Journal of Species Research 14(1):96-105, 2025

Taxonomic reassessment of the Korean *Leptochiton rugatus* (P. P. Carpenter, 1892) (Leptochitonidae: Polyplacophora)

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Leptochiton Gray, 1847 is the most well-known and species-rich genus within the family Leptochitonidae. Species of this genus inhabit a wide range of marine environments, from shallow coastal waters to cold, deep-sea habitats. Due to the lack of distinctive morphological characters among congeneric species, the taxonomy of the genus has been complicated, making it difficult to distinguish between species based solely on external features. Recent studies using detailed morphological data obtained from scanning electron microscopy (SEM) have uncovered many cryptic species within the genus. *L. rugatus* (P. P. Carpenter, 1892) was once considered a single, widely distributed species across the northern Pacific. However, recent analysis incorporating morphological and molecular data have revealed that it is species complex that comprises several cryptic species. Over the last several decades, *L. rugatus* has been included in the National list of species in Korea with detailed descriptions, illustrations, SEM images, and distribution information. In this study, we reassessed the taxonomy of Korean *L. rugatus* species based on a comprehensive analysis of both morphological and molecular data (mtDNA *cox1*). The results from morphological and molecular phylogenetic analyses, referring to their geographic distribution information, revealed that *L. rugatus* species previously recorded in Korean waters should be taxonomically revised as *L. subrugatus* Sirenko & Sigwart, 2021. Based on this updated taxonomic information, we provide a detailed description of the microstructures of valves, girdle (perinotum and hyponotum), and radula for *L. subrugatus* from Korea.

Keywords: chiton, Korea, *Leptochiton subrugatus*, microscopic characters, mtDNA *cox1*, SEM

DOI:10.12651/JSR.2025.14.1.096

INTRODUCTION

Leptochitonidae Dall, 1889 is a family of small, ancient chitons, comprising approximately 180 species from six genera (MolluscaBase eds., 2024). The members of the family are distributed worldwide from tropical oceans to Antarctic seas, with notable species diversity in the North Pacific (Sigwart *et al*., 2011; Sigwart, 2017). While the majority of species are found in benthic habitats in cold waters and deep-sea environments, a few species also occur in shallow coastal waters (Sigwart, 2017). Leptochitonidae species are characterized by their small body size, generally uncolored, granulated tegmentum, and the absence of insertion plates (Kaas and Van Belle, 1985).

Among the family Leptochitonidae, *Leptochiton* Gray, 1847 is the most well-known and species-rich genus. Species of this genus inhabit a diverse array of marine environments, ranging from shallow coastal waters to cold, deep-sea habitats. However, recent morphological and molecular analyses have revealed the non-monophyly of the genus (Sigwart, 2009; 2017; Sigwart *et al*., 2011). Identifying species within the *Leptochiton* genus remains challenging when relying solely on external morphology, due to the lack of distinctive morphological characteristics among congeneric species. Fortunately, the recent application of scanning electron microscopy (SEM) for the microscopic characters of valves (shell plates), girdles, and radula morphologies has significantly facilitated species identification, resulting in the discovery of unexpected cryptic species within the genus (Sigwart and Chen, 2018; Sirenko and Sigwart, 2021).

In Korea, three species of *Leptochiton* have been recorded: *L. fuliginatus* (Reeve, 1847) [Reeve, 1847], *L. hakodatensis* (Thiele, 1909) [Park *et al*., 2022], and *L. rugatus* (P. P. Carpenter, 1892) [Dell'Angelo *et al*., 1990]. Among these, *L. rugatus* has long been documented in the National list of species in Korea without further updates since it was first reported with detailed descriptions, illustrations, SEM images, and distribution information by Dell'Angelo *et al*. (1990). A recent comprehensive analysis of morphological, molecular, ecological, and biogeographical data discovered several cryptic species within *L. rugatus* that were previously considered to be widely distributed across the northern Pacific (Sigwart and Chen, 2018; Sirenko and Sigwart, 2021). Most notably, Sirenko and Sigwart (2021) revised the taxonomy of *L. rugatus* populations distributed from the Sea of Japan [East Sea] (near Possjet Bay) to the Yellow Sea (near Qingdao) and reclassified them as a new species, *L. subrugatus* Sirenko & Sigwart, 2021. Given the geographic overlap of Korean populations of *L. rugatus* with the newly described species *L. subrugatus*, it is necessary to reassess the taxonomy of Korean *L. rugatus* populations to determine whether they represent *L. rugatus* or the recently described *L. subrugatus* species.

In this study, we reassessed the taxonomy of Korean *L. rugatus* species based on a comprehensive analysis of morphological and molecular data (mtDNA *cox1*). The comparative analysis of morphological microstructure characteristics, coupled with molecular phylogenetic analysis using the mtDNA *cox1* sequences, revealed that the previously designated Korean *L. rugatus* should be reclassified as *L. subrugatus*. Based on this updated taxonomic reappraisal, we provide a detailed description of the microstructures of the valves (tegmentum), girdle (including perinotum and hyponotum), and radula of *L. subrugatus* in Korea, using scanning electron microscopy (SEM).

MATERIALS AND METHODS

The specimens were collected from subtidal zones at a depth of around 30 meters in the chilly waters (4−6°C) of the East Sea (Goseong) in Korea (see examined materials for each species) and preserved in 95% ethyl alcohol. For species identification, we examined morphological characteristics of valves and girdle using a stereoscopic microscope (Leica M205C; Wetzlar, Germany). Animals were dissected to examine the microstructure of the tegmentum sculpture on the valves, girdle (perinotum and hyponotum), and radula using a SEM. The valves, girdle, and radula were respectively separated and incubated at 50°C in a 10% KOH solution for approximately 1−3 min, then washed with distilled water. After washing, they were cleaned to remove residual tissues using an ultrasonic cleaner (Shinhan 200H3L; Shinhan-Sonic, Korea), coated with platinum ions after drying, and then photographed using a SEM (Ultra Plus; Zeiss, Germany).

