

Research Article

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Unveiling a novel species, *Pachymeniopsis shinchorai* sp. nov., from Korea, with reference to phylogenetic relationships within the Grateloupiaceae (Halymeniales, Rhodophyta)

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Abstract: Recent comprehensive phylogenetic and morphological analyses have led to the recognition of the Grateloupiaceae as a distinct family within the Halymeniales. Despite strong support for its monophyly, the genera within the Grateloupiaceae display diverse morphological traits and share external features that prevent accurate generic identification without additional molecular analyses. This study conducted detailed morphological observations and assessed the phylogenetic relationships of a *Grateloupia*-like species found in Korea, which superficially resembles "*G. imbricata*". We describe *Pachymeniopsis shinchorai* sp. nov., characterized by erect, compressed axes branching dichotomously to subdichotomously, maturing into a dome-shape thallus. This species is distinguished from related species by its densely arranged thallus, which forms a hemispherical shape, its abundant secondary attachments adhering to adjacent branches and the substratum, and its phylogenetic position in the *rbcL* tree. This species contributes to the biodiversity of the intertidal zone on Jeju Island, Korea. Our phylogenetic analysis confirms the monophyly of nine clades within the Grateloupiaceae and underscores the need for further studies to resolve the generic status of *Pachymeniopsis*, *Prionitis*, and *Phyllymenia*, which cannot be readily distinguished by morphological criteria alone. Due to the lack of support for several genera, comprehensive collections and multi-gene analyses are essential to accurately delineate the internal generic relationships within the family.

Keywords: Grateloupiaceae; morphology; *Pachymeniopsis*; phylogeny; *rbcL*

1 Introduction

Members of *Grateloupia* *sensu lato*, which belong to the order Halymeniales, have received considerable attention for both morphological and molecular analyses (Gargiulo et al. 2013; Montes et al. 2017; Rodríguez-Prieto et al. 2022). They exhibit a diverse range of morphological characters, from pinnate forms like *G. filicina* (J.V.Lamouroux) C. Agardh, designated as a lectotype species, to dichotomous forms such as *G. dichotoma* J.Agardh, and foliose blades as seen in *G. elliptica* Holmes. *Grateloupia* C.Agardh is the largest genus in the order Halymeniales, comprising 92 currently recognized species (Guiry and Guiry 2024). Another genus, *Phyllymenia* J.Agardh, was originally described from South Africa based on a single species, *Phyllymenia hieroglyphica* J.Agardh (later synonymized as *P. belangeri*; Setchell and Gardner 1936), characterized by foliose blades which range from simple and cuneate to lacerate (De Clerk et al. 2005). However, as *Phyllymenia* was described without comparison to other genera (Agardh 1848), its generic status has been debated and reassessed through both morphological and molecular studies (De Clerck et al. 2005; Gargiulo et al. 2013; Nguyen et al. 2023; Setchell and Gardner 1936). Similarly, *Prionitis* J.Agardh was initially described with nine species, with *Prionitis lanceolata* later designated as the lectotype (Schmitz 1889). The distinction between *Grateloupia*, *Phyllymenia*, and *Prionitis* and several related genera such as *Carpopeltis* Schmitz, *Cryptonemia* J.Agardh and *Polyopes* J.Agardh remains unclear due to overlapping morphological traits (Kawaguchi 1989). Subsequently, the genus *Pachymeniopsis* Yamada ex Kawabata was proposed to accommodate three Japanese species having foliose blades, with *Pachymeniopsis lanceolata* (Okamura) Yamada ex Kawabata as the type species. Among these groups, vegetative features such as overall habit and branching patterns show little

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taxonomic utility (Kim et al. 2021; Wang et al. 2001; Wilkes et al. 2005).

Historically, the auxiliary cell ampullae have been emphasized as a crucial characteristic for distinguishing genera within the Halymeniales (Chiang 1970; Gargiulo et al. 2013). To date, six types of auxiliary cell ampulla structure have been identified in this group. Chiang (1970) initially classified five types: *Grateloupia*-type, *Thamnochonium*-type, *Halymenia*-type, *Aeodes*-type, and *Cryptonemia*-type. Later, Lee and Kim (2019) introduced an additional type, the *Nesoa*-type. Extensive studies have focused on the development of ampullar structures both before and after fertilization in *Grateloupia sensu lato* (De Clerck et al. 2005; Kawaguchi 1989; Kawaguchi et al. 2001; Lin et al. 2008). Owing to similarities in these structures, several genera, including *Dermocorynus* P.Crouan et H.Crouan, *Pachymeniopsis*, *Phyllymenia*, and *Prionitis*, were either fully or partially merged into *Grateloupia* (De Clerck et al. 2005; Kawaguchi 1997; Wang et al. 2001; Wilkes et al. 2005). However, Gargiulo et al. (2013) later reinstated several genera based on combined evidence from *rbcL* phylogenies and reinterpretation of female reproductive structures. After that, newly described genera, such as *Neorubra* M.S.Calderon, G.H.Boo et S.M.Boo and *Mariaramirezia* M.S.Calderon, G.H.Boo et S.M.Boo, were phylogenetically clarified, having been previously recognized as *Grateloupia denticulata* and *Prionitis decipiens*, respectively (Calderon et al. 2014a, 2014b).

Recently, Kim et al. (2021) conducted a comprehensive molecular phylogenetic study on the order Halymeniales, analyzing 33 of 38 recognized genera, including 30 type species. Their findings strongly supported the segregation of the family Grateloupiaceae from Halymeniaceae, based on both phylogenetic data and distinct morphological characteristics, particularly in terms of female and tetrasporangial developments. The emended family Grateloupiaceae now comprises nine genera: *Grateloupia*, *Dermocorynus*, *Mariaramirezia*, *Neorubra*, *Pachymeniopsis*, *Kintokiocolax*, *Phyllymenia*, *Prionitis*, and *Yonagunia* Kawaguchi et Masuda (Kim et al. 2021). Among them, the genus *Pachymeniopsis* was originally delineated based on species such as *Pa. lanceolata*, *Pa. elliptica*, and *Pa. yendoi*, all of which exhibit a foliose blade form. The initial circumscription of this genus focused on vegetative anatomy (e.g. an outer cortex of dichotomously branched, anticlinal filaments of small cells linked by numerous secondary pit-connections, and an inner cortex of large cells that become larger and more stellate towards the medulla), female reproductive features (e.g., absence of pericarps surrounding the ostiolate cystocarps), and the arrangement of reproductive structures (e.g. carpogonial branch ampullae located in the transitional region between

outer and inner cortex, and cystocarps and tetrasporangia scattered over the thallus) (Kawaguchi 1997). Despite ongoing molecular studies, the generic criteria for *Pachymeniopsis* remain ambiguous due to the inclusion of both foliose blade and branching types within the *Pachymeniopsis* clade (Kim et al. 2014; Yang et al. 2015). Nevertheless, recent phylogenetic analyses have consistently demonstrated that *Pachymeniopsis* is well-resolved with high bootstrap values, confirming its distinct genetic identity within the Grateloupiaceae, including three currently recognized species (Calderon et al. 2014b; Gargiulo et al. 2013; Kim et al. 2021).

