shell and become closed when the plates meet again as diametrical growth of the barnacle proceeds. The plate boundary is clearly visible as a seam extending from the outer end of the hollow to the wall's perimeter. The two hollows in the carina are formed by the fusion of ribs at the perimeter of the carina (Fig. 136)

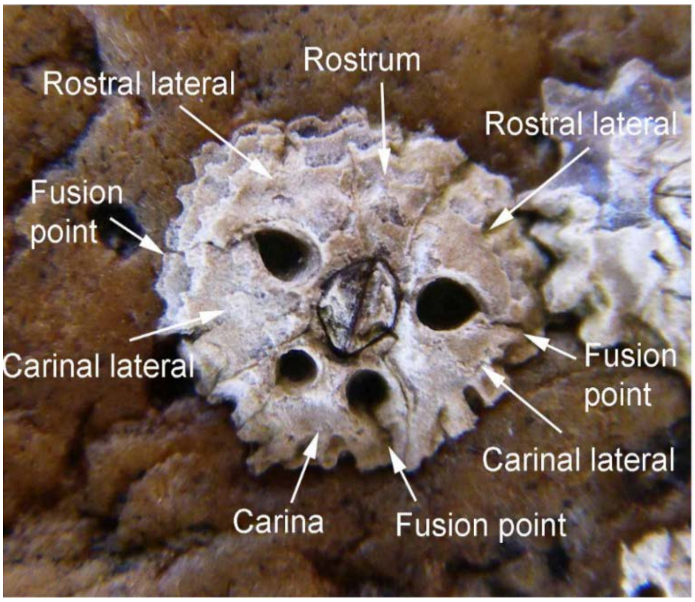

Fig. 136. Specimen of *Chinochthamalus scutelliforms* from Hainan Island, China with four hollows in its six-plated shell. The two hollows flanking the operculum are formed by the separation and later re-meeting of the growing rostral lateral and carinal lateral plates on each side. The two hollows in the carina are formed by the fusion of once-separated ribs at the outer perimeter of the growing shell.

in a manner similar to that whereby the two hollows form in the carina of *T. chinensis*, and the seams thus formed remain visible as the carina continues to grow. The functional significance of such hollows, however, remains uncertain. Darwin (1854) suggested these hollows may give support to the much depressed and thin shell in *C. scutelliformis*. This question should be addressed by investigations of the hydrodynamics of barnacles and by a transcriptomic analysis of gene expression in the tissues of barnacles with shells that lack or have hollows.

Conclusions

In the work described here, intertidal and sublittoral Balanomorpha barnacles were collected from 44 localities including Korea marine national park areas from 2016 to 2018. A total of 23 species of 15 genera under seven families were identified and classified for biogeographical studies, and morphological and molecular taxonomic studies were conducted.

In Chapter 1, the marine ecosystems and associated intertidal and sublittoral barnacle species of Korea provide an excellent opportunity to study and monitor the processes of climate change. The coastal water of Korea was divided into three regions (the Yellow Sea, the Southern coast affected by the Kuroshio and the Eastern coast) in consideration of the species diversity, the community, and the geographical distribution which are influenced by oceanogeographic currents and seawater temperature differences among the several marine ecosystems. There are five species distributing in all parts of Korea, of which the following three species are the most predominant and widely distributed all over in intertidal and shallow water: *Chthalamlus challengeri*, *Balanus trigonus*, and *Megabalanus rosa*. The Yellow Sea and Kuroshio Ecosystems share a great proportion of species in common. However, *Tetraclitella* species and coral-associated barnacles were only detected on the Southern coast (= the Korea Strait affected by the Kuroshio). The abundance of two cold-water species including *Chthamalus dalli* and *Semibalanus cariosus* decreases in the Eastern coast of Korea. Under the effects of global warming, one of the cold-water species, *Balanus rostrarus*, expanded its distributional range to the Yellow Sea and the Southern coast. Also, four invasive barnacle species, *Amphibalanus amphitrite*, *A. eburneus*, *A. improvisus*, and *Perforatus perforates*, have been expanding their range. The abundance of warm-and cold-water species and invasive barnacle species can be used as indicators for global warming and ocean acidification.

