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New records of *Pseudoderma sinicarum* and *Lithophyllum nagaokaense* (Lithophylloideae, Lithophyllaceae, Rhodophyta) from Korea

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Abstract

The subfamily Lithophylloideae includes non-geniculate coralline algal genera for which taxonomic uncertainty persists due to pronounced morphological plasticity and the limited availability of type-anchored molecular data. Here, we report *Pseudoderma sinicarum* and *Lithophyllum nagaokaense* as new records from Korea, identified based on plastid DNA markers (*psb*A and *rbc*L) and morpho-anatomical observations. Phylogenetic analyses showed that sequences from Korean specimens were identical and nearly identical to the corresponding holotype sequences, providing strong molecular support for their taxonomic identities. Morpho-anatomical comparisons showed that Korean specimens of *L. nagaokaense* were consistent with the original description from Japan, whereas those of *P. sinicarum* exhibited previously undocumented variation in hypothallial cell type (palisade vs. non-palisade), cell dimensions, and the persistence of bistratose construction compared with the original description from China. These findings demonstrate that characters traditionally used for generic delimitation in Lithophylloideae can exhibit intraspecific variation. By integrating type-anchored molecular evidence with morpho-anatomical assessment, this study expands the known geographic distributions of both species and contributes to understanding taxonomic complexity within Lithophylloideae.

Keywords: Molecular phylogeny, Morpho-anatomy, Non-geniculate coralline algae, *psb*A, *rbc*L

Introduction

The subfamily Lithophylloideae Setchell (1943: 134) comprises both non-geniculate and geniculate coralline algae, distinguished by a combination of morpho-anatomical characteristics that includes species bearing palisade cells, cell fusions, secondary pit-connections, and trichocytes (Van der Merwe & Maneveldt 2016; Peña *et al.* 2020; Baba & Kato 2023). Within this morphologically complex subfamily, generic delimitation has been problematic, especially among taxa assigned to *Lithophyllum* Philippi (1837: 387) and *Titanoderma* Nägeli (1858: 532) (Lee *et al.* 2026a). *Titanoderma* has been treated either as a heterotypic synonym of *Lithophyllum* (Campbell & Woelkerling 1990; Woelkerling & Campbell 1992) or as a distinct genus based primarily on thallus construction and hypothallial cell type (Chamberlain 1991, 1996; Chamberlain & Irvine 1994; Van der Merwe & Maneveldt 2016). Under the latter concept, *Lithophyllum* lacks persistent bistratose thallus margins because thallus thickening begins behind the margin and has non-palisade hypothallial cells, whereas *Titanoderma* has persistent bistratose margins and palisade hypothallial cells (Van der Merwe & Maneveldt 2016; Lee *et al.* 2026a). Nevertheless, the taxonomic status of *Titanoderma* remains unresolved, as these morphological characters may vary or overlap among taxa and molecular studies have yet to establish an accepted generic framework (Richards *et al.* 2014; Jesionek *et al.* 2016; Lee *et al.* 2026a).

Despite these unresolved generic boundaries, *Lithophyllum* currently comprises 153 taxonomically accepted species of non-geniculate coralline algae (NGCA) (Guiry & Guiry 2026). Recent advances in integrative taxonomy incorporating morpho-anatomical and molecular data, including DNA sequences obtained from historical type

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specimens, have improved species identification and clarified the distributions of several taxa (Basso *et al.* 2015; Hernández-Kantún *et al.* 2015; Richards *et al.* 2018; Kato & Baba 2019; Pezzolesi *et al.* 2019; Kato *et al.* 2022a). *Lithophyllum nagaokaense* Min-Khant-Kyaw, A.Kato & M.Baba (2024: 171) is one such species that was recently described from Japan based on this integrative taxonomic approach (Min-Khant-Kyaw *et al.* 2024). The occurrence of *L. nagaokaense* outside Japan has also not been verified, and its distribution in neighboring regions, including Korea, remains undocumented.

Multi-gene concatenated phylogenetic analyses, combined with morpho-anatomical assessments, revealed a new genus, *Pseudoderma* S.-H.Yan, X.-L.Wang & G.-C.Wang (2025: 7), within Lithophylloideae (Yan *et al.* 2025). *Pseudoderma* is represented by a single species, *P. sinicarum* S.-H.Yan, X.-L.Wang & G.-C.Wang (2025: 8), which was established based on analyses of plastid (*psb*A), mitochondrial (COI-5P), and SSU markers (Yan *et al.* 2025). The species has been recorded only from China, and its distribution in adjacent regions remains unverified. Phylogenetic analyses have shown that *Pseudoderma* is closely related to *Lithophyllum* and *Titanoderma*, and shares morpho-anatomical similarities with both genera. Yan *et al.* (2025) distinguished *Pseudoderma* from the *Lithophyllum/ Titanoderma* complex based on differences in thallus thickening patterns associated with hypothallial cell type, particularly the relative contribution of palisade and non-palisade hypothallial cells to thallus development. Their interpretation builds on earlier concepts used to distinguish *Lithophyllum* and *Titanoderma*, in which hypothallial cell type and the persistence of a bistratose thallus were considered important generic characters (Chamberlain 1991, 1996; Chamberlain & Irvine 1994; Van der Merwe & Maneveldt 2016).

In Korea, ten species of NGCA in the subfamily Lithophylloideae have thus far been reported (Lee *et al.* 2026a; National Institute of Biological Resources 2026). These comprise nine species of *Lithophyllum*, including *L. canescens* (Foslie 1900a: 6) Foslie (1905: 8), *L. corallinae* (P.Crouan & H.Crouan 1867: 150) Heydrich (1897a: 47), *L. dispar* (Foslie 1907: 29) Foslie (1909: 50), *L. jejuense* K.Lee & M.Kim (2026: 152), *L. neo-okamurae* A.Kato, D.Basso, Caragnano, Rodondi, V.Peña & M.Baba (2022a: 122), *L. okamurae* Foslie (1900a: 4), *L. shioense* Foslie (1906: 23), *L. tumidulum* Foslie (1901: 5), *L. yessoense* Foslie (1909: 17), and one species of *Pseudolithophyllum* Me.Lemoine (1913: 45), *P. whidbeyense* (Foslie 1906: 21) Steneck & R.T.Paine (1986: 229). Among these, DNA sequence data are available for only three species, *L. jejuense*, *L. neo-okamurae* and *L. okamurae* (Kato *et al.* 2022a; Lee *et al.* 2026a). Given the high degree of morphological plasticity and cryptic diversity documented within the Lithophylloideae, the lack of DNA-based verification raises concerns regarding taxonomic accuracy.

In this study, we document *P. sinicarum* and *L. nagaokaense* as new records from Korea based on an integrative approach that combines analyses of plastid markers (*psb*A and *rbc*L) with morpho-anatomical observations. DNA sequences from Korean specimens were compared with reference sequences obtained from type specimens to support species-level identifications, and their morpho-anatomical features were compared with the original descriptions. Additionally, an unresolved *Pseudoderma* lineage was detected, highlighting the need for further taxonomic investigation within the genus.

Materials and methods

Specimen collection

Specimens were collected from intertidal and subtidal zones across Korea between 2024 and 2025 by wading, snorkeling, and SCUBA diving to a maximum depth of 15 m (Table S1). In situ and ex situ photographs were taken of the specimens using a TG-7 digital camera (OM SYSTEM, Japan). Portions of specimens were dried in fine silica gel (approximately 0.2–1 mm beads) for molecular analyses and scanning electron microscopy (SEM) observations. Fragments from the same specimens were preserved in 70% ethanol for morpho-anatomical analyses. Voucher specimens were deposited in the Herbarium of Jeju National University (JNUB), Jeju Island, Korea. Herbarium acronyms follow Thiers (2026, continuously updated).

Molecular analyses

Total genomic DNA was extracted from field-collected specimens dried in silica gel using the MagPurix® Plant DNA Extraction Kit v.1.3 (Zinext Life Science, Taiwan) according to the manufacturer's protocol. Algal material was processed after grinding in proximity ligation assay (PLA) buffer and incubated for 2 h at 60 °C in a shaking microplate incubator (Provocell, ESCO, Singapore). The DNA extract was stored at −20 °C prior to amplification.

The chloroplast photosystem II D1 protein (*psb*A) was used as a marker, with amplification attempted for all collected specimens. Following lineage identification based on the *psb*A gene, the chloroplast ribulose-bisphosphate carboxylase gene (*rbc*L) was amplified from a subset of samples representing each *psb*A lineage. The primer pairs used for amplification and sequencing were *psb*A-F1/*psb*A-R2 for *psb*A (Yoon *et al.* 2002) and F-753/R-*rbc*S start together with F-57/R-1150 for *rbc*L (Freshwater & Rueness 1994). Polymerase chain reactions (PCRs) were carried out in 20 μL reaction volumes in tube strips using AccuPower® Taq PCR Premix kit (Bioneer Corp., South Korea). PCRs were performed using an AllInOneCycler 96-well PCR system (A-2041-1N; Bioneer Corp., South Korea), with marker-specific thermocycling profiles. PCR products were commercially sequenced by Macrogen Co. (Seoul, South Korea).