Korea is one of the most well-documented regions for the taxonomy of *Grateloupia sensu lato* (Kim et al. 2023; Lee et al. 2009; Yang et al. 2015). A detailed taxonomic study, including precise morphological investigations, delineated two foliose *Pachymeniopsis* species distributed in Korea (Lee and Lee 1993). Additionally, Yang and Kim (2015) employed DNA barcoding analysis to confirm the presence of 14 species within this region, including the description of *Pachymeniopsis volvita*. More recently, Kim et al. (2023) concentrated on *Grateloupia filicina*-like species in the Northwest Pacific, with a particular focus on refining the species distributions in Korea. Furthermore, since most species within *Grateloupia sensu lato* occur in the intertidal zone, they provide a valuable opportunity for the comprehensive phylogeographic studies aimed at exploring their population genetic structure (Yang et al. 2021a, 2021b). During a survey of intertidal macroalgae, an unidentified *Grateloupia* species was abundantly distributed on rocky substrata in Shinchon, Jeju, Korea, but had never been found anywhere else. To identify the species, we conducted phylogenetic analyses using both morphological and molecular methods. The aims of this study are: (i) to describe a new intertidal species of *Grateloupia sensu lato* from Korea based on detailed morphological observations, (ii) to resolve its taxonomic placement within the group through phylogenetic comparisons. This research enhances our understanding the diversity of *Grateloupia sensu lato* and supports the accurate documentation of marine biodiversity in the region.

2 Materials and methods

2.1 Sampling

The specimens of the unidentified species used in this study were collected in the intertidal zone at Shinchon, Jeju-si, Jeju Island, Korea (33°32'18"N, 126°37'15"E). When the populations were discovered, *in situ* photographs were taken. Several plants were first kept alive in a plastic cooler

and transported to the laboratory. Most collections were pressed fresh as herbarium specimens with serial numbers. Several remaining plants were preserved in 5 % formalin-seawater for morphological observations, whereas materials used in molecular studies were desiccated in silica gel. Pressed herbarium specimens are deposited in the Herbarium of Jeju National University (JNUB), Jeju and the National Marine Biodiversity Institute of Korea (MABIK), Seocheon, Korea.

2.2 Morphological observation

For morphological observations, sections were prepared manually using a razor blade or freezing microtome (Nippon Optical Works Co., Ltd., NH-101II, Tokyo, Japan). The sections were stained on slides with Wittmann's aceto-iron-hematoxylin-chloral hydrate and mounted in 50 % Hoyer's mounting medium, or with 1 % aqueous aniline blue acidified with 0.1 % HCl and mounted in 40 % Karo corn syrup. Photomicrographs of plant habit were captured with a TG-7 digital camera (Olympus, Japan), and anatomical images were taken using an Olympus BX51 microscope (Tokyo, Japan) with a Q-imaging digital camera (Burnaby, British Columbia, Canada).

2.3 Molecular analysis

Genomic DNA of samples was extracted from small portions of the upper branches using a MagPurix DNA Isolation Kit (Zinext Life Science, Taiwan), according to the manufacturer's instructions. The extracted DNA was stored at -20°C and underwent polymerase chain reaction (PCR) amplification using AccuPower PCR Premix (Bioneer, Korea) in final volume of 20 μl . To amplify the plastid *rbcL* and mitochondrial COI-5P portions from the total DNA, we used the primer sets F7-R898 and F762-R1442 for *rbcL* (Kim et al. 2010) and GazF2-GazR1 for COI-5P (Saunders 2005). PCR was performed on an All-In-One-cycler (Bioneer, Daejeon, Korea), as described by Yang et al. (2015). PCR products were visuallyyed on a 1 % agarose gel, then purified and sequenced by Macrogen Co. (Daejeon, Korea). Finally, five sequences were generated from the unidentified species. In addition, we obtained a sequence of *Grateloupia imbricata* from the same collecting site.

All successful amplifications of the gene were sequenced in both directions. Assembly and manual editing were performed using Geneious Prime v. 2022.2.2 (<http://www.geneious.com>). We downloaded *rbcL* sequences from GenBank to compare with representative taxa of the genera

within the Grateloupiaceae (Kim et al. 2021; Nguyen et al. 2023; Rodríguez-Prieto et al. 2022). Newly generated sequences were deposited in GenBank and combined with downloaded GenBank sequences. Sequences were aligned using the MISCLE algorithm in Geneious and used to infer the phylogenetic analyses. Outgroup was designated with *Halymenia durvillei*, *Halymenia dilatata*, and *Carpopeltis phyllophora*, which belong to the family Halymeniaceae.

To infer phylogenetic relationships, we conducted maximum likelihood (ML) method with the GTR substitution model in Geneious. We used 1,000 replications under the same model settings to generate the bootstrap values. Genetic divergences were calculated using MEGA-X ver. 10.0.5 (Kumar et al. 2018). We also performed the Bayesian inference (BI) with MrBayes v.3.2.1 software (Ronquist et al. 2012). Two independent searches were done under the default setting, such as four chains of Metropolis-coupled Markov Chain Monte Carlo, sampling every 100 trees, for 20 million generations, and the same evolution model (GTR + G) used in the ML search. The burn-in point was identified graphically by tracking the likelihood for plateau. Eventually, 14,700 trees sampled in the stationary state were used to infer Bayesian posterior probabilities (BPP).