In Chapter 2, the study of diversity and host usage of coral-associated barnacles in Korea, and the northern coral distribution limit in the East China Sea was conducted. As a result, only three coral-associated barnacles, *Cantellius arcuatus*, *Cantellius* sp., and *Pyrgomina oulastreae,* belonging to two genera in two subfamilies were identified. Of these, one coral-associated barnacle species *Cantellius arcuatus* (Hiro, 1938) is newly recorded from Korean waters. *Cantellius* sp. remained as an unknown species, indicating a possibility of new species differing from the congeneric species. The host usage of these three barnacles does not overlap. The Pyrgomatinid barnacles *C. arcuatus* and *Cantellius* sp. were found only on the corals *Montipora millepora* and *Alveopora japonica,* respectively. The Megatrematinid barnacle *P. oulastreae,* relatively a generalist, was found on *Psammocora* spp. and *Oulastrea crispata* corals. Also, molecular taxonomic study using two mitochondrial markers, 12S rDNA and cytochrome *c* oxidase subunit I (COI) were applied to compare the distribution in Korea and neighboring countries. *C. arcuatus* covers a wider host range in Taiwan waters, inhabiting *Montipora* spp. and *Porites* spp., which suggests that the host specificity of coral-associated barnacles varies with host availability. The sequences of *Cantellius* sp. do not match those of any known sequences of *Cantellius* barnacles in the Indo-Pacific region. It is therefore proposed that a new species be erected for *Cantellius* sp., *P. oulastreae* probably prefers cold waters because it has been reported in temperate regions. It suggests that marginal coral-associated barnacles exhibit higher host specificity than do those in subtropical and tropical reef systems when host availability is limited. This chapter was published in *PLoS One* by the author.

In Chapter 3, a revision of the genus *Tetraclitella* based on the formation of hollows in the shells as the main identification key was conducted in order to describe how these hollows form. During this investigation, some characteristic confusions between *T. chinensis* and *T. multicostata* were found. Specimens are occasionally found that share characteristics with both *T. chinensis* and *T. multicostata*, such as having fewer than six hollows and their shell plates without the hollows having longitudinal ribs. Also, there are no obvious morphological differences in the cirri, mouthparts, and opercular plates (tergum and scutum), and a combined gene phylogenetic tree using the partial sequences of two mitochondrial genes (12S rDNA and COI) and one nuclear gene (ITS1) showed that both species formed a single, unbranched lineage. Both morphological and molecular data suggest that *T. chinensis* and *T. multicostata* are conspecific. As a result, the two nominal species were formally synonymized, with *T. multicostata* being reduced to a junior synonym of *T. chinensis*, and a key to identify the genus *Tetraclitella* was provided. This chapter was published in the *Journal of Crustacean Biology* by the author.

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Abstract in Korean

완흉상목에 속하는 따개비류는 거의 모든 해양환경에 서식하며, 해양 갑각류 중 유일하게 성체시에 고착생활을 하는 종이다. 따개비류의 종 분포는 다른종의 풍부도와 생태에 영향을 미친다. 따개비류는 대표적인 오손 생물 중 하나로, 선박 평형수에 의한 유입과 선박 하단에 빠르게 부착하여 경제적 손실을 야기하기 때문에, 분포현황 조사와 개체군의 생태적 특성 연구가 필요하다. 하지만, Kim (1998)의 형태분류학적 연구 이후에 한국 따개비류의 단편적인 연구만 수행되어왔다. 본 연구에서는, 한국따개비류의 생물지리학적 분포, 종 풍부도, 종 다양성 및 분류학적 연구를 수행하였다. 모든 표본들은 2016 년부터 2018 년까지 조간대 및 조하대에서 수집되었다. 7 개의 과, 15 개의 속에 속하는 22 종의 따개비가 동정 및 분류되었으며, 이중에서 1 종의 산호따개비는 신종으로 기재하였으며, 1 종의 미기록종을 발굴하였다. 분자학적 형질 및 분포를 비교하기 위해 다계통분석을 수행하였다.