All PCR products were sequenced bidirectionally using forward and reverse primers. Raw sequence reads were assembled and aligned using MAFFT v7.490 (Katoh & Standley 2013) within Geneious Prime v.2026.0.2 (Biomatters Ltd., Auckland, New Zealand). All newly generated sequences were deposited in GenBank and analyzed together with Lithophylloideae sequences retrieved from GenBank (Table S2). The dataset included the generitype sequences of *Lithophyllum incrustans* Philippi (1837: 388) (*psb*A: KR708604; *rbc*L: KR708583; Hernández-Kantún *et al.* 2015) and *P. sinicarum* (*psb*A: OQ943654; *rbc*L: OQ943756; Yan *et al.* 2025), to anchor generic names in the phylogenetic analyses. *Chamberlainium agulhense* (Maneveldt, E.van der Merwe & P.W.Gabrielson 2015: 475) Caragnano, Foetisch, Maneveldt & Payri (2018: 399) and *C. decipiens* (Foslie 1897: 20) Caragnano, Foetisch, Maneveldt & Payri (2018: 399) were used as outgroup taxa for both the *psb*A and *rbc*L datasets.

Phylogenetic analyses were implemented within Geneious Prime, and pairwise genetic divergences were estimated in MEGA11 (Tamura *et al.* 2021). Phylogenetic relationships for *psb*A and *rbc*L were reconstructed using both maximum likelihood (ML) and Bayesian inference (BI) under the General Time Reversible model with a gamma distribution and a proportion of invariant sites (GTR + I + G). Maximum likelihood trees were generated in RAxML with nodal support evaluated by 1,000 bootstrap replicates. Bayesian analyses were performed using the MrBayes v.3.2.6 plugin (Huelsenbeck & Ronquist 2001). Four Markov chain Monte Carlo (MCMC) chains were run for 2 million generations, sampling every 1,000 generations, with the initial 25% of samples excluded as burn-in.

Morpho-anatomical observations

Morpho-anatomical analyses were conducted only on molecularly confirmed specimens of *P. sinicarum* and *L. nagaokaense*. Paraffin microtomy and sectioning were performed according to Lee *et al.* (2026a). For scanning electron microscopy (SEM), samples were prepared following Min-Khant-Kyaw *et al.* (2024) and examined using a high-resolution SEM (JSM-6510LV; JEOL, Tokyo, Japan) at an accelerating voltage of 20 kV.

Anatomical terminology was adopted from Adey & Adey (1973) and Woelkerling (1988), and growth forms were described following Woelkerling *et al.* (1993) and Maneveldt *et al.* (2026). Cell and conceptacle measurements were conducted according to Irvine & Chamberlain (1994) and Maneveldt *et al.* (2019). For vegetative structures, ten cells (epithallial, subepithallial initial, perithallial, and hypothallial cells) per specimen were measured. For conceptacle chambers, sections through the pore canal were measured in *P. sinicarum* (2 specimens, 10 conceptacles) and *L. nagaokaense* (2 specimens, 21 conceptacles). Measurements are presented as minimum–maximum ranges, followed by the mean ± standard deviation (SD), with ranges given in brackets.

Results

In total, 18 gene sequences were newly generated in this study, comprising 10 *psb*A and 8 *rbc*L sequences (Table S1). Phylogenetic trees inferred from the *psb*A and *rbc*L datasets showed similar topologies in ML and BI analyses (Figs 1, 2). Across both datasets, sequences of *P. sinicarum* and *L. nagaokaense* generated in this study were each nested within clades containing their respective holotype sequences, while *Pseudoderma* sp. 1 formed an unresolved lineage within *Pseudoderma* and could not be assigned to any sequenced congener (Fig. 1).

In the *psb*A gene tree (Fig. 1), seven Korean specimens of *P. sinicarum* and two specimens of *L. nagaokaense* had sequences identical or nearly identical to those of their respective holotypes (GenBank accessions: OQ943654 and LC795589), with pairwise divergences of 0–0.4% and 0–0.1%, respectively. *Pseudoderma* sp. 1, also from Korea, clustered with an unidentified *Pseudoderma* sp. 6 from China (GenBank accessions: PP598288 and PP598310) and *Lithophyllum* sp. from Japan (GenBank accessions: MZ438316, MZ438343 and MZ438356), with pairwise

divergences of 0.5–0.9%. *Pseudoderma sinicarum* was recovered as sister to an unidentified *Pseudoderma* sp. 3 from China (GenBank accession: PP598223), with a pairwise divergence of 5.4–5.6%. *Lithophyllum nagaokaense* was recovered as sister to a clade comprising *L. atlanticum* Vieira-Pinto, M.C.Oliveira & P.A.Horta (2014: 361), *L. neo-okamurae*, *L. tomitae* M.Lyra, Bahia & L.Sagado (2024: 350), *L. trincomaliense* (Foslie 1906: 23) A.Kato & M.Baba (2022b: 671), and *L. validum* (Foslie 1906: 23) Foslie (1909: 32).

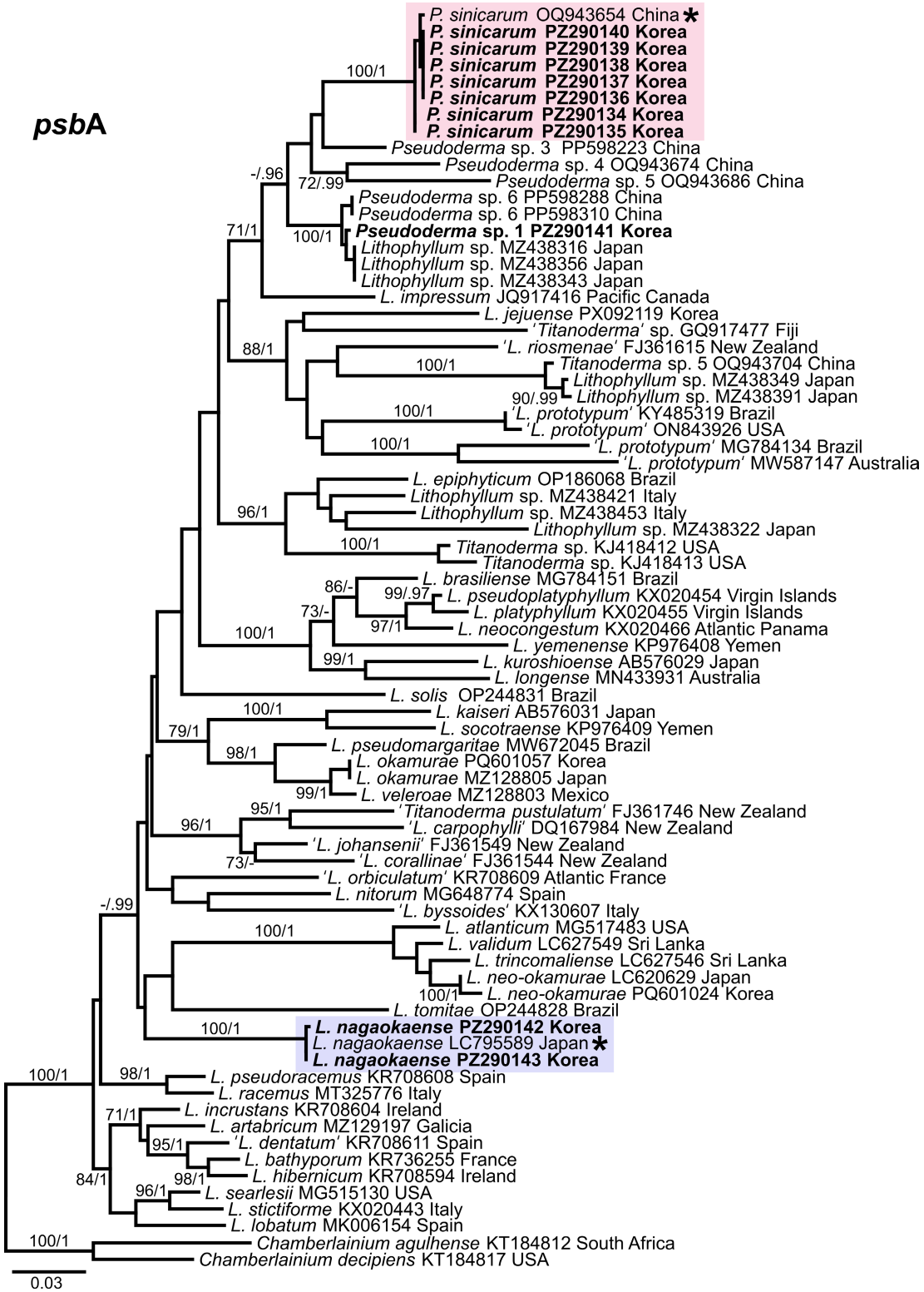


FIGURE 1. Phylogenetic tree of the subfamily Lithophylloideae based on *psb*A sequences, estimated using maximum likelihood (ML) and Bayesian inference (BI). Sequences generated in the present study are shown in bold. The sequences of the holotype are indicated by an asterisk (*). Species denoted by single quotes have not been confirmed through comparison with the DNA sequences of their respective type specimens. Values above branch nodes represent ML bootstrap values (BS) and Bayesian inference posterior probabilities (PP). Only bootstrap values > 70% and posterior probabilities > 0.95 are shown.