3 Results

3.1 Molecular phylogeny

Phylogenetic analyses containing 95 sequences identified clades corresponding to the nine recognized genera of the Grateloupiaceae, including *Pachymeniopsis* (incorporating *Kintokiocolax*), *Prionitis*, *Phyllymenia*, *Neorubra*, *Grateloupia*, *Mariaramirezia*, *Dermocorynus*, *Yonagunia*, and an additional "*G.* *subpectinata* clade (=*G. subpectinata* group in Gargiulo et al. 2013) (Figure 1 and Supplementary Figures S1–S2). Specimens newly collected from Shinchon were phylogenetically positioned within the *Pachymeniopsis* clade, and did not correspond to any congeneric species (Figure 1). Consequently, we propose *Pachymeniopsis shinchonai* M.Y. Yang et M.S. Kim sp. nov. as a new member of the Grateloupiaceae from Korea. *Pachymeniopsis shinchonai* sp. nov. was resolved as a sister taxon to "*G. chiangii*" and "*G. cornea*" with an interspecific divergence of 1.9–3.0 % (ML Bootstrap [MLB] 94 %, Bayesian posterior probability [BPP] 1.0), but was distinctly separated from the morphologically similar "*G. imbricata*" (PV053169), which was sympatrically collected with the new species, by a divergence of 3.9 %.

The phylogenetic integrity of the Grateloupiaceae was robustly supported in both ML and BI trees (100 % MLB, 1.0 BPP), but support for the internal genera was variable

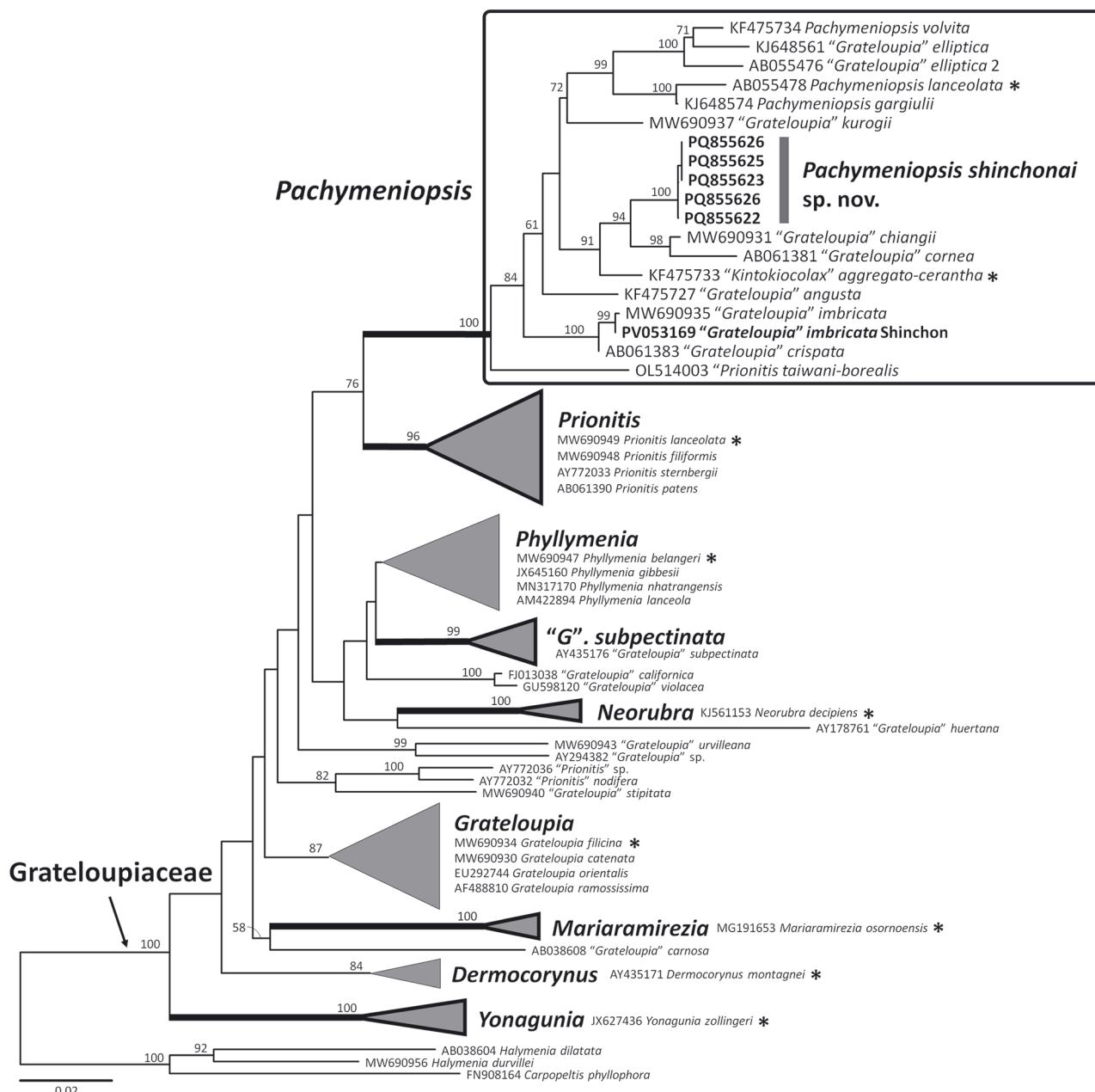


Figure 1: Phylogenetic tree of the Grateloupiaceae based on *rbcL* sequences, estimated using the maximum likelihood (ML) criterion. Clades labeled with a generic name include the type species for each genus. Grey triangles indicate a condensed representation of the clades related to *Pachymeniopsis*, with the selected sequences assigned to their respective genera. Bootstrap values are provided at each node to indicate the level of support, with thick black lines emphasizing genera that received strong bootstrap support (>95%). Asterisks (*) indicate the type species for each genus.

(Figure 1 and Supplementary Figures S1–S2). The monophyly of six clades – *Pachymeniopsis* (including *Kintokiocolax*), *Prionitis*, *Neorubra*, *Mariaramirezia*, *Yonagunia*, and “*G.* subpectinata” – received strong support (>95%). In contrast, the monophyly of *Grateloupia* and *Dermocorynus* was moderately supported (84–87% MLB), while *Phyllymenia* lacked support (Figure 1). The phylogenetic tree using the BI methods presented slightly different topologies compared to

those generated by the ML method (Supplementary Figure S2). Specifically, the clades of *Prionitis* and “*G.* subpectinata” are shown as sister taxa in the ML analysis (Figure 1), whereas *Neorubra* is positioned between these two genera in the BI analysis (Supplementary Figure S2). In the BI tree, the support for the monophyly of *Grateloupia* and *Dermocorynus* increased, but *Phyllymenia* still did not receive support.