Total genomic DNA was extracted from the foot tissue of specimens using the E.Z.N.A. mollusc DNA extraction kit (Omega Bio-tek, Norcross, USA) following the manufacturer's protocols. To amplify a partial sequence of the mtDNA *cox1* (658 bp) and 16S (512 bp) genes, a polymerase chain reaction (PCR) was conducted using TaKaRa Ex Taq (Takara Bio, Shiga, Japan) with the universal primer sets (*cox1*: LCO1490/HCO2198, 16S: 16sar-L/16sbr-H) (Palumbi *et al*., 1991; Folmer *et al*., 1994). The PCR was prepared in a total volume of 50 μL consisting of 33.75 μL of distilled water, 5 μL of 10X Ex Taq buffer, 4 μL of dNTP Mixture (2.5 mM each), 2 μL of each primer (LCO1490: 5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′, HCO2198: 5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′, 16sar-L: 5′-CGC CTG TTT ATC AAA AAC AT-3′, and 16sbr-H: 5′-CCG GTC TGA ACT CAG ATC ACG T-3′), 0.25 μL of TaKaRa Ex Taq, and 3 μL of genomic DNA template. The PCR conditions were as follow: an initial denaturation at 95°C for 1 min, followed by 40 cycles of denaturation at 94°C for 30 s, annealing at 46°C for 30 s, extension at 72°C for 30 s, and a final extension at 72°C for 10 min. The amplified PCR products were isolated on a 1% agarose gel and purified using a QIAquick gel extraction kit (Qiagen, Valencia, CA, USA). Sequencing of the partial mtDNA *cox1* gene was performed bidirectionally using an ABI PRISM 3700 DNA analyzer (Applied Biosystems, Foster City, CA, USA).

Phylogenetic analyses were conducted using mtDNA *cox1* sequences data from Korean *Leptochiton subrugatus* and other *Leptochiton* species available on GenBank from previous studies (Kelly and Eernisse, 2007; Sigwart *et al*., 2011; Layton *et al*., 2014; Sigwart and Chen, 2018). Due to the shorter length of some GenBank sequences compared to those obtained in this study, a 555 bp homologous region was prepared for subsequent analysis by trimming both ends of sequences using Geneious Prime v. 2023.2.1 (Biomaters, Auckland, New Zealand). Multiple DNA sequence alignment was performed using MAFFT v7.490 (Katoh and Standley, 2013) with default parameters in Geneious Prime. Genetic distances (*p*-distance) between and within species were calculated using MEGA X (Kumar *et al*., 2018). The resulting phylogenetic tree was reconstructed in RAxML v8.2.12 (Stamatakis, 2014) using the maximum likelihood (ML) method with 1,000 bootstrap replications.

RESULTS AND DISCUSSION

Systematic accounts

Phylum Mollusca Linnaeus, 1758
Class Polyplacophora Gray, 1821
Order Lepidopleurida Thiele, 1909
Family Leptochitonidae Dall, 1889

Genus *Leptochiton* Gray, 1847

Type species: *Chiton cinereus* Montagu, 1803 (non Linnaeus, 1767) [=*Chiton asellus* Gmelin, 1791, fide Lovén, 1846], by subsequent designation (Gray, 1847).

Diagnosis. Body small; valves thin with hardly raised lateral areas; tegmentum generally pale with finely granulose; mucro subcentral; no insertion plates; girdle with small scales, sometimes interspersed with spicules or entirely spiculose; major lateral radula teeth with uni-, bi-, or tricuspid cap, the denticle (s) always pointed.
Genus distribution. Worldwide. Triassic to Recent (Laghi, 2005; Sigwart, 2017).

***Leptochiton subrugatus* Sirenko & Sigwart, 2021**
(Figs. 1-4) 아기군부 (국명승계)

Leptochiton subrugatus Sirenko and Sigwart, 2021: 3-8, figs. 1-4.
Lepidopleurus assimilis: Taki, 1938: 328-331, pl. 14, fig. 2, pl. 16, figs. 5, 9-13, 15, pl. 17, figs. 9-11; Jakovleva, 1952: 55, fig. 16, pl. 1, fig. 4 (non *Lepidopleurus assimilis* Thiele, 1909, partim).
Leptochiton assimilis: Saito, 1995: 100; 2000: 4, 5, fig. 1; 2017: 728, pl. 2, fig. 3 (non *Lepidopleurus assimilis* Thiele, 1909, partim).
Leptochiton (*Leptochiton*) *rugatus*: Kaas and Van Belle, 1985: 85-87, fig. 37, map 15; Dell'Angelo *et al.*, 1990: 32-34, pl. 1, figs. 1-6, pl. 2, figs. 1-7, textfig. 2 (non *Lepidopleurus rugatus* Carpenter in Pilsbry, 1892, partim).
Leptochiton rugatus: Ferreira, 1979: 146-149, figs. 1, 2, 7, 33, 34; Slieker, 2000: 82, 83, pl. 29, fig. 3; Qi, 2004: 3, pl. 1A; Sigwart *et al.*, 2011; Sirenko, 2013: 148; Sigwart, 2017 (non *Lepidopleurus rugatus* Carpenter in Pilsbry, 1892, partim).
Leptochiton sp. 2: Sigwart and Chen, 2018.