In the *rbc*L gene tree (Fig. 2), seven Korean specimens of *P. sinicarum* and one specimen of *L. nagaokaense* had sequences identical or nearly identical to those of their respective holotypes (GenBank accessions: OQ943756 and LC795600), with pairwise divergences of 0.5–1.2% and 0%, respectively. *Pseudoderma sinicarum* was recovered as sister to a clade comprising *Pseudoderma* sp. 4 and *Pseudoderma* sp. 5 (GenBank accessions: OQ943752 and OQ943764), with strong statistical support. *Lithophyllum nagaokaense* was recovered as sister to a clade comprising *L. byssoides* (Lamarck 1801) Foslie (1900c: 20), *L. intermedium*, *L. orbiculatum* (Foslie 1895: 171) Foslie (1900: 19), and *L. subtenellum* (Foslie 1899: 11) Foslie (1900c: 20), although this relationship lacked statistical support. Additionally, Korean *L. nagaokaense* differed from other *Lithophyllum* species reported from Korea and Japan, namely *L. jejuense*, *L. kaiseri* (Heydrich) Heydrich (1897b: 412), *L. kuroshioense* A.Kato & M.Baba (2019: 652), *L. neo-okamurae* and *L. okamurae,* by 7.7–11.8% in *psb*A sequence divergence and 15.3–19.7% in *rbc*L sequence divergence.

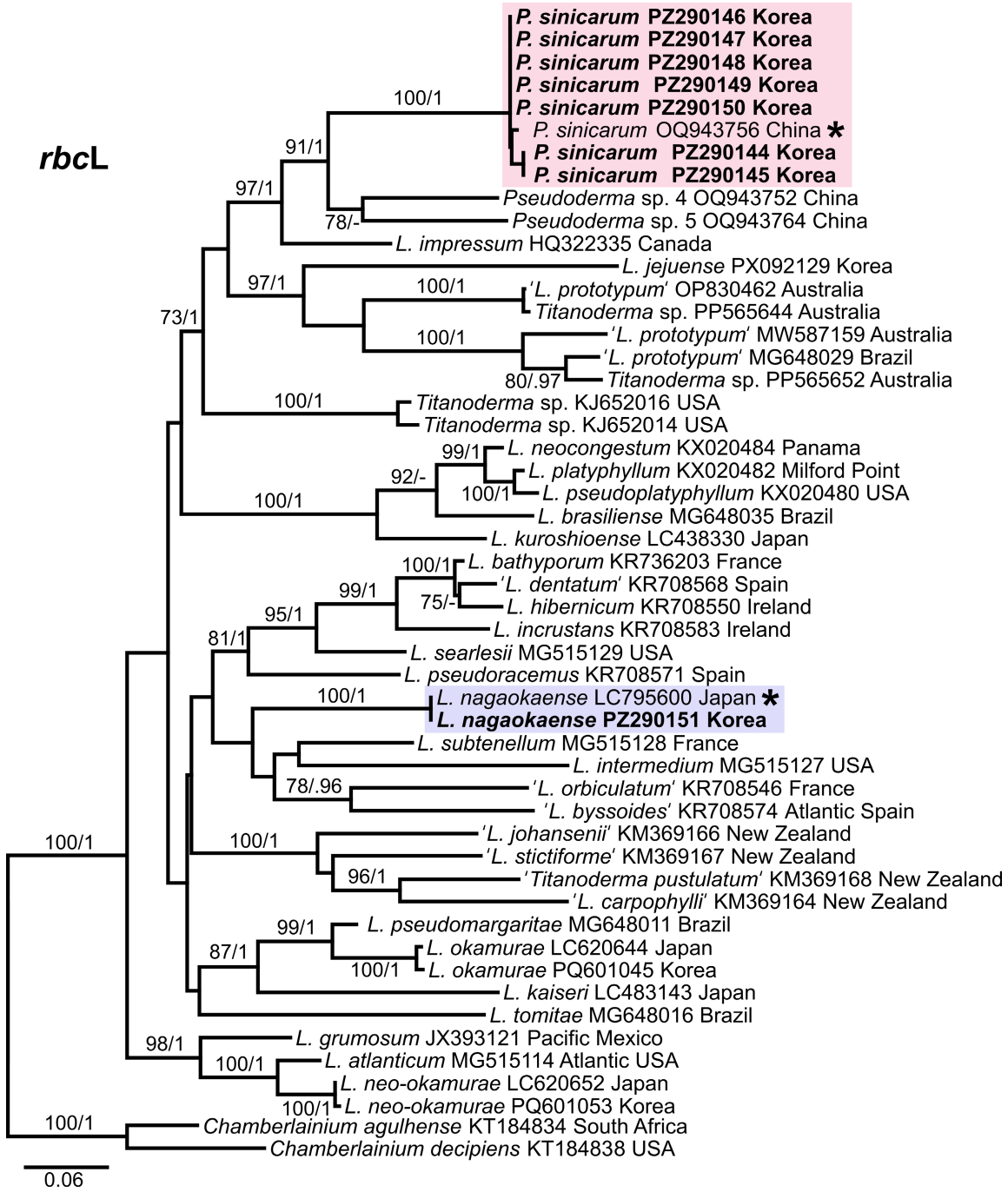


FIGURE 2. Phylogenetic tree of the subfamily Lithophylloideae based on *rbc*L sequences, estimated using maximum likelihood (ML) and Bayesian inference (BI). Sequences generated in the present study are shown in bold. The sequences of the holotype are indicated by an asterisk (*). Species denoted by single quotes have not been confirmed through comparison with the DNA sequences of their respective type specimens. Values above branch nodes represent ML bootstrap values (BS) and Bayesian inference posterior probabilities (PP). Only bootstrap values > 70% and posterior probabilities > 0.95 are shown.

Pseudoderma sinicarum S.-H.Yan, X.-L.Wang & G.-C.Wang (2025: 8)

Holotype:—QD344E (MBMCAS), 3 November 2020, *leg.* X.-L. Wang & S.-H. Yan, epiphytic in the intertidal zone (Yan *et al.* 2025).

Type locality:—China, Shandong Province, Qingdao, Zhanshan Bay.

Etymology:—The specific epithet *sinicarum* refers to China.

Distribution:—Previously known only from the western Pacific coast of China (Shandong, Zhejiang, Fujian, and Hainan provinces), and is here newly recorded from Korea.

Specimens examined:—REPUBLIC OF KOREA. Jeju Province: Seongsan, Jeju-si, intertidal zone, epiphytic on *Pterocladiella* sp., 20 December 2024, *leg.* K.T. Lee, JNUB000000059 (*psb*A: PZ290134; *rbc*L: PZ290144), JNUB000000060 (*psb*A: PZ290135; *rbc*L: PZ290145). Jeollanam-do: Ocheon-ri, Geogeumdo, intertidal zone, 30 January 2025, *leg.* K.T. Lee, JNUB000000061 (epiphytic on *Pterocladiella* sp.; *psb*A: PZ290136; *rbc*L: PZ290146), JNUB000000062 (epiphytic on *Grateloupia* sp.; *psb*A: PZ290137; *rbc*L: PZ290147), JNUB000000063 (epiphytic on *Grateloupia* sp.; *psb*A: PZ290138; *rbc*L: PZ290148), JNUB000000064 (epiphytic on *Pterocladiella* sp.; *psb*A: PZ290139; *rbc*L: PZ290149), JNUB000000065 (epiphytic on *Pterocladiella* sp.; *psb*A: PZ290140; *rbc*L: PZ290150).

Description

Habit:—Thalli grew epiphytically on red algae in the intertidal zone, including *Pterocladiella* and *Grateloupia*. Some thalli were also observed growing epiphytically on other NGCA (Figs 3G, H).

Vegetative anatomy:—Thalli were encrusting, forming a thin, hard crust wrapped around the host alga (Figs 3A, B, G, H). Living thalli were purplish-pink to dark pink in color. Thalli were dorsiventral and dimerous (Figs 3C, F). The hypothallus consisted of a single layer of both sinuous palisade and non-palisade cells, 11–70 µm in length and 6–12 µm in diameter (Figs 3C–F, 3H). The perithallus also consisted of both palisade and non-palisade cells, 7–48 µm in length and 6–13 µm in diameter (Figs 3C–F, 3H). Subepithallial initials were isodiametric to elongate, 7–35 µm in length and 6–11 µm in diameter (Figs 3C–F, 3H). Secondary pit-connections were common; cell fusions were not observed. The epithallus comprised one to two layers of rounded to flattened cells, 2–5 µm in length and 6–10 µm in diameter (Fig. 3C). Trichocytes were present, measuring 20–48 µm in length and 5–7 µm in diameter (Fig. 3D). Thallus margins were bistratose (Figs 3G, H). Data on measured vegetative features are summarized in Table 1.