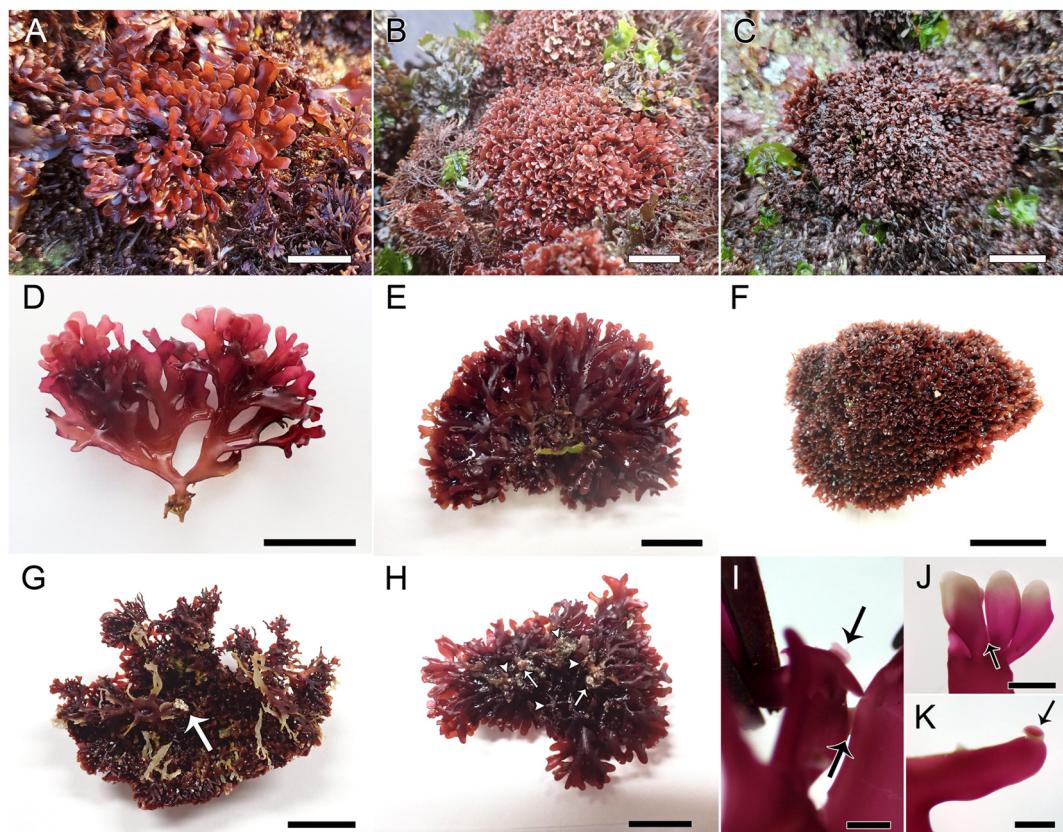


Figure 2: External morphology of *Pachymeniopsis shinchorai* M.Y. Yang et M.S. Kim sp. nov. (A–C) *In situ* habit of plants growing at Shinchon, Jeju Island, showing young plant collected February 13, 2024 (A), densely arranged thallus becoming hemispherical in form, collected July 6, 2024 (B), fertile plant collected November 27, 2023 (C). (D) A partial thallus detached from the mass showing dichotomous to sub-dichotomous branching pattern, collected February 13, 2024. (E) Ventral view of hemispherical thallus collected July 6, 2024. (F) Dorsal view of hemispherical thallus collected July 6, 2024. (G) Ventral view of thallus showing a main holdfast (arrow), collected August 22, 2024. (H) Ventral view of thallus showing two holdfasts (arrows) and several secondary attachments (arrowheads), collected August 22, 2024. (I–K) Branches adhering to adjacent branches by secondary attachments (arrows). Scale bars = 2 cm (A–C, F, G), 1 cm (D–E, H), and 0.2 cm (I–K).

3.2 Description of a new species

Pachymeniopsis shinchorai M.Y. Yang et M.S. Kim sp. nov. (Figures 2–4).

3.2.1 Description

Thalli erect and epilithic with discoid holdfast; cartilaginous and up to 2–6 cm long; red to dark red; composed of 3–6 (–10) compressed main axes, 1–2 mm wide, dichotomously to subdichotomously branched in 3–4 orders with blunt apices; densely arranged and overlapped forming a hemispherical mass; often attached to adjacent branches or branchlets through secondary attachments. Thallus structure multiaxial, composed of cortical and medullary layers; thickness varied from 220 to 280 μm in the upper parts of branches, 350–380 μm in middle, and 400–450 μm in the lower parts of the thallus; outer cortex rounded to

oblong, 5–8 μm in diameter, with 4–7 cells layers; subcortical cells loosely arranged, rounded to oblong, 8–12 μm in diameter; medulla densely arranged with tubular filaments, 15–35 μm long. Gametophytes and tetrasporophytes were isomorphic. Tetrasporangia transversely divided; restricted on circular proliferations; 11–13 μm wide and 40–55 μm long. Cystocarps confined to circular proliferations; non-procarpic; spherical to ovoid carposporangia, 9–15 μm wide by 10–12 μm long; gonimoblasts 110–150 μm in diameter.

3.2.2 Holotype

Designated here MABIK AL00100769, vegetative, Shinchon, Jeju-si, Jeju Island, Korea (33°32'18"N, 126°37'15"E), 06 July 2024, deposited in the herbarium of National Marine Biodiversity Institute of Korea (MABIK). GenBank accession Number: PQ855622 for *rbcL*; PV053166 for *COI-5P*.