Material examined. Korea: total 14 individuals: 4 individuals: Munamjin-ri, Jugwang-myeon, Goseong-gun, Gangwon-do (38°18′04.4″N, 128°34′10.8″E), collected by SCUBA diving at depth of 29 m, 05 May 2021; 7 individuals: Munamjin-ri, Jugwang-myeon, Goseong-gun, Gangwon-do (38°18′02.4″N, 128°34′12.2″E), collected by SCUBA diving at depth of 28 m, 06 May 2021; 3 individuals: Munamjin-ri, Jugwang-myeon, Goseong-gun, Gangwon-do (38°18′04.2″N, 128°34′15.0″E), collected by SCUBA diving at depth of 32 m, 06 May 2021. All specimens are deposited in the Animal Phylogenomics Laboratory at Ewha Womans University in Seoul, Korea.
Description. Body elongate-oval, small in size (Fig. 1A; in examined specimen, Body Length 4.85 mm, Body Width 2.28 mm). Valves thin, creamy-white in color, sometimes stained with yellow-brown to black by environmental deposits. Girdle very narrow, white to dirty yellow in color. Gills arrangement adanal and merobranchial on both sides, from 6th valve to the anus (Fig. 1B).

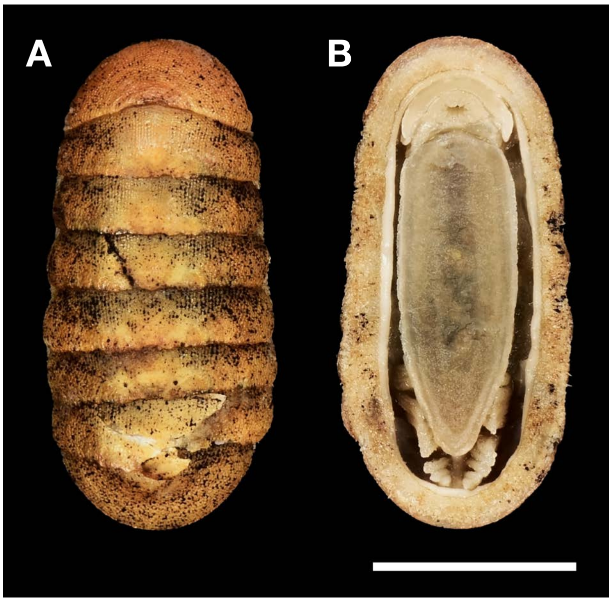

Fig. 1. *Leptochiton subrugatus* Sirenko & Sigwart, 2021. A, Dorsal view; B, Ventral view. Scale bar: A, B = 2 mm.

Head valve semicircular with dense granules arranged in indistinct radial lines and concentric growth lines; granules very small, uniform in size, rounded oval in shape; posterior margin widely V-shaped and nearly straight (Fig. 2A). Intermediate valves similar from 2nd valve to 7th valve in width, broadly rectangular in shape, not beaked; anterior and posterior margins nearly straight, lateral margins rounded (Fig. 2B, C). Intermediate valves dorso-ventrally rounded, not carinated, and moderately elevated in frontal view (Fig. 2E; elevation ratio of 0.64-0.79 in the 5th valve); tegmentum of central area (ca) sculptured with small rounded granules densely arranged in longitudinal rows (Fig. 2B, C, H, I); lateral areas (la) not raised, with granules arranged in fine radial rows and several growth lines (Fig. 2B, C, I); each granule with 3-5 aesthete pores, comprising one megalaesthete (me) and two to four micraesthetes (mi). Tail valve semicircular and wider than head valve; mucro (m) antemedian, protruding, slightly pointed; sculpture of antemucronal area (ama) same as central area of intermediate valves; postmucronal area (pma) similar to head valve and lateral area of intermediate valves (Fig. 2D); anterior margin slightly convex; antemucronal and postmucronal slope (ams, pms) almost straight (Fig. 2G). Articulamentum white, no insertion plate; apophyses (ap; sutural laminae) widely separated, short, triangular in shape, and hyaline; jugal sinus (js) wide and shallow; central calluses (cc) relatively thick and prominent (Fig. 2F); numerous pores in radial rows,