Reproductive anatomy:—Gametangial thalli were not found. Tetra- and bisporangial conceptacles were uniporate, measured 185–232 µm in diameter and 92–120 µm in height. Pore canals were triangular, 31–50 µm in length, and tapered towards the surface (Figs 4A–C); cells lining the pore canal were arranged obliquely or horizontally relative to the thallus surface (Fig. 4B). Pore canals were either unoccluded (Figs 4A, B) or occluded by a mucilage plug (Fig. 4C). Conceptacle roofs comprised two to four cell layers and were 30–41 µm thick. Conceptacle chamber floors were situated five to eight cells below the surrounding thallus surface. A central columella was often present, with a calcified hump below (Figs 4A, C). Remnants of interspersed cavity cells that gave rise to the roof were observed (Fig. 4D). Tetra- and bisporangia were zonately divided, 25–105 µm in length and 15–50 µm in diameter, and developed at the periphery (Figs 4A, C, D). Conceptacles appeared buried within the thallus. Data on measured reproductive features are summarized in Table 2.

Lithophyllum nagaokaense Min-Khant-Kyaw, A.Kato & M.Baba (2024: 171)

Holotype:—SAP 115668, 13 November 2008, *leg*. M. Baba, epilithic on boulders in the shallow subtidal zone (Min-Khant-Kyaw *et al.* 2024).

Type locality:—Japan, Niigata Prefecture, Nagaoka City, Teradomari, Yamada.

Etymology:—The specific epithet *nagaokaense* refers to the type locality.

Distribution:—Previously known only from Japan, occurring along temperate coasts on both the Sea of Japan and Pacific Ocean sides, and is here newly recorded from Korea.

Specimens examined:—REPUBLIC OF KOREA. Jeju Province: Sinheung, Jeju-si, intertidal zone, epilithic on rocky substrata, 6 December 2024, *leg*. K.T. Lee, JNUB000000067 (*psb*A: PZ290142); Biyangdo, Jeju-si, subtidal rhodolith bed at 10 m depth, 10 March 2025, *leg*. K.T. Lee, JNUB000000068 (*psb*A: PZ290143; *rbc*L: PZ290151).

TABLE 1. Comparison of the morphology and vegetative anatomy of *Pseudoderma* and *Lithophyllum* species. Measurements are presented as means ± standard deviation, with ranges provided in brackets.

Character	***P. sinicarum*** **(This study)**	***P. sinicarum*** **(Yan *et al.* 2025)**	***L. nagaokaense*** **(This study)**	***L. nagaokaense*** **(Min-Khant-Kyaw *et al.* 2024)**	***L. neo-okamurae*** **(Kato *et al.* 2022a)**	***L. okamurae*** **(Kato *et al.* 2022a)**	***L. jejuense*** **(Lee *et al.* 2026a)**
Gross morphology	Attached	Attached	Attached or free-living	Attached or free-living	Attached or free-living	Attached or free-living	Attached
Basal layer of palisade cell	Present	Absent	Absent	Absent	Absent	Absent	Present
Vegetative structures	(5 specimens, 50 cells)	ND	(2 specimens, 20 cells)	(6 specimens, 60 cells)	(6 specimens, 30 cells)	(1 specimen, 30 cells)	(5 specimens, 50 cells)
Epithallial cell							
Number	1–2	1–2	1–3	1–4	1–2	1	1
Length (μm)	3.2 ± 0.7 [2–5]	5.0 ± 1.4 [4–6]	3.9 ± 1.1 [3–6]	3.7 ± 0.8 [2.5–5.5]	3.3 ± 0.6 [2–5]	3.7 ± 1 [2–6]	6.4 ± 1.2 [4–9]
Diameter (μm)	7.9 ± 0.9 [6–10]	8.5 ± 2.3 [6–11]	8.7 ± 1.3 [7–11]	8.4 ± 1.0 [7–11]	8.5 ± 0.7 [7–10.5]	9.8 ± 1.7 [6–12]	9.1 ± 1.6 [7–14]
Subepithallial initial							
Length (μm)	14.4 ± 6.5 [7–35]	12.5 ± 5.0 [6–17]	9.7 ± 1.6 [6–13]	9.8 ± 1.8 [6–13.5]	8.3 ± 1.5 [6–12]	11.9 ± 2.5 [7–15]	37.0 ± 12.8 [10–76]
Diameter (μm)	8.5 ± 1.3 [6–11]	9.7 ± 2.8 [7–13]	8.6 ± 1.7 [6–12]	8.7 ± 1.0 [6–11.5]	8.2 ± 0.9 [7–10]	9.8 ± 1.5 [7–12]	10.4 ± 1.9 [6–15]
Perithallial cell							
Length (μm)	17.1 ± 8.6 [7–48]	19.4 ± 7.8 [12–27]	12.1 ± 4.6 [5–20]	12.2 ± 3.4 [6–20.5]	12.3 ± 3.4 [8–19]	12.6 ± 2.8 [7–19]	8–44
Diameter (μm)	8.6 ± 1.7 [6–13]	8.3 ± 1.9 [6–10]	9.6 ± 1.5 [6–13]	8.7 ± 0.9 [7–11]	8.2 ± 0.7 [6–9]	11 ± 1.5 [9–13]	6–16
Hypothallial cell							
Length (μm)	28.7 ± 12.6 [11–70]	20.4 ± 8.6 [12–29]	13.3 ± 2.6 [8–18]	14.4 ± 2.2 [9.5–20.5]	13.4 ± 2.7 [8–22]	16.1 ± 3.3 [12–25]	9–90
Diameter (μm)	8.1 ± 1.5 [6–12]	6.0 ± 1.8 [4–8]	10.8 ± 2.0 [6–14]	11.8 ± 2.3 [4–15]	8.9 ± 1.9 [5.5–14]	9.8 ± 2.5 [6–15]	8–20
Trichocytes	Present	Present	Absent	Absent	Absent	Absent	Absent