제 1 장에서는 한국의 다양한 해양생태계 중 조간대 및 천해지역에 분포하고 있는 따개비류의 생물 지리학적 연구를 수행하였다. 먼저, 다변량분석 (multivariate analysis)을 이용하여 해양생태계와 관련된 종구성을 확인하였다. 다음으로, 종 다양성에 영향을 미치는 환경요인 (해수표층온도, 엽록소 농도 및 염도)은 Giovanni 데이터 베이스를 통해서 확보하였다. 또한, 외래 따개비류의 분류학적 형질 기재 및 현 분포현황을 기록하였다. 본 연구 결과, 한국 해역의 조간대 및 천해지역에 분포하고 있는

따개비는 해류, 해수표층온도 및 염도 차의 영향을 받는것으로 확인되었다. 각 종의 원기재를 기반으로 주요형질과 정보들도 재정리하였다. 분자 분류학적 연구 결과, 확보된 22 종의 따개비류는 각각 단계통군을 형성하였고, 12S rDNA 와 COI 유전자는 따개비류 종들의 동정과 은둔종 (cryptic diversity) 및 따개비류의 형태적 유연성 (phenotypic plasticity)을 발견하는데에도 유용한 분자적 마커임을 확인하였다.

제 2 장에서는 한국산 산호따개비류의 생물다양성과 숙주특이성에 대한 연구가 이루어졌다. 오로지 3 종의 산호따개비 *Cantellius arcuatus*, *Cantellius* sp., *Pyrgomina oulastreae* 가 서로 다른 3 종의 산호에 공생하고 있었다. 12S rDNA 와 COI 유전자를 이용한 분자학적 형질 분석에 따르면, *C. arcuatus* 는 일본, 대만, 말레이시아 및 파푸아뉴기니에서 수집된 표본들과 일치하였으며, 이 종은 지리적 분포가 넓고 산호따개비의 숙주특이성은 가용 숙주종의 풍부도에 따라 다양함을 보여주었다. 또한, 1 종의 신종후보종 *Cantellius* sp. 을 기재하였다. 기존에 보고되었던 *C. euspinulosum* 을 포함하여 국내에 분포하고 있는 총 4 종의 산호따개비류의 형태분류학적 기재를 추가적으로 진행하였다. 본 연구 결과, 태평양 서북부의 연안해에 분포하고 있는 산호따개비는 아열대 및 열대지역보다 상당히 낮은 종다양성을 나타내었고, 아열대 및 열대지역의 산호초의 생태시스템보다 높은 숙주 특이성을 보였다.

제 3 장에서는 패각의 활꼴모양 구멍을 주요 형태학적 형질로 사용하는 *Tetraclitella* 속의 분류학적 재정립을 수행하였다. 구멍형성과정을 확인하기 위해 한국, 대만과 중국에서 다양한

크기의 표본들을 확보하였다. 형태 분류 보완 및 개체군의 생물지리학적 분포 조사를 위하여 미토콘드리아 12S rDNA와 COI, 핵 리보솜 ITS1 유전자를 이용하였다. 추가적으로, 원기재를 기반으로 형태분류학적 재기재 및 *Tetraclitella*속 분류 검색표를 최신화 하였다. 본 연구 결과, *T. chinensis*는 패각 형태의 형태학적 (hollowed 및 multicostate) 형질이 재검증되었으며, 이를 바탕으로 *T. multicostata*로 보고되었던 종은 *T. chinensis*로 동종이명 처리하였다.

주요어: 완흉상목 따개비류, 생물지리학. 생물다양성, 산호따개비류, 숙주특이성, 분류학, 분자계통학

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