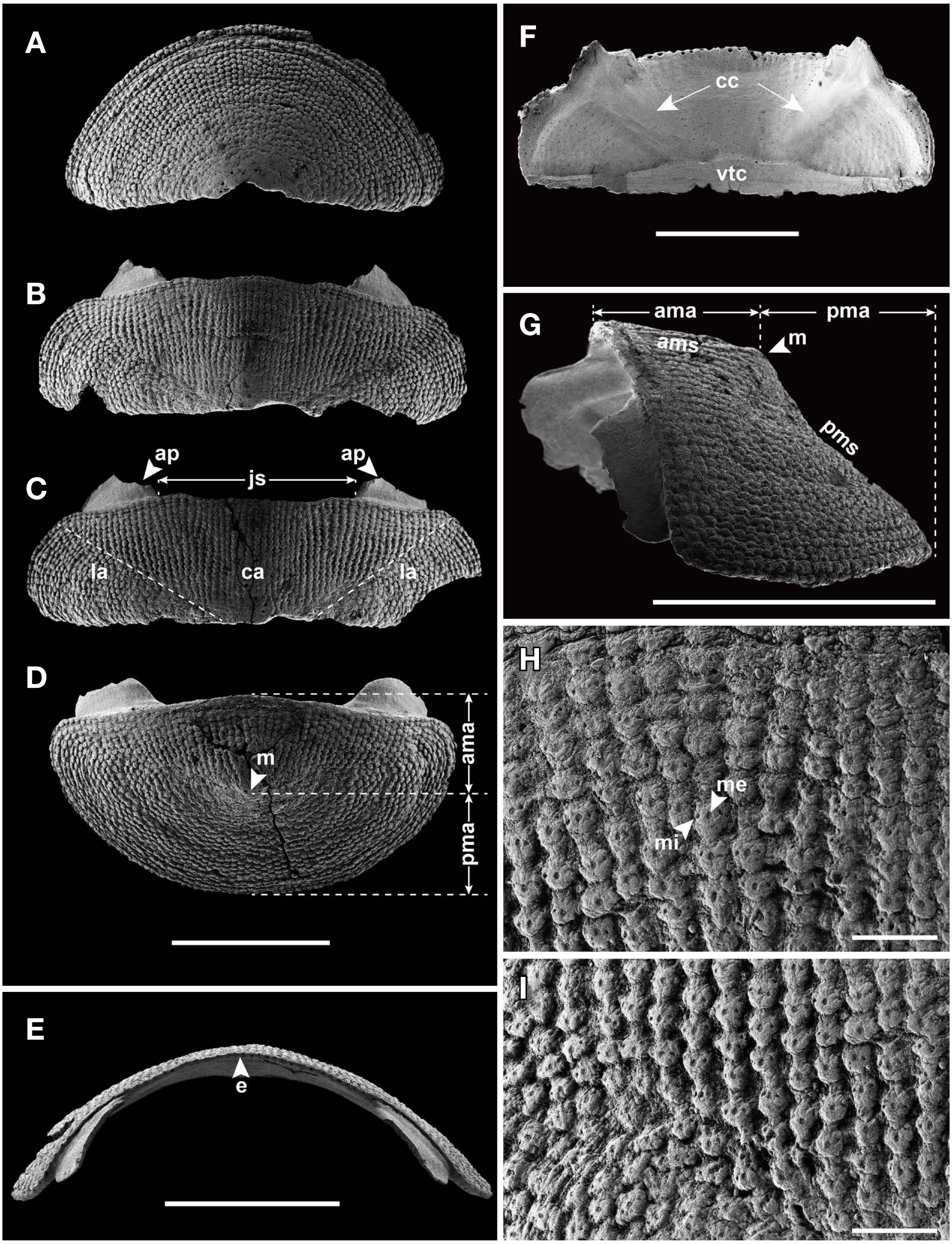

Fig. 2. Scanning electron microscope images of valves of *Leptochiton subrugatus*. A, Head valve, dorsal view; B, 2nd valve, dorsal view; C, 4th valve, dorsal view; D, Tail valve, dorsal view; E, 5th valve, frontal view; F, 4th valve, ventral view; G, Tail valve, lateral view; H, 4th valve, detail of tegmentum surface of central area; I, 4th valve, detail of tegmentum surface of central and lateral area. Abbreviations: ama, antemucronal area; ams, antemucronal slope; ap, apophyses; ca, central area; cc, central callus; e, eave; js, jugal sinus; la, lateral area; m, mucro; me, megalaesthete; mi, micraesthetes; pma, postmucronal area; pms, postmucronal slope; vtc, ventral tegmental callus. Scale bars: A–G = 1 mm, H, I = 100 μm.