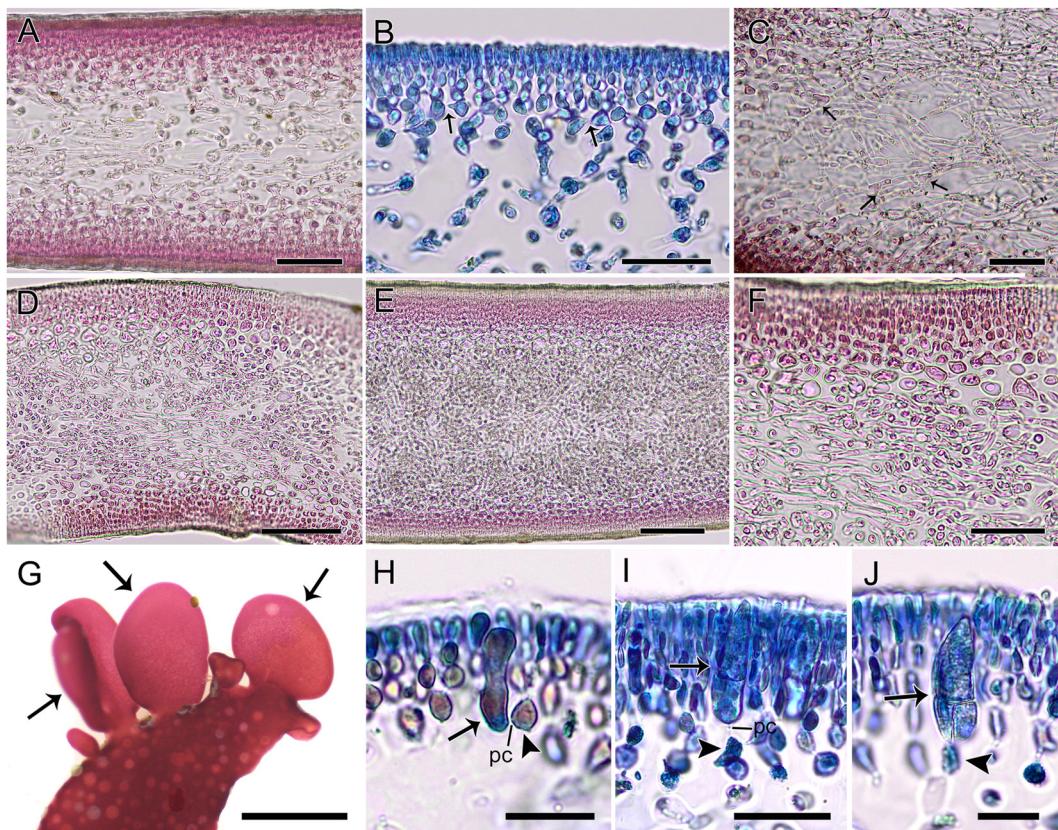


Figure 3: Vegetative structure and development of tetrasporangia of *Pachymeniopsis shinchonai* M.Y. Yang et M.S. Kim sp. nov. (A) Transverse section through a young branch showing the cortex and medulla. (B) Detail of cortex showing cellular cortex composed of five-cells and a network of stellate inner cortical cells. Note secondary pit-connections appear between adjacent cortical cells (arrows). (C) Longitudinal section through a young branch showing entangled tubular medullary cells with numerous branches (arrows). (D) Transverse section through middle part of a thallus showing enlarged sub-cortex and densely filled medulla. (E) Transverse section through basal part of a thallus showing a thickened cortex and dense medulla. (F) Cortex of basal part of a thallus showing a thickened cortex composed of six to seven cell layers. (G) Tetrasporangia restricted to the proliferations (arrows). (H) Tetrasporangia initial (arrow) born laterally on inner cortical cell (arrowhead) connected by pit connection (pc). (I) A transverse division of developed tetrasporangium (arrow), which is basally connected to inner cortical cell (arrowhead) by pit connection (pc). (J) Cruciate division of tetrasporangium (arrow), still basally connected to inner cortical cell. Scale bars = 60 μ m (A), 40 μ m (B, I), 50 μ m (C, F), 100 μ m (D, E), 1 mm (G), and 20 μ m (H, J).

3.2.3 Isotype

JNUB-240706-2, vegetative, Shinchon, Jeju-si, Jeju Island, Korea, 06 July 2024, deposited in the herbarium of Jeju National University (JNUB). GenBank accession Number: PQ855623 for *rbcL*; PV053167 for *COI-5P*.

3.2.4 Etymology

The specific epithet ‘*Shinchon*’ refers to the type locality in Shinchon, Jeju, Korea, and ‘*ai*’ means children in Korean language as this alga was initially collected by children from Shinchon Elementary School. Therefore, the name literally means ‘Shinchon children’.

3.2.5 Korean name

덩이개도박 (Deongigaedobak).

3.2.6 Other specimens examined

May 6, 2023 (vegetative); July 1, 2023 (vegetative); July 3, 2023 (vegetative); October 13, 2023 (vegetative); November 27, 2023 (vegetative); February 13, 2024 (vegetative); April 21, 2024 (vegetative); April 24, 2024 (vegetative); June 23, 2024 (vegetative); July 6, 2024 (vegetative); August 17, 2024 (female); August 22, 2024 (female & tetrasporic). All specimens are collected from Shinchon, Jeju-si, Jeju Island, Korea.