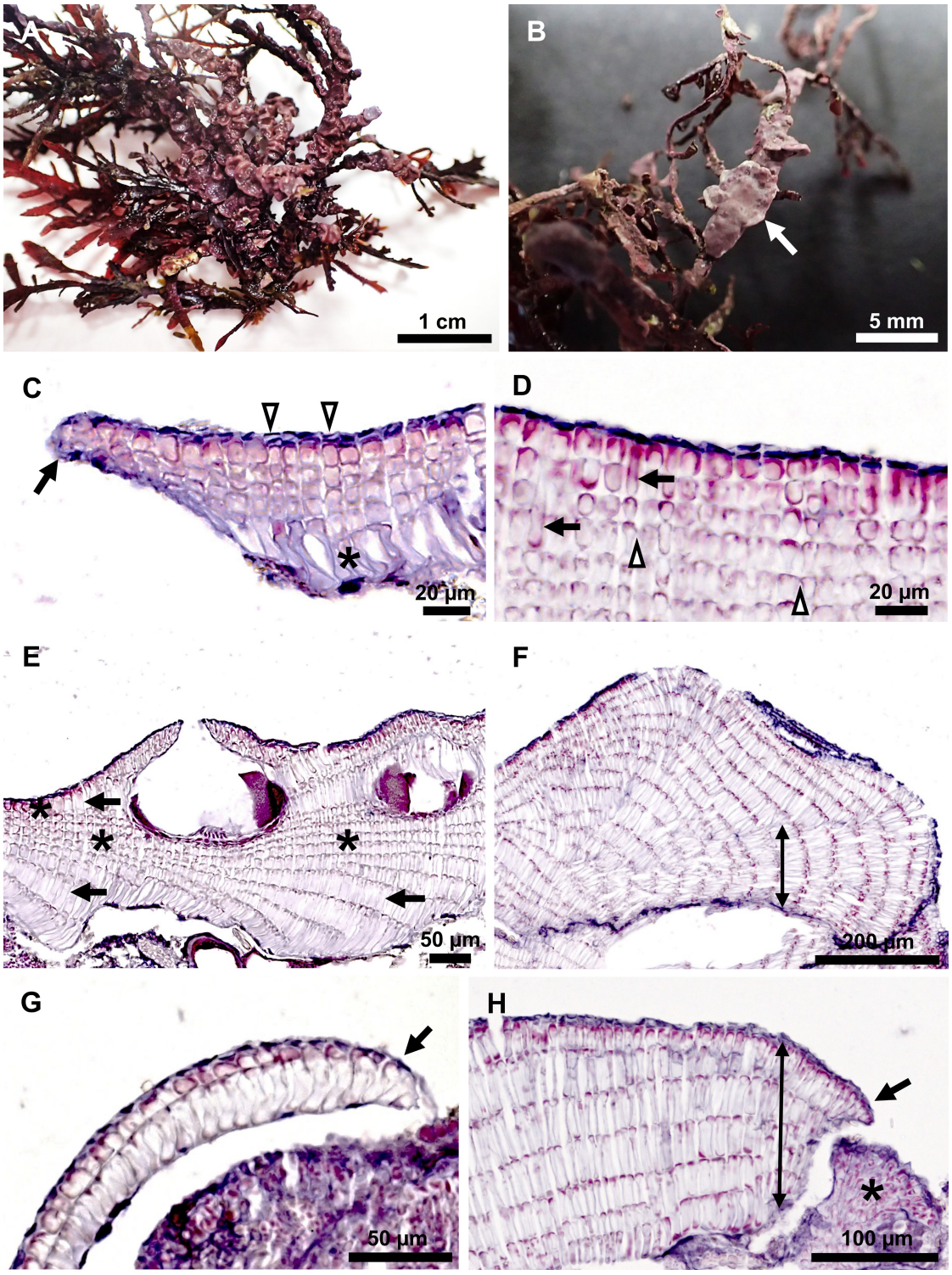


FIGURE 3. External morphology and vegetative anatomy of *Pseudoderma sinicarum*. (A) Habit of epiphytic thalli growing on a red algal host (*Pterocladiella* sp.) (JNUB000000064). (B) Close-up view of an encrusting thallus tightly adhering to the host surface (arrow) (JNUB000000060). (C) Vertical section through a dimerous, bistratose margin showing the terminal initial (arrow), palisade hypothallial cells (asterisk), and two layers of epithallial cells (arrowheads) (JNUB000000060). The bistratose condition was restricted to the thallus margin and was lost shortly behind the margin. (D) Vertical section of the outer thallus showing trichocytes (arrows) and secondary pit-connections (arrowheads) (JNUB000000060). (E) Vertical section through the thallus showing isodiametric to elongate perithallial and subepithallial cells (arrows) and shorter perithallial and subepithallial cells (asterisks) (JNUB000000060). (F) Vertical section through the thallus showing perithallial cells bending toward the thallus margin (double-headed arrow) (JNUB000000060). (G) Vertical section of the margin and thallus showing a uniform bistratose pattern (arrow) (JNUB000000059). (H) Vertical section through the thallus showing a bistratose margin (arrow) that quickly thickens to form a multistratose thallus behind the margin (double-headed arrow) (JNUB000000059). The asterisk indicates another NGCA.

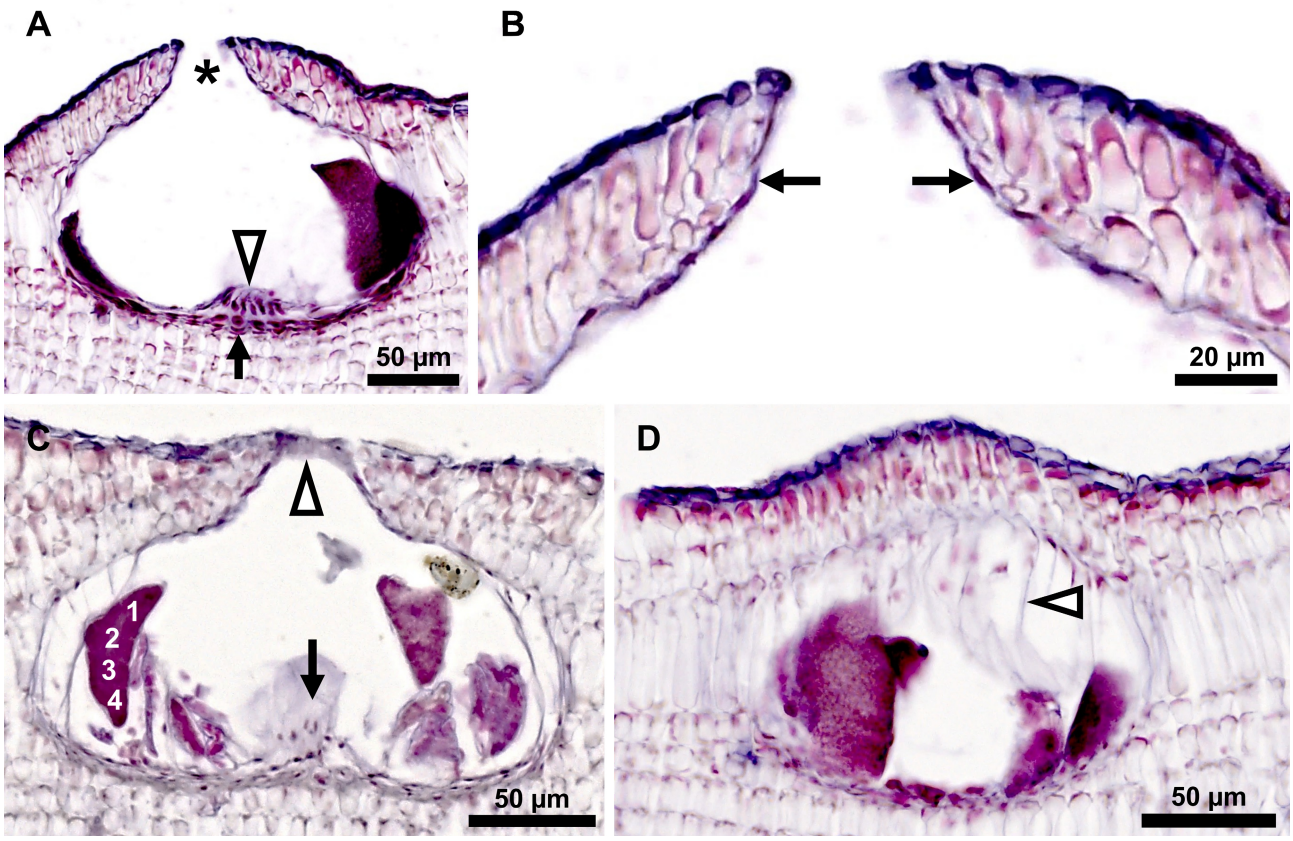


FIGURE 4. Tetrasporangial anatomy of *Pseudoderma sinicarum*. (A) Vertical section through a uniporate tetrasporangial conceptacle showing a triangular pore canal (asterisk), a central columella (arrowhead), and a calcified hump below the columella (arrow) (JNUB000000060). (B) Enlarged view of the pore canal showing cells lining the canal arranged obliquely to horizontally relative to the thallus surface (arrows) (JNUB000000060). (C) Vertical section through a tetrasporangial conceptacle showing a mucilage plug (arrowheads) blocking the pore canal and zonately divided tetrasporangia arranged peripherally to the remains of a central columella (arrow) (JNUB000000060). (D) Vertical section through the side of a tetrasporangial conceptacle showing remnants of interspersed cavity cells forming the conceptacle roof (arrowhead) (JNUB000000060).

Description

Habit:—Thalli were epilithic on rocky substrata in the intertidal zone (Fig. 5A), or occurred as free-living forms in subtidal rhodolith beds (Fig. 5B).

Vegetative anatomy:—Thalli ranged from lumpy to columnar (Figs 5A, B). Branches were knobby, up to 16 mm in length and 3–7 mm in diameter, and dichotomously branched or anastomosing. Living thalli were purplish-pink to dark pink in color. Thalli were dorsiventral and dimerous. The hypothallus consisted of a single layer of non-palisade isodiametric to slightly rectangular cells, 8–18 µm in length and 6–14 µm in diameter (Fig. 5C). Cells of perithallial filaments were 5–20 µm in length and 6–13 µm in diameter. Secondary pit-connections were common; cell fusions were not observed. Subepithallial initials were square to rectangular, 6–13 µm in length and 6–12 µm in diameter. The epithallus comprised one to three layers of cells that were rounded to flattened, 3–6 µm in length and 7–11 µm in diameter (Fig. 5D). Trichocytes were not observed. Bistratose margins were also not observed. Data on measured vegetative features are summarized in Table 1.

Reproductive anatomy:—Gametangial thalli were not found. Only tetrasporangial conceptacles were observed, which were uniporate and measured 133–178 µm in diameter and 68–97 µm in height. Pore canals were square to triangular and tapered towards the surface, 27–51 µm in length (Figs 6A–C). Cells surrounding the pore canal were enlarged, angular, and oriented more or less perpendicular to the roof surface (Figs 6A, B), and were unoccluded (Fig. 6B). Conceptacle roofs comprised three to five cell layers and were 25–44 µm thick. Conceptacle chamber floors were situated eight to eleven cells below the surrounding thallus surface. A central columella was usually absent but occasionally present; when present, the columella was composed of sterile filaments. A calcified hump was not observed. Remnants of interspersed cavity cells that gave rise to the roof were observed (Fig. 6C). Tetrasporangia

were zonately divided, 26–52 µm in length and 13–27 µm in diameter, and developed at the periphery (Fig. 6D). Conceptacles were observed buried within the thallus and were either not infilled or partially infilled (Fig. 5F). Data on measured reproductive features are summarized in Table 2.