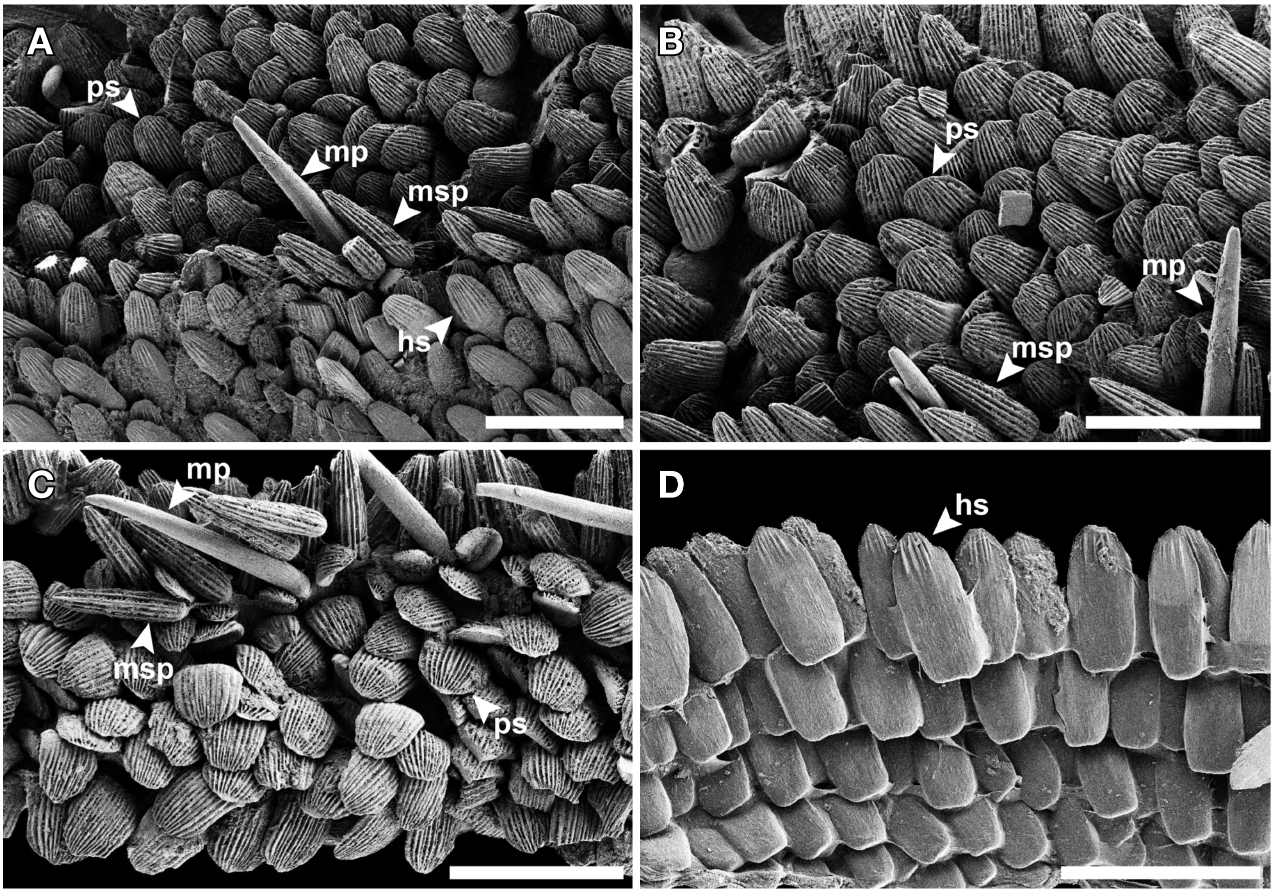

Fig. 3. Scanning electron microscope images of microstructure of girdle in *Leptochiton subrugatus*. A, Perinotum and hyponotum scales, marginal spicules and spines; B, C, Perinotum scales, marginal spicules and spines; D, Hyponotum scales. Abbreviations: hs, hyponotum scale; mp, marginal spine; msp, marginal spicule; ps, perinotum scale. Scale bars: A–D = 100 μm.

except for two central calluses connected from apophyses to ventral tegmental callus (vtc); eaves (e) very thin.

Perinotum densely covered with flat, curved, ovate scales (perinotum scale; ps: length 51.1 μm, width 31.3 μm) with blunted-tip and 13–18 longitudinal ribs, longer near sutures (Fig. 3A–C); outer margin densely covered with small marginal spicules (msp: length 77.4 μm, width 15.7 μm) with obtusely pointed tip and strong radial ribs (Fig. 3A–C); sporadic marginal spines (mp: length 139 μm, width 12.5 μm) long, slender, pointed, almost smooth, with faint longitudinal lines (Fig. 3A–C); hyponotum covered with elongate, flat, overlapping scales (hyponotum scale; hs: length 77.8 μm, width 33.1 μm) with obtusely pointed tip and 6–9 longitudinal ribs at the tip (Fig. 3A, D).

Radula teeth (Fig. 4) symmetrical, measuring 2.57 mm length, with 96 transverse rows of mature teeth. Central tooth (c) narrow with a small cusp bent forward; two centro-lateral teeth (cl) long with blades bent inwardly; head (h) of major lateral teeth (mlt) unicuspid, each cusp narrow, bluntly pointed; major uncinal teeth (mu)

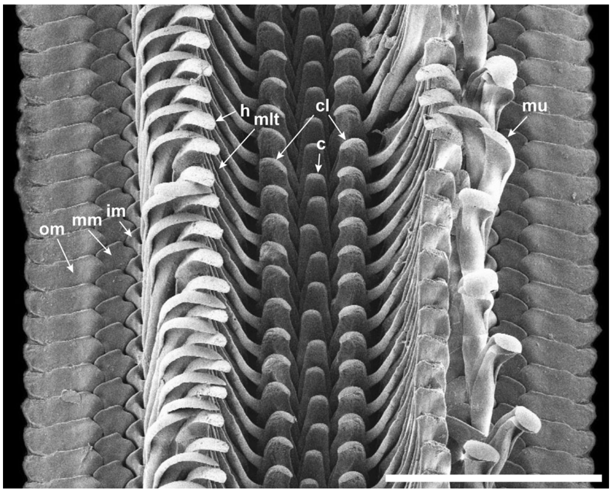

Fig. 4. Scanning electron microscope image of microstructure of radula of *Leptochiton subrugatus*. Abbreviations: c, central tooth; cl, centro-lateral tooth; h, head of major lateral tooth; im, inner marginal tooth; mlt, major lateral tooth; mm, middle marginal tooth; mu, major uncinus tooth; om, outer marginal tooth. Scale bar = 100 μm.