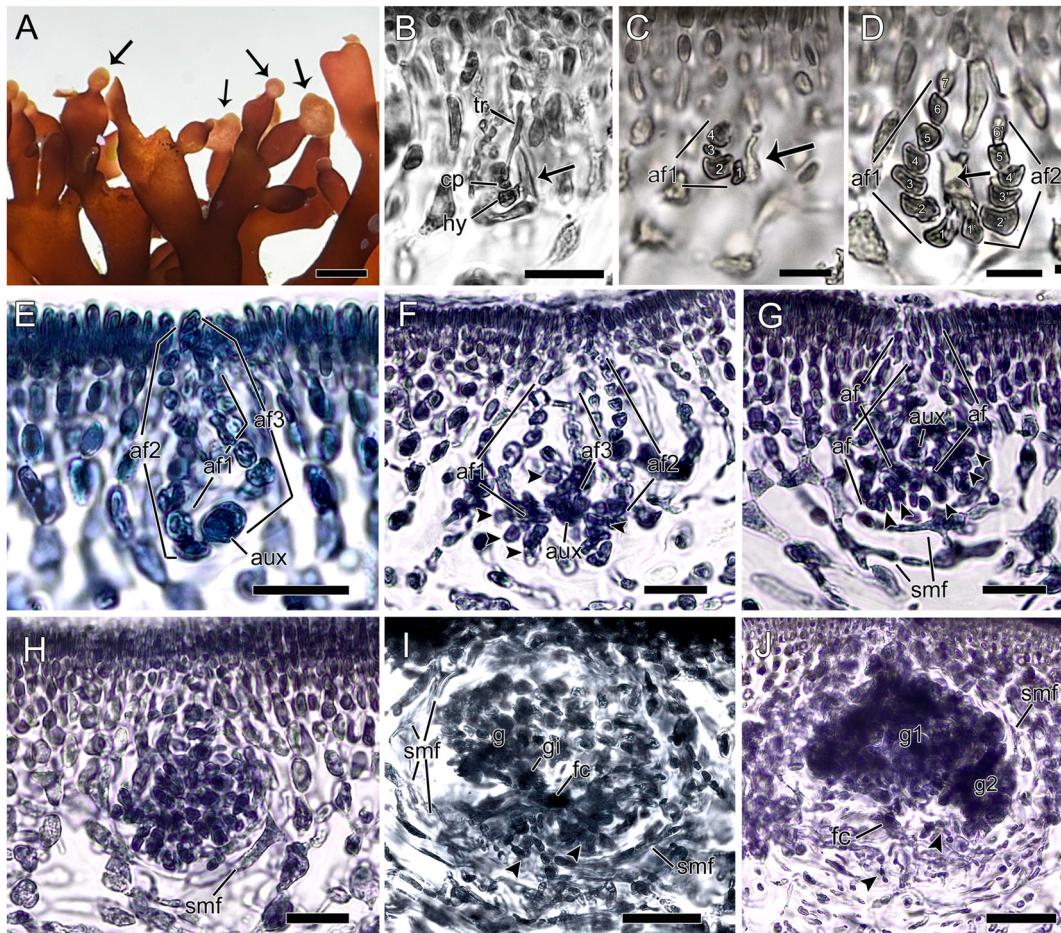


Figure 4: Female reproductive structure of *Pachymeniopsis shinchorai* M.Y. Yang et M.S. Kim sp. nov. (A) Cystocarp-bearing proliferations (arrows) showing circular to widely expanded shapes. (B) Two-celled carpogonial branch composed of a carpogonium (cp) with a long trichogyne (tr), and hypogenous cell (hy) borne on an elongated cortical cell (arrow). (C) Auxiliary cell ampulla showing the four-celled stage of a first-order ampullar filament (af1) borne on an elongated cortical cell (arrow). (D) Further development of first-order (af1, labeled 1–7) and second-order (af2, labeled 1'–6') ampullar filaments. (E) A later stage showing the third-order filament (af3) and auxiliary cell (aux). (F) Early post-diploidization showing the auxiliary cell (aux) and three ampullar filaments (af1–af3), which bear branches of each of the ampullar filaments (arrowheads). (G) A later stage of (F) showing the auxiliary cell (aux) enclosed by ampullar filaments (af1–af3) and numerous branches of the ampullar filaments (arrowheads). Note secondary medullar filaments (smf) surrounding the whole cystocarp. (H) Highly branched ampullar filaments and remnants of secondary medullar filaments (smf) surrounding the cystocarp. (I) Carposporophyte showing the gonimoblast initial (gi) producing gonimoblasts (g) and formation of fusion cell (fc). Note remaining branched ampullar filaments (arrowheads) and secondary medullar filaments (smf) forming the pericarp. (J) Gonimogloves (g1, g2) differentiating into carposporangia and remains of secondary medullar filaments (smf) forming the pericarp. Scale bars = 1 mm (A), 20 μ m (B, C, E–H), 10 μ m (D), and 40 μ m (I, J).

3.2.7 Distribution

The species has been found only in Shinchoron, Jeju Island, Korea until date.

3.2.8 Habit and vegetative morphology

Thalli are erect, up to 2–6 cm long, from discoid holdfasts. They consist of 3–6 (–10) compressed main axes, each 1–2 mm wide (Figure 2A–C). Thallus is cartilaginous, red to dark red in color. The margins of the axes slightly curve

inwards (Figure 2D). Main axes are dichotomously to sub-dichotomously branched in 3–4 orders, with blunt apices (Figure 2D and E). As they age, the thalli become densely arranged and overlap, forming a subspherical to hemispherical mass (Figure 2F) originating from single or 2–3 holdfasts (Figure 2G and H). Thalli often form secondary attachments to adjacent branches or branchlets (Figure 2I–K), enhancing adhesion both between the branches and to the substratum. Thallus structure is multiaxial (Figure 3A–F) and composed of cortical and medullary layers (Figure 3A). The thallus thickness varies, measuring 220–280 μ m in the

upper parts of branches, 350–380 μm in middle, and 400–450 μm in the lower parts of the thallus. The outer cortex consists of anticlinal filaments, which are rounded to oblong and 5–8 μm in diameter, with 4–5 cell layers in upper branches (Figure 3A and B) and 6–7 cell layers in lower part of thallus (Figure 3D–F). Secondary pit-connections between adjacent cell rows are frequently observed in this layer (Figure 3B). Subcortical cells are loosely arranged, rounded to oblong, measure 8–12 μm in diameter (Figure 3B). The medulla is densely arranged with tubular filaments in longitudinal sections, featuring oblong cells, 15–35 μm long (Figure 3C). Medullary filaments are secondarily pit-connected and occasionally branch to form a network (Figure 3C).

3.2.9 Reproductive morphology

Gametophytes and tetrasporophytes were isomorphic. Gametophytes are morphologically similar to tetrasporophytes. Tetrasporangial sori are restricted on circular proliferations (Figure 3G). Tetrasporangial initials are cut off laterally from subcortical cells in the cortex, elongate, and are pit-connected (Figure 3H). They initially divide transversely, with the tetrasporangium basally pit-connected with the subcortical cell (Figure 3I), and subsequently divide longitudinally to form cruciate arranged tetraspores (Figure 3J). Mature tetrasporangia are 11–13 μm wide and 40–55 μm long.

Cystocarps are confined to circular proliferations at the distal end of branchlets, which commonly become broader than the branchlets (Figure 4A). Gonioblasts are visible directly under a dissecting microscope as transparent dots without the need for sectioning (Figure 4A). The female reproductive system is non-procarpic, which means the auxiliary cells and carpogonial branches arise from separate cortical filaments, termed carpogonial branch ampullae (Figure 4B) and auxiliary cell ampullae (Figure 4C–F). Carpogonial branches are rare and borne on a supporting cell, and two-celled, including the hypogynous cell and carpogonium with a terminal trichogyne (Figure 4B). Auxiliary cell ampullae are more abundant than the carpogonial branch ampullae and composed of three orders of ampullar filaments. Initially, the first order of ampullar filaments in auxiliary cell ampullae is produced laterally from a subcortical cell (Figure 4C). Afterwards, the initial of the second-order ampullar filament is produced from the basal cell of the first order of ampullae filament (Figure 4D). The ampullar filaments in fully developed auxiliary cell ampullae are unbranched, 8–12 cells long, and the basal cell of the third ampullar filament enlarges and becomes darkly stained, functioning as the auxiliary cell (Figure 4E). Direct

diploidization was not seen. After diploidization, the cell of the ampullar filaments branch once or twice (Figure 4F). Secondary medullary cells are then produced from surrounding vegetative cells (Figure 4G), and subsequently envelop the cystocarp. The branched ampullar filaments branch a few more times to form a cluster (Figure 4H). The secondary medullary filaments become pit-connected to the cortical layers (Figure 4G–I). The auxiliary cell produces a gonimoblast initial and subsequently fuses with its neighboring ampullar cell (Figure 4I), which is not branched. As the development of gonimoblast continues, a cavity is formed around the developing gonimoblasts (Figure 4I). One or two gonimogloves are produced from a gonimoblast initial and mature gonimoblasts are up to 110–150 μm in diameter (Figure 4J). Most cells of gonimoblasts differentiate into spherical to ovoid carposporangia, 9–15 μm wide by 10–12 μm long (Figure 4J). The cystocarp is imbedded in the thallus and has a distinct ostiole.