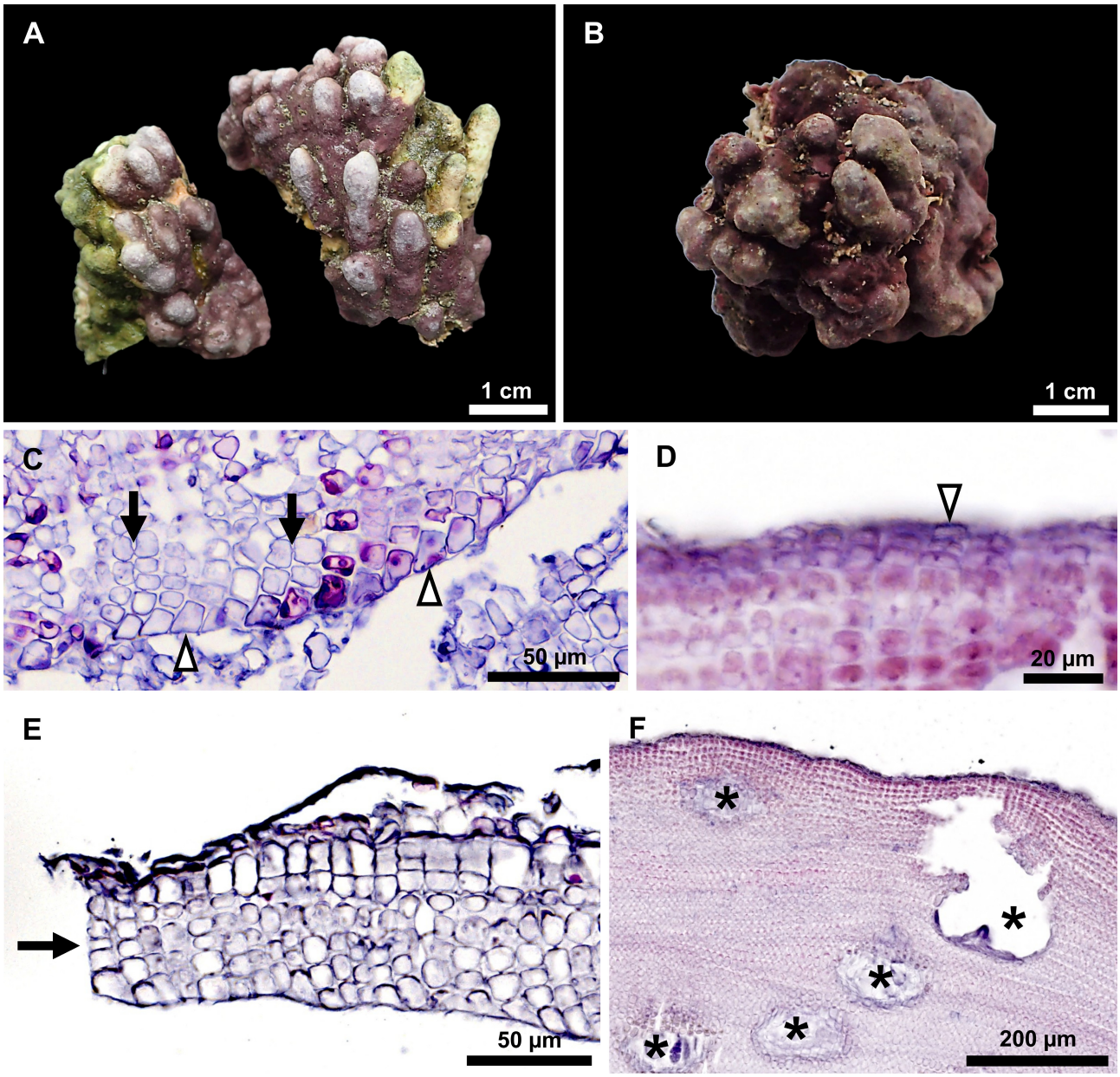


FIGURE 5. External morphology and vegetative anatomy of *Lithophyllum nagaokaense*. (A) Habit of a detached epilithic columnar specimen (JNUB000000067). (B) Habit of a rhodolith specimen with lumpy growth form (JNUB000000068). (C) Vertical section through the lower thallus showing a dimerous thallus with a unistratose hypothallus composed of non-palisade cells (arrowheads) (JNUB000000067). The arrows indicate secondary pit-connections. (D) Vertical section through the outer thallus showing an epithallus comprised of three layers of cells (arrowhead) (JNUB000000067). (E) Vertical section through the thallus showing the dimerous construction with a unistratose hypothallus composed of non-palisade cells giving rise to perithallial cells dorsally (arrow) (JNUB000000068). (F) Vertical section of the thallus showing buried conceptacles that are both infilled and not infilled (asterisks) (JNUB000000067).

Discussion

Molecular evidence for new records

Recent regional sequencing efforts have revealed remarkable cryptic diversity among non-geniculate coralline algae, refining species distributions and uncovering lineages previously overlooked under morphology-based taxonomy

TABLE 2. Comparison of the reproductive anatomy of *Pseudoderma* and *Lithophyllum* species. Measurements are presented as means ± standard deviation, with ranges provided in brackets.

Character	*P. sinicarum* (This study)	*P. sinicarum* (Yan *et al.* 2025)	*L. nagaokaense* (This study)	*L. nagaokaense* (Min-Khant-Kyaw *et al.* 2024)	*L. neo-okamurae* (Kato *et al.* 2022a)	*L. okamurae* (Kato *et al.* 2022a)	*L. jejuense* (Lee *et al.* 2026a)
Tetrasporangial conceptacle	(2 specimens, 10 conceptacles)	(50 conceptacles)	(2 specimens, 21 conceptacles)	(5 specimens, 34 conceptacles)	(7 specimens, 35 conceptacles)	(1 specimen, 4 conceptacles)	(5 specimens, 20 conceptacles)
Chamber diameter (µm)	205 ± 14 [185–232]	198.3 ± 36.1 [162–234]	161 ± 11 [133–178]	163 ± 18 [124–199]	309 ± 33 [248–380]	235–295	406 ± 35 [329–458]
Chamber height (µm)	106 ± 10 [92–120]	105.7 ± 23 [83–129]	82 ± 9 [68–97]	81 ± 12 [58–101]	104 ± 10 [86–121]	94–105	146 ± 22 [104–185]
Pore canal length (µm)	41 ± 5 [31–50]	ND	38 ± 8 [27–51]	35 ± 6 [23–43]	57 ± 10 [40–78]	53	60 ± 7 [45–70]
Shape of pore canal	Triangular	Triangular	Triangular to square	Triangular to square	Triangular	Triangular	Triangular
Occlusion of pore canals	Present	ND	Absent	Absent	Absent	Absent	Present
Shape of cells lining conceptacle pore canals	Obliquely oriented pore-canal lining cells	ND	Enlarged angular cells, oriented more or less perpendicular to roof surface	Enlarged angular cells, oriented more or less perpendicular to roof surface	Papillate cells, oriented more or less parallel to roof surface	Papillate cells, oriented more or less parallel to roof surface	Papillate cells, oriented more or less parallel to roof surface
Roof thickness (µm)	35 ± 3 [30–41]	37.6 ± 10.2 [27–48]	34 ± 6 [25–44]	34 ± 6 [23–48]	58 ± 10 [43–78]	48	52 ± 6 [41–62]
Number of roof cells (including epithallial cell)	3 ± 1 [2–4]	2–3	4 ± 1 [3–5]	3 ± 0 [3–4]	6 ± 1 [4–8]	4–5	2 ± 0 [2–3]
Depth from chamber floor to surface (no. of cells)	6 ± 1 [5–8]	4–7	10 ± 1 [8–11]	9 ± 1 [6–12]	13 ± 2 [10–16]	8–12	4 ± 0 [4–5]
Depth from chamber floor to surface (µm)	147 ± 10 [131–164]	144.2 ± 26.0 [118–170]	119 ± 12 [102–144]	103 ± 21 [66–154]	156 ± 22 [114–202]	88–141	191 ± 24 [145–240]
Occurrence of calcified hump below central columella	Present	Present	Absent	Absent	Present	Present	Present
Number of cells forming calcified hump below central columella	1	1	0	0	4–7	2–4	1–3

.....continued on the next page

TABLE 2. (Continued)

Character	*P. sinicarum* (This study)	*P. sinicarum* (Yan *et al.* 2025)	*L. nagaokaense* (This study)	*L. nagaokaense* (Min-Khant-Kyaw *et al.* 2024)	*L. neo-okamurae* (Kato *et al.* 2022a)	*L. okamurae* (Kato *et al.* 2022a)	*L. jejuense* (Lee *et al.* 2026a)
Tetra (bi-) sporangium	Tetrasporangial & bisporangial (N = 21)	Tetrasporangial (N = 38) & bisporangial (N = 20)	Tetrasporangial (N = 16)	Tetrasporangial (N = 20)	Tetrasporangial	ND	Tetrasporangial (N = 21)
Length (μm)	62 ± 18 [25–105]	78.8 ± 18.9 [60–98] (Tetrasporangial) 72.6 ± 14.1 [59–87] (Bisporangial)	40 ± 9 [26–52]	68 ± 11 [42–88]	68 ± 8 [47–79]	ND	58 ± 15 [30–84]
Diameter (μm)	24 ± 10 [15–50]	30.1 ± 9.4 [21–40] (Tetrasporangial) 33.8 ± 12.7 [21–46] (Bisporangial)	17 ± 4 [13–27]	33 ± 9 [15–52]	28 ± 4 [20–34]	ND	28 ± 9 [12–56]

N, number of tetra (bi-) sporangium; ND, no data available.