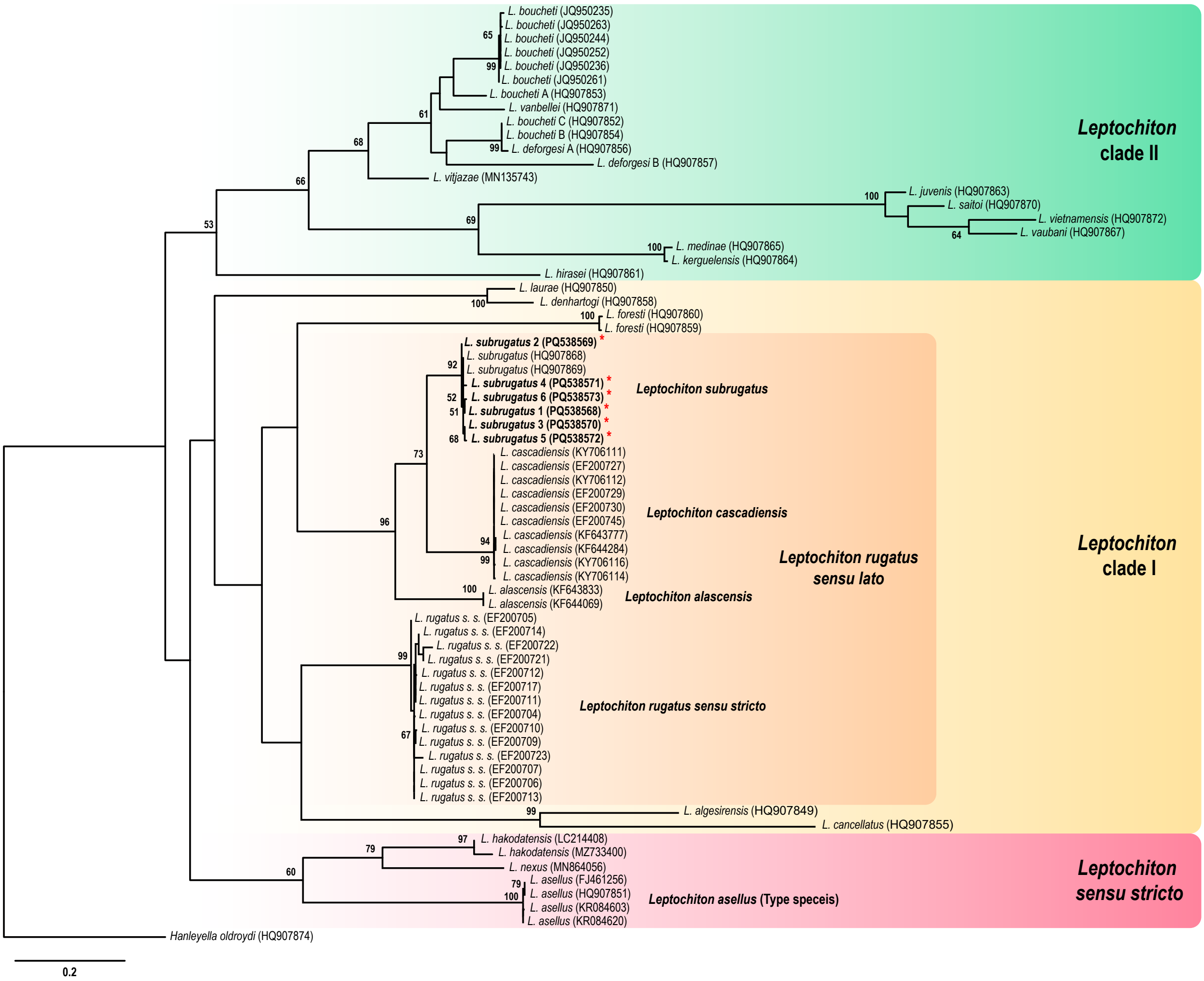

Fig. 5. Phylogenetic relationships among *Leptochiton* species based on the mtDNA *cox1* sequences, inferred from the maximum likelihood method. Node supporting values are indicated as bootstrap support values (≥ 50). Sequences used in this study are denoted by red asterisks (*).

slender oar shaped, bent inwardly, with a rounded tip; marginal teeth (im, mm, om) flat, outer marginal teeth widest.

Habitat. Intertidal to 30 m depth on hard substrates such as stones, rocks, or shells (e.g., mussels).

Type locality. Sea of Japan [East Sea]: Novgorodskaya Inlet, Possjet Bay (42°39′50″N, 130°40′51″E), 1.2–1.8 m depth.

Distribution. Russia (Sea of Japan [East Sea]: Vostok Bay, Peter the Great Bay, and Possjet Bay; Southwest Sakhalin: Moneron Island), Japan (Kunashir Island, South Kurile Islands; Hokkaido), China (Yellow Sea, near Qingdao), and Korea (Goseong).

Remarks. For nearly a century, this species was often misidentified as *Leptochiton assimilis* (Thiele, 1909) and *L. rugatus* (P. P. Carpenter, 1892) due to their morphological similarities (Taki, 1938; Jakovleva, 1952; Ferreira, 1979; Kaas and Van Belle, 1985; Dell'Angelo *et al*., 1990; Saito, 1995; 2000; 2017; Slieker, 2000; Qi, 2004; Sirenko, 2013). However, a recent comprehensive analysis of morphological and molecular data from *L. rugatus* samples collected from the Northwestern part (near Possjet Bay) of the Sea of Japan [East Sea] and the Yellow Sea (near Qingdao) concluded that they were separate species from *L. assimilis* and *L. rugatus*, and described the new species, *L. subrugatus* (Sirenko and Sigwart, 2021). In Korea, this species was initially reported as *L. rugatus* by Dell'Angelo *et al*. (1990), providing detailed descriptions, illustrations, SEM images, and their distribution information. A careful comparison of the morphological data described by Dell'Angelo *et al*. (1990) with the taxonomic information for *L. subrugatus* and *L. rugatus sensu stricto* (referring strictly to populations in California and Mexico, the type locations) provided by Sirenko

Table 1. Morphological comparison of three Korean *Leptochiton* species with *Leptochiton rugatus sensu stricto*.