The male reproductive structure was not observed.

4 Discussion

The Grateloupiaceae is a species-rich family that still requires further investigation to resolve its non-monophyletic genera. Recent extensive molecular studies have demonstrated several strongly supported genera within Grateloupiaceae, including *Pachymeniopsis*, *Prionitis*, *Neorubra*, *Yonagunia*, *Dermocorynus*, and *Mariaramirezia* (Kim et al. 2021). Despite the strong phylogenetic support for these genera, members of these genera often exhibit diverse morphological traits and share external features, highlighting the need for additional molecular analyses to ensure accurate identification at the generic levels (Calderon et al. 2014b; Kim et al. 2014; Lin et al. 2008, 2011; Nguyen et al. 2023). In this study, our molecular analyses combined with morphological observation have revealed the existence of a novel species within *Pachymeniopsis*, namely, *P. shinchorai* sp. nov. from Korea.

The new species was initially presumed to be a member of *Grateloupia*, due to its morphological resemblance to “*G. imbricata*” and “*G. crispata*”, with flattened blade branching dichotomously (Yoshida 1998 as *Pr. imbricata* and *Pr. crispata*). The phylogenetic analyses revealed that the new species belongs to the *Pachymeniopsis* clade, which has been recognized as a distinct genus supporting the monophyly with the type species (Calderon et al. 2014a, 2014b; Gargiulo et al. 2013; Kim et al. 2021). In the phylogenetic tree (Figure 1), the clade of *Pachymeniopsis* consists of 13 species that exhibit two thallus types; (1) branching forms as seen in *Pa. shinchorai* sp. nov., “*G. cornea*”, “*G. chiangii*”, “*G. angusta*”,

“G”. *imbricata*, “G”. *crispata*, and “Pr”. *taiwani-borealis* (Kawaguchi 1989; Okamura 1937; Rodríguez-Prieto et al. 2022; Yoshida 1998), and (2) foliose blade forms, as seen in *Pa. lanceolata*, “G”. *elliptica*, *Pa. volvita*, *Pa. gargiuloi*, and “G”. *kurogii* (Kawaguchi 1990, 1997; Yang et al. 2015; Yoshida 1998), except for the parasite *Kintokiocolax aggregatocerantha*. Interestingly, all species within the *Pachymeniopsis* clade are native to Asia. Although several species, such as “G”. *imbricata*, *Pa. lanceolata*, and *Pa. gargiuloi*, have been artificially introduced to Europe, America, and New Zealand (D’Archino et al. 2021; García-Jiménez et al. 2008; Montes et al. 2016, 2017; Verlaque et al. 2005), most species in the clade were originally described from Japan, Korea, and Taiwan (Guiry and Guiry 2024).

Among the species in the clade, *Pa. shinchorai* sp. nov. shares similarities with other related species exhibiting branching forms, particularly “G”. *imbricata*, “G”. *crispata*, and “Pr”. *taiwani-borealis* (Kawaguchi 1989; Okamura 1937; Rodríguez-Prieto et al. 2022; Yoshida 1998), in terms of their diochotomously to subdichotomously branched thallus, vegetative anatomical features, and the development and size of the tetrasporangium (Table 1). Notably, *Pa. shinchorai* sp. nov. most closely resembles “G”. *crispata*, sharing the crowded, overlapped apical portion that forms a hemispherical-shaped appearance (Kawaguchi 1989; Yoshida 1998). However, *Pa. shinchorai* sp. nov. is distinguished by its formation of abundant secondary attachments that contribute to a firmly arranged hemispherical shape by adhering not only to adjacent branches but also to the substratum, a feature not developed in “G”. *crispata*. In contrast, *Pa. shinchorai* sp. nov. differs from “G”. *imbricata*, which also exhibits a flabellate appearance but without overlapped branches (Yoshida 1998). Furthermore, the reproductive structure (i.e. tetrasporangia and cystocarps) of *Pa. shinchorai* sp. nov. are restricted to circular proliferations that become wide and sometimes bifurcate when fully mature, whereas in other related species, the tetrasporangia are scattered across the thallus or branches, as seen in “G”. *imbricata* (Okamura 1937), or are located at the tips of the branches, as in “G”. *crispata*, “G”. *cornea*, “G”. *chiangii*, and “Pr”. *taiwani-borealis* (Kawaguchi 1989; Rodríguez-Prieto et al. 2022; Yoshida 1998).

Female reproductive features, such as the number of cells in carpogonial branch ampullae and the type of auxiliary cell ampullae, are key distinguishing characteristics among genera in the Halymeniales (Calderon et al. 2014b; Gargiulo et al. 2013; Lin et al. 2008; Rodríguez-Prieto et al. 2022). Of the six types of auxiliary cell ampullae identified by Chiang (1970) and later expanded by Lee and Kim (2019), *Pa. shinchorai* sp. nov. exhibits *Grateloupia*-type, which features a simple ampillary filament structure composed of