(Hernández-Kantún *et al.* 2016; Richards *et al.* 2018; Maneveldt *et al.* 2019; Min-Khant-Kyaw *et al.* 2026). The present study contributes to this ongoing taxonomic clarification through molecular confirmation of two newly recorded Lithophylloideae species, *P. sinicarum* and *L. nagaokaense*, in Korea. Previous studies delimited these species using molecular and morpho-anatomical evidence, including available type-linked sequences (Min-Khant-Kyaw *et al.* 2024), while Yan *et al.* (2025) additionally applied algorithmic species delimitation methods.

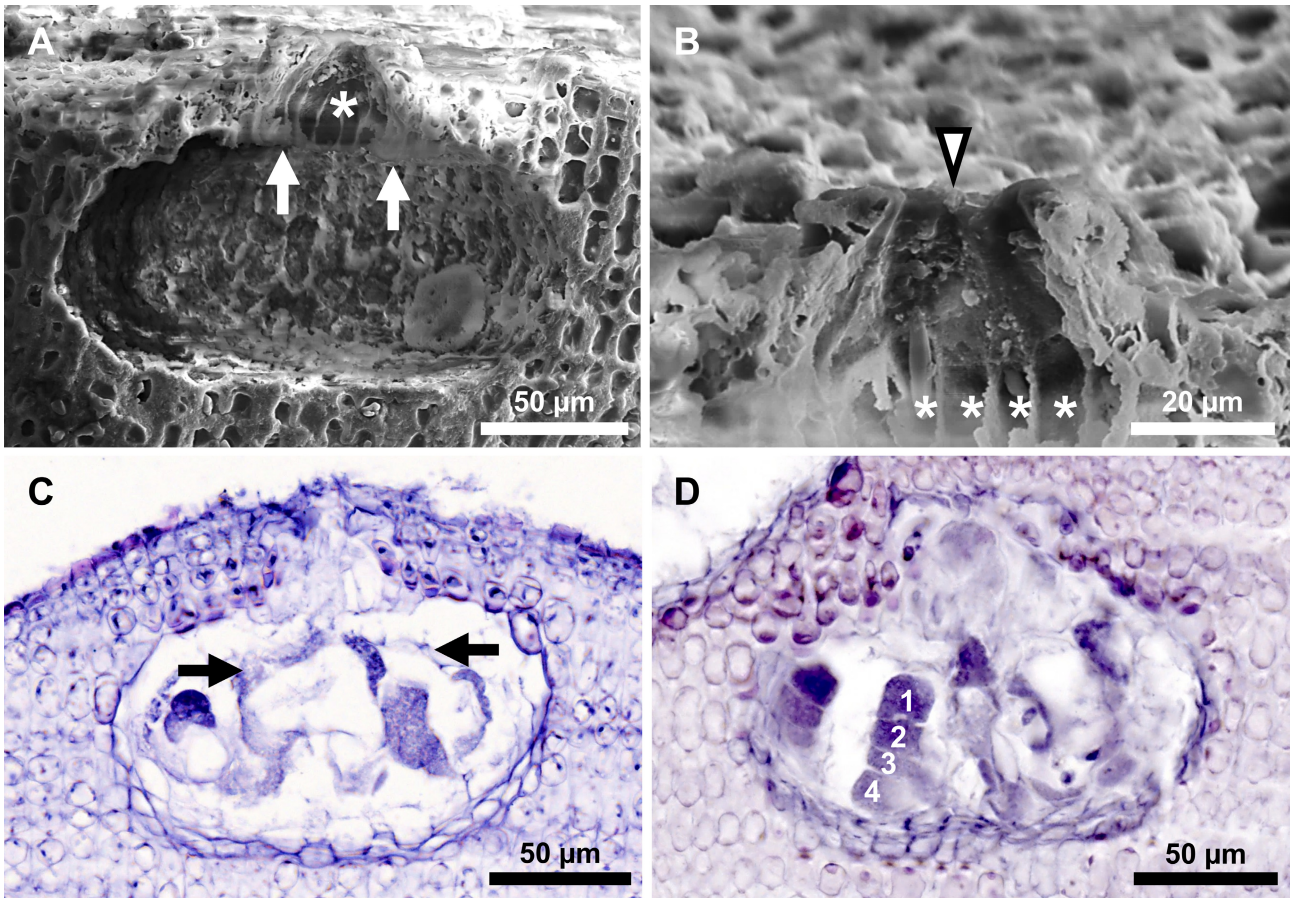


FIGURE 6. Tetrasporangial anatomy of *Lithophyllum nagaokaense*. (A) Vertical fracture through a uniporate tetrasporangial conceptacle showing a slightly tapered pore canal (asterisk) and enlarged angular pore canal cells oriented more or less perpendicular to the roof surface (arrows) (JNUB000000068). (B) Vertical fracture through a tapered pore canal showing enlarged angular cells (asterisks) surrounding the canal opening (arrowhead) (JNUB000000068). (C) Vertical section through a uniporate tetrasporangial conceptacle showing remnants of interspersed cavity cells that contributed to the roof formation (arrows) (JNUB000000068). (D) Vertical section through a buried tetrasporangial conceptacle showing zonately divided tetrasporangia (JNUB000000067).

In the present study, sequence divergences between Korean specimens and holotype sequences were 0–0.4% in *psb*A and 0–1.2% in *rbc*L for *P. sinicarum*, and 0–0.1% in *psb*A and 0% in *rbc*L for *L. nagaokaense*. Previously, Min-Khant-Kyaw *et al.* (2024) reported intraspecific divergences of up to 0.5% in *psb*A and 0.4% in *rbc*L for *L. nagaokaense*, and the divergences observed in the Korean specimens were within these ranges. Intraspecific sequence divergences were not explicitly reported by Yan *et al.* (2025); however, our comparisons of GenBank sequences from specimens examined in their study, including the holotype QD344E (*psb*A: OQ943654; *rbc*L: OQ943756) and additional specimens listed in Table S2, revealed divergences of 0–0.9% in *psb*A and 0–3.6% in *rbc*L for *P. sinicarum*. In *Lithophyllum*, interspecific *rbcL* divergence of 1.9% was reported between *L. platyphyllum* (Foslie 1899: 13) Foslie (1900b: 26) and *L. pseudoplatyphyllum* Hernández-Kantún, W.H.Adey & P.W.Gabrielson (2016: 632) (Hernández-Kantún *et al.* 2016), whereas intraspecific *rbcL* divergence of up to 0.9% was reported for *L. neo-okamurae* (Kato *et al.* 2022a). The maximum *rbc*L divergence of 1.2% between Korean specimens and the holotype sequence of *P. sinicarum* is relatively high but falls within the sequence variation observed among Chinese specimens identified as *P. sinicarum* by Yan et al. (2025). Considering the phylogenetic placement and morpho-anatomical characteristics of the Korean specimens, the available evidence supports their identification as *P. sinicarum*, although further studies are needed to clarify species boundaries and genetic variation within the genus.

Korean material identified here as *Pseudoderma* sp. 1 forms a well-supported clade in the *psb*A analyses together with sequences previously designated as *Pseudoderma* sp. 6 from China (GenBank accessions: PP598288 and PP598310; Yan *et al.* 2025) and *Lithophyllum* sp. from Japan (GenBank accessions: MZ438316, MZ438356 and MZ438343; Peña & Torres 2021). The low divergence among these lineages (0.5–0.9%) suggests that they represent a single, genetically coherent lineage distributed across the Northwest Pacific. These sequences were assigned to different genera in previous regional studies, likely reflecting the high morpho-anatomical similarity among Lithophylloideae taxa (Van der Merwe & Maneveldt 2016; Torrano-Silva *et al.* 2018). Further integrative phylogenetic and taxonomic investigation of this clade is thus needed (Hernández-Kantún *et al.* 2015; Maneveldt *et al.* 2019; Kato *et al.* 2022a). Future studies should include detailed morpho-anatomical comparisons and, where possible, sequence data from type or topotype material of taxa potentially related to this lineage (Hernández-Kantún *et al.* 2015; Wade *et al.* 2023).

Morpho-anatomical variation in *Pseudoderma* and diagnostic implications

Overall, the Korean specimens of *P. sinicarum* and *L. nagaokaense* are morpho-anatomically consistent with those of the original descriptions of these species from China and Japan, respectively. However, the Korean specimens of *P. sinicarum* revealed additional morpho-anatomical variation not documented in the original description (Tables 1 and 2).