	L. fuliginatus	*L. hakodatensis*	*L. rugatus s. s.*	*L. subrugatus*
Type locality	Korean archipelago	Japan: Hakodate	Mexico: Baja California	Sea of Japan: Possjet Bay
Body shape	Elongate-oval	Elongate-oval	Oval to elongate-oval	Elongate-oval
Adult body size	Medium	Small	Small	Small
Dorsal elevation	Moderate	Moderate	Moderate	Low to moderate
Back shape (in frontal view)	Subcarinated	Rounded	Carinated	Rounded
Central area of intermediate valve	Rounded granules in longitudinal rows	Rounded granules in longitudinal rows	Small granules in longitudinal rows	Small, rounded granules in longitudinal rows
Lateral area of intermediate valve	Slightly raised, with 6–10 concentric growth lines	Not raised, granules in radial rows	Granulate with several concentric growth lines	Not raised, granules in fine radial rows
The number of aesthete pores per granule	No data	5–8	7	3–5
Mucro	Slightly postmedian	Slightly antemedian, distinct	Subcentral	Antemedian, protruding
Antemucronal slope	Slightly convex	Slightly convex	Convex	Almost straight
Postmucronal slope	Steep, little concave	Concave	Steep, straight	Almost straight
Perinotum scales	Elongate scales with 4 ribs	Flat, ovate scales with 4–7 fine ribs	Broad ovate scales with 13–16 ribs	Flat, ovate scales with 13–18 ribs
Radula: major lateral teeth	Bicuspid, sharp	Bicuspid, bluntly pointed	Unicuspid, long, sharp	Unicuspid, bluntly pointed

and Sigwart (2021), along with the morphological analyses conducted in this study, leads us to concluded that the Korean populations described as *L. rugatus* species in previous taxonomic literatures (Dell'Angelo *et al.*, 1990) correspond to the taxonomic characters described for *L. subrugatus* (Sirenko and Sigwart, 2021). This taxonomic reassessment is supported by some key morphological characteristics resulting from morphological comparison of the three Korean *Leptochiton* species with *L. rugatus s. s.* (see Table 1 for detailed information): (1) the back shape of *L. subrugatus* is dorso-ventrally rounded, in contrast to the carinated shape of *L. rugatus s. s.*; (2) the number of aesthete pores per granule on the tegmentum is 3–5 in *L. subrugatus*, while 7 in *L. rugatus s. s.*; and (3) the slope of the front of the mucro (antemucronal slope) is nearly straight in *L. subrugatus*, compared to convex in *L. rugatus s. s.*. In addition, the distribution range of the Korean *L. rugaus* previously described by Dell'Angelo *et al.* (1990) included Karorim Bay in the West Sea, which overlaps with the distribution range of *L. subrugatus* (Sirenko and Sigwart, 2021).

Our phylogenetic analyses using the mtDNA *cox1* sequences were conducted to validate the morphological identification of Korean *L. subrugatus* and infer their phylogenetic relationships within the genus *Leptochiton*. The phylogenetic tree revealed that the species belonging to *Leptochiton* formed a monophyletic group and divided into three clades (*Leptochiton sensu stricto*, the *Leptochiton* clades I, and II), consistent with previous studies (Sigwart *et al.*, 2011; Sigwart, 2017), but each receiving low bootstrap value (Fig. 5). In phylogenetic tree, *L. subrugatus* grouped within the *Leptochiton* clade I that contains *L. rugatus sensu lato*, previously considered as *L. rugatus*, but is now recognized as a separate species complex comprising *L. alascensis* (Thiele, 1909), *L. cascadiensis* Sigwart & Chen, 2018, and *L. rugatus s. s.*. Genetic distances between *L. subrugatus* and other species belonging to the *Leptochiton* ranged from 7.57% (from *L. cascadiensis*) to 27.75% (from *L. juvenis* (Leloup, 1981) belonging to the *Leptochiton* clade II) (Table 2). In contrast to this high interspecific divergence, the within-species genetic difference among different *L. subrugatus* populations, represented by six Korean specimens and two Russian specimens of *L.* sp. 2 (Sigwart and Chen, 2018), was very low, ranging from 0 to 0.73%. Note that the pairwise sequence distance between *L. subrugatus* and *L. rugatus s. s.* ranged from 13.72 to 15.32%. Given their sister relationship with *L. cascadiensis* in the phylogenetic tree, molecular data from the Korean *L. subrugatus* populations strongly support the revision of *L. rugatus s. s.* (P. P. Carpenter, 1892) previously included in the National list of species in Korea, as *L. subrugatus* Sirenko & Sigwart, 2021.

Molecular sequence data: mtDNA *cox1* (GenBank accession nos. PQ538568–PQ538573); 16S rDNA (GenBank accession nos. PQ538574–PQ538579).

Table 2. Uncorrected *p*-distances (%) for the mtDNA *cox1* sequences among *Leptochiton* species.

	L. subrugatus	*L. cascadiensis*	*L. alascensis*	*L. rugatus s. s.*	*L. asellus*	*L. hakodatensis*	*L. nexus*	*L. foresti*	*L. denhartogi*	*L. laurae*	*L. boucheti* C	*L. boucheti* B	*L. deforgesi* A	*L. boucheti* A	*L. boucheti*	*L. vanbellei*	*L. deforgesi* B	*L. vitjazae*	*L. kerguelensis*	*L. medinae*	*L. hirasei*	*L. algesirensis*	*L. cancellatus*	*L. juvenis*	*L. saitoi*	*L. vaubani*	*L. vietnamensis*
L. subrugatus	**0-0.72**																										
L. cascadiensis	7.57−8.47	**0−0.36**																									
L. alascensis	9.75−10.27	11.17−11.35	**0**																								
L. rugatus s. s.	13.72−15.32	15.32−17.12	14.59−15.68	**0−2.52**																							
L. asellus	18.20−19.10	17.48−18.20	16.94−17.30	17.66−18.95	**0−0.36**																						
L. hakodatensis	17.30−18.56	18.02−17.56	17.30−17.48	16.40−17.84	14.26−14.77	**1.98**																					
L. nexus	16.22−16.76	16.40−16.76	17.30	18.02−18.56	16.76−16.94	11.53−12.43	−																				
L. foresti	15.32−16.04	16.76−17.12	16.94−17.12	16.76−18.38	18.38−18.56	16.58−17.66	18.02−18.20	**0.54**																			
L. denhartogi	17.12−17.30	17.84−18.20	19.10	18.56−19.28	19.10−19.31	18.92−19.10	18.38	18.74	−																		
L. laurae	17.30−17.48	17.12−17.48	18.20	17.30−18.02	18.56−18.77	17.84−18.74	18.74	20.18	6.31	−																	
L. boucheti C	19.86−20.22	20.40−20.76	20.22	17.87−18.95	19.13−19.49	17.69−18.41	19.13	17.33−17.51	19.13	18.59	−																
L. boucheti B	19.82−20.18	20.36−20.72	20.18	17.84−18.92	19.10−19.46	17.66−18.38	19.10	17.48−17.66	19.28	18.74	0.00	−															
L. deforgesi A	20.18−20.54	20.72−21.08	20.54	18.02−19.10	19.10−19.46	18.20−18.56	19.28	17.84−18.02	19.46	18.56	0.72	0.72	−														
L. boucheti A	20.36−20.72	19.82−20.18	19.46	16.94−18.02	18.92−19.10	16.40−16.58	16.94	16.58−16.76	19.46	20.00	8.48	8.47	8.47	−													
L. boucheti	18.77−19.46	20.18−20.90	19.10−19.46	17.48−18.92	19.82−20.36	16.04−17.12	16.94−17.30	16.94−17.48	18.92−19.28	18.92−19.28	8.84−9.21	8.83−9.19	9.19−9.55	6.67−7.21	**0−0.54**												
L. vanbellei	19.64−20.18	20.18−20.54	19.46	17.12−17.84	19.64−19.82	16.04−17.12	17.66	17.84−18.02	18.74	18.74	9.75	9.73	10.09	7.93	9.01−9.19	−											
L. deforgesi B	20.00−20.36	19.28−19.64	18.38	18.56−19.64	19.68−19.82	16.40−17.12	16.76	17.84−18.02	20.36	19.64	11.37	11.35	11.71	10.45	10.99−11.35	13.15	−										
L. vitjazae	18.23−18.56	19.82−20.18	18.74	17.30−18.20	19.10−19.46	17.30−18.20	17.66	17.84	18.92	18.92	11.73	11.71	11.71	10.45	10.27−10.63	11.71	13.51	−									
L. kerguelensis	22.92−23.42	24.50−24.68	22.34	21.26−21.98	21.80−21.98	20.54−21.08	21.62	21.80−22.16	24.32	21.98	18.77	18.74	18.56	18.56	18.20−18.56	18.74	20.36	18.38	−								
L. medinae	23.29−23.78	24.86−25.05	22.70	21.44−22.16	22.16−22.34	20.18−21.72	21.44	22.34−22.70	23.96	21.62	18.59	18.56	18.74	18.56	17.66−18.02	18.74	19.46	18.56	1.44	−							
L. hirasei	17.84−18.20	18.74−19.10	17.48	17.84−18.38	20.04−20.18	19.82	21.08	18.56−18.92	22.34	21.80	17.15	17.12	17.12	16.76	18.20−18.56	19.10	18.74	17.84	20.00	20.54	−						
L. algesirensis	21.44−22.16	20.00−20.36	20.54	17.12−18.38	19.49−19.64	18.38−19.46	19.46	18.38−18.74	20.90	19.10	19.86	19.82	20.00	19.82	20.00−20.18	19.28	21.26	20.18	23.24	23.24	21.26	−					
L. cancellatus	22.52−23.06	21.62−21.98	22.88	18.74−19.82	21.66−21.80	20.18−21.08	20.72	19.46−19.82	23.60	22.88	21.48	21.44	21.62	20.00	20.72−20.90	19.28	21.98	20.18	22.34	22.16	19.82	15.86	−				
L. juvenis	27.39−27.75	26.49−26.67	24.68	25.05−26.31	25.77−26.13	25.05−25.41	25.95	25.05−25.23	26.67	25.23	22.02	21.98	21.62	20.54	22.88−23.24	20.54	21.62	21.62	20.54	20.36	22.52	24.32	24.14	−			
L. saitoi	26.49−26.67	25.23−25.41	23.78	23.78−25.05	25.77−26.13	25.23	24.86	25.23−25.41	25.59	24.50	22.56	22.52	22.16	20.54	21.62−21.80	21.44	20.72	21.80	20.54	20.54	21.98	23.06	24.14	7.75	−		
L. vaubani	25.41−25.77	26.31−26.49	24.68	22.34−23.06	25.05−25.41	22.88−23.06	23.96	25.41	24.32	24.14	22.02	21.98	22.34	21.08	22.16−22.34	20.90	21.44	21.62	21.62	21.08	22.34	23.42	25.95	11.53	12.25	−	
L. vietnamensis	25.23−25.59	25.05−25.41	25.05	23.60−24.68	26.17−26.31	25.41−25.95	25.77	25.59	25.23	24.14	21.48	21.44	21.80	21.80	22.16−22.52	22.70	23.24	24.50	21.44	20.90	23.24	23.78	26.85	13.51	11.71	10.45	−

The bold type indicates p-distances among individuals of the same species.

CONFLICTS OF INTEREST

These authors of this paper have no affiliation with any interests and is solely responsible for the paper.

ACKNOWLEDGEMENTS

This work was supported by a grant from the National Institute of Biological Resources (NIBR), funded by the Ministry of Environment (MOE) of the Republic of Korea (NIBR202231206) and the management of Marine and Fishery Bio-resources Center (2025) funded by the National Marine Biodiversity Institute of Korea (MABIK).

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Submitted: October 11, 2024
Revised: October 30, 2024
Accepted: November 13, 2024