three orders of ampillary filaments (Figure 4). The *Grateloupia*-type auxiliary cell ampullae are a characteristic found in members of the Grateloupiaceae (Kim et al. 2021). Within the Grateloupiaceae, Lin et al. (2008) proposed two distinct patterns of auxiliary cell ampullae development; (1) *G. taiwanensis* type, characterized by ampullae consisting of three orders of unbranched filaments that branch after diploidization of the auxiliary cell, and (2) the *G. orientalis* type, in which the ampullae are composed of two orders of unbranched filaments, with only a few cells incorporated into a basal fusion cell after diploidization of the auxiliary cell. Our observation of *Pa. shinchorai* sp. nov. revealed the presence of three orders of unbranched ampillary filaments that divide several times to form a cellular cluster (Figure 4), which aligns with the *G. taiwanensis* type. This type of auxiliary cell ampullae development has also been found in *Pa. lanceolata* (Kawabata 1962; Kawaguchi 1997), “G”. *elliptica* (Kawabata 1962), “G”. *kurogii* (Kawaguchi 1990), “G”. *angusta* (Kawaguchi 1989), “Pr”. *taiwani-borealis* (Rodríguez-Prieto et al. 2022), which are included in the *Pachymeniopsis* clade, and “G”. *patens* and “G”. *schmitziana* (Kawaguchi 1989), of the *Prionitis* clade, as well as *Ph. gibbesii* (Rodríguez-Prieto et al. 2022), *Ph. taiwanensis* (Lin et al. 2008), *Ph. nhatrangensis* (Nguyen et al. 2023), and “G”. *sparsa* (Kawabata 1963) of the *Phyllymenia* clade. Currently, the *G. orientalis* type of auxiliary cell ampullae is recognized as characteristic of the *Grateloupia* clade (Lin et al. 2008, Rodríguez et al. 2022).

The generic distinctions among *Pachymeniopsis*, *Prionitis*, and *Phyllymenia* are obscure when molecular data are excluded, and this historically led to their merger with *Grateloupia* (Kawaguchi 1997; Wang et al. 2001). These genera exhibit similar auxiliary cell ampullae (*G. taiwanensis* type), as previously mentioned, and lack consistent diagnostic characteristics both superficially and anatomically (Kim et al. 2023). However, a large-scale phylogenetic analysis of the Halymeniales using *rbcL* data has strongly supported the separation of *Pachymeniopsis* and *Prionitis* as distinct genera, while *Phyllymenia* remains unsupported (Kim et al. 2021), findings that are corroborated by this study (Figure 1, Supplementary Figures S1–S2). Recently, Rodríguez et al. (2022) suggested that the clade including “G”. *subpectorata* and *Dermocorynus dichotomus* belong to the *Phyllymenia* clade, based on concatenated *rbcL* and LSU rDNA data, which received high support. However, our study, dealing with the full range of analyzed taxa within the Grateloupiaceae (Kim et al. 2021), reveals instability of *Phyllymenia*, notably the node splitting with *Neorubra* in the middle in the BI tree (Supplementary Figure S2).

In contrast, the generic status of *Pachymeniopsis* and *Prionitis* are stable in both ML and BI trees (Supplementary

Table 1: Comparison of morphological characters between *Pachymeniopsis shinchorai* sp. nov. and phylogenetically related species.

Morphological characters	<i>Pachymeniopsis shinchorai</i>	<i>'Grateloupia' imbricata</i>	<i>'Prionitis' taiwan-borealis</i>	<i>'Grateloupia' crispata</i>	<i>'Grateloupia' cornea</i>	<i>'Grateloupia' chiangii</i>
Habit	Erect, flattened blade branched dichotomously to subdichotomously, hemispherical appearance	Erect, flattened blade branched dichotomously or irregularly, fan-like appearance	Prostrate, compressed blade branched subdichotomously	Erect, flattened blade branched dichotomously, hemispherical appearance	Erect, linear and compressed blades branched dichotomously	Erect, linear and compressed blades branched dichotomously, flatellate appearance
Color	Red to dark red	Yellowish brown to dark red	Red to dark red, yellowish in the distal end of branches	Purplish red, or sometimes greenish, or yellowish	Bright red to purplish red	Red to purplish red
Thallus height	Up to 6 cm	Up to 10 cm	Up to 5 cm	Up to 6 cm	Up to 30 cm	Up to 15 cm
Blade width	1–2 mm	7–15 µm	1–1.5 mm	2–8 mm	Up to 2 mm	Up to 8 mm
Apices	Blunt	Blunt	Acute to blunt	Blunt and often bifurcate	Acute and bifurcate	Blunt and often bifurcate
Thallus thickness	220–450 µm	300–400 µm	480–550 µm	500 µm	400–600 µm	650 µm
Cortex	8–11 cell layers, laterally connected by secondary pit-connections	4–6 cell layers, laterally connected by secondary pit-connections	8–9 cell layers, laterally connected by secondary pit-connections	11 cell layers, laterally connected by secondary pit-connections	7–8 cell layers in upper and 17 cell layers in lower, laterally connected by secondary pit-connections	8–12 cell layers, laterally connected by secondary pit-connections
Medulla	Simple or branched, densely arranged filaments	Densely arranged filaments	Densely arranged filaments	Simple or branched filaments	Densely arranged filaments	Simple or branched, densely arranged filaments
Position of tetrasporangia	On the circular proliferations	Scattered over the thallus	Scattered over the distal ends of branchlets or on the swollen apices	On the distal end of branchlets or on the swollen apices	On the distal end of branches or proliferations	On the distal end of branches
Size of tetrasporangium	11–13 × 40–55 µm	13–18 × 43–55 µm	10–11 × 46–52 µm	11–12 × 42–45 µm	13–17 × 40–48 µm	13–17 × 40–52 µm
Cystocarps	On the circular proliferations	Scattered over the thallus	Scattered over the distal ends of branches or the swollen apices as sorus-like groups	On the distal end of branches	On the distal end of branches and proliferations as sorus-like groups	On the distal end of branches as sorus-like groups
Pericarp	Secondary medullary filaments	N/A	Secondary medullary filaments	Poorly developed	Vegetative cells and ampullar filament	Vegetative cells and ampullar filament
Habitat	Rocky lower intertidal zone or tide pools	Rocky lower intertidal zone	Shallow coral reef or rocky shores or 2–12 m in depth	Rocky lower intertidal zone or tide pools	Rocky lower intertidal zone to upper subtidal zone	Rocky lower intertidal zone
References	This study	Okamura 1937; Yoshida 1998	Rodríguez-Prieto et al. (2022)	Kawaguchi 1989; Yoshida 1998 (as <i>Prionitis crispata</i>)	Okamura 1937; Kawaguchi 1989 (as <i>Prionitis cornea</i>)	Kawaguchi 1989 (as <i>Prionitis divaricata</i>)

N/A, not applicable.

Figures S1–S2), which strongly support their monophyly. Unfortunately, this study does not identify clear morphological characteristics that distinctly separate the two genera, as each encompasses a mixture of species with variable morphological features. Additionally, different views among researchers regarding the