Traditional taxonomic concepts distinguished *Lithophyllum* and *Titanoderma* using a combination of hypothallial cell type and thallus construction (Chamberlain 1991, 1996; Chamberlain & Irvine 1994). *Lithophyllum* was characterized by the absence or limited persistence of bistratose margins and mainly non-palisade hypothallial cells, whereas *Titanoderma* was characterized by persistent bistratose margins and predominantly palisade hypothallial cells, except in reproductive or overgrowing portions (Chamberlain 1991, 1996; Chamberlain & Irvine 1994; Van der Merwe & Maneveldt 2016; Lee *et al.* 2026a). In this context, Yan *et al.* (2025) characterized *Pseudoderma* by bistratose margins with non-palisade hypothallial cells, distinguishing it from the *Lithophyllum/Titanoderma* complex.

The Korean specimens of *P. sinicarum* exhibited bistratose margins and possessed both palisade and non-palisade hypothallial cells. Furthermore, the persistence of bistratose construction varied among *P. sinicarum* thalli, with some thalli exhibiting a relatively uniform bistratose pattern, whereas others rapidly developed multistratose regions behind the margin (Figs. 3C, G, H). The co-occurrence of both cell types in *P. sinicarum* is consistent with variation previously reported in *Lithophyllum* by Woelkerling & Campbell (1992). However, those earlier observations were based solely on morpho-anatomical evidence and may have included cryptic species in the absence of molecular verification. These observations demonstrate that hypothallial cell type and thallus thickening patterns, traditionally used for generic delimitation in Lithophylloideae, can vary within a single species, highlighting the need to reassess their taxonomic significance.

Korean specimens of *P. sinicarum* also possessed longer subepithallial and perithallial cells than Chinese material (Yan *et al.* 2025). Subepithallial initials in Korean specimens ranged from 7 to 35 μm in length and perithallial cells from 7 to 48 μm in length, with upper limits nearly twice those of Chinese material (6 to 17 μm and 12 to 27 μm, respectively). These discrepancies may reflect differences in cell selection and measurement criteria, including section orientation and developmental position (Woelkerling & Campbell 1992), as cell dimensions may also be influenced by ontogenetic stage, environmental conditions, or individual variation (Peña *et al.* 2020; McCoy *et al.* 2023). Because factors such as cell selection, section orientation, and measurement criteria can be standardized, consistent, fine-scale morpho-anatomical examination may help separate methodological variation from biological variation (Korshunova *et al.* 2019). Collectively, these anatomical observations underscore the value of morpho-anatomical approaches for refining species boundaries and understanding intraspecific morphological plasticity in Lithophylloideae (Farr *et al.* 2009; Rösler *et al.* 2016; Lee *et al.* 2026b).

In addition, the occurrence of a calcified hump and columellar structure in *P. sinicarum* warrants further consideration. Yan *et al.* (2025) reported a calcified hump in Fig. 5j, but its structural extent remains unclear across Figs. 5j–m of the tetrasporangial conceptacle. In the present study, we use the term "calcified hump" to describe a convex-upward floor of the conceptacle chamber, whereas filamentous structures arising from the conceptacle floor are treated separately as a "columella," following the classical usage of Woelkerling (1988), Irvine & Chamberlain (1994), and Basso *et al.* (2014). However, the structural extent denoted by "columella" is not always clearly defined, particularly where a convex conceptacle floor or calcified hump is present (Basso *et al*. 2014). For example, Basso *et al.* (2014) used the term columella in association with a convex-upward conceptacle floor while also referring to a central columellar structure. These differing usages suggest that the terms calcified humps, convex conceptacle floors, central columella and columella-like structures, remain inconsistently used. Further comparative anatomical observations are needed to clarify their structural limits and potential taxonomic significance.

Rather than reflecting an intrinsic limitation of morphology, morpho-anatomical ambiguity within Lithophylloideae may stem from the uneven accumulation of molecular and type-anchored data across the subfamily (Yan *et al.* 2024, 2025). Taxonomic studies within Lithophylloideae have focused on thick-crust and rhodolith-forming taxa, for which extensive molecular and type-based data are available (Kato *et al.* 2022a; Gomes *et al.* 2024; Min-Khant-Kyaw *et al.* 2024), while such data remain limited for taxa with thin crustose thalli (Yan *et al.* 2025). Consequently, taxonomic boundaries remain poorly resolved for many Lithophylloideae lineages, making it difficult to determine whether morpho-anatomical characters are consistent within molecularly defined groups (Bittner *et al.* 2011; Richards *et al.* 2014; Peña *et al.* 2020). Few Lithophylloideae species possessing palisade hypothallial cells have been characterized using molecular data linked to type material (Lyra *et al.* 2023; Yan *et al.* 2025; Lee *et al.* 2026a). Yan *et al.* (2025) used principal component analysis (PCA) to assess morpho-anatomical variation in *Pseudoderma* and *Titanoderma*, illustrating the potential complementary role of multivariate analyses in integrative species delimitation. The importance of integrating molecular and morpho-anatomical evidence is also illustrated in the Hapalidiales, where sequencing type-associated material, including the *Lithothamnion* generitype, helped clarify generic boundaries and provided a framework for reassessing morpho-anatomical characters across several genera (Jeong *et al.* 2021; Min-Khant-Kyaw *et al.* 2025, 2026).

Future taxonomic investigations within Lithophylloideae should prioritize lineages exhibiting high genetic divergence, uncertain species boundaries, or limited type-linked molecular data (Gomes *et al.* 2024), as well as ecologically important taxa such as rhodolith-forming species (Min-Khant-Kyaw *et al.* 2024; Lee *et al.* 2026b). Comprehensive sampling across diverse habitats and geographic regions, including the collection of reproductively mature specimens whenever possible, is essential for obtaining the molecular and morpho-anatomical evidence needed to resolve taxonomic uncertainties (Pezzolesi *et al.* 2019; Jeong *et al.* 2021; Kato *et al.* 2022b; Lee *et al.* 2026a). Broad molecular screening, including metabarcoding, may further assist in identifying overlooked lineages and guiding targeted collections for integrative taxonomic analyses (Lee *et al.* 2024; Fontana *et al.* 2026; van der Reis *et al.* 2026).

Diversity of Korean Lithophylloideae

Korean Lithophylloideae exhibit a broad ecological and morphological spectrum, ranging from diminutive epiphytic crusts to rhodolith-forming species of considerable structural complexity (Lee 2008; Lee *et al.* 2026a). Korean records of Lithophylloideae include *L. canescens*, *L. corallinae*, *L. dispar*, *L. shioense*, *L. tumidulum*, *L. yessoense*, and *P. whidbeyense*, which were listed as checklist records by Lee & Kang (2001), but remain unsupported by voucher-based revision or DNA sequence data from Korea (Lee *et al.* 2026a). These records indicate that a substantial portion of Korean Lithophylloideae diversity remains taxonomically unresolved.

Pseudoderma sinicarum represents the first epiphytic Lithophylloideae species from Korea to be confirmed by type-anchored molecular data. Among epiphytic species, four Lithophylloideae (*L. canescens*, *L. corallinae*, *L. dispar*, and *L. tumidulum*) are currently recognized from Korea (National Institute of Biological Resources 2026), yet these records are based on unsubstantiated checklist entries or brief regional accounts (Lee 2008). According to Baba & Kato (2023), these four species were distinguished in a Japanese account on the basis of growth habit, host specificity, and surface luster; however, the absence of DNA sequence data renders their taxonomic reliability uncertain. Given the high diversity of epiphytic NGCA documented from China (Yan *et al.* 2025), further systematic surveys are needed to characterize the epiphytic Lithophylloideae of Korea.

Among rhodolith-forming species, two Lithophylloideae (*L. neo-okamurae* and *L. okamurae*) are currently recognized from Korea (Lee *et al.* 2026b). The present study adds *L. nagaokaense* to the list of rhodolith-forming species documented from subtidal rhodolith beds in Korea. In addition to their close molecular affinity, the Korean specimens were morpho-anatomically consistent with Japanese *L. nagaokaense*, sharing attached or free-living thalli, the absence of trichocytes, triangular to square pore canals, similarly oriented enlarged roof cells, and closely overlapping vegetative and conceptacle dimensions (Min-Khant-Kyaw *et al.* 2024). The Korean specimens of *L. nagaokaense* examined here exhibited a columnar growth form. Notably, both *L. nagaokaense* and *L. neo-okamurae* exhibit columnar growth along Japanese coasts (Kato *et al.* 2022a; Min-Khant-Kyaw *et al.* 2024), whereas Korean *L. neo-okamurae* has been documented only in encrusting to fruticose forms (Kim *et al.* 2024; Lee *et al.* 2026b). This geographic difference in growth form suggests that thallus morphology may vary within species and should therefore be used cautiously as a species-level diagnostic character in *Lithophyllum* (Pezzolesi *et al*. 2017; Kim *et al.* 2024; Lee *et al.* 2026b).

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Data availability: Newly generated DNA sequences have been deposited in GenBank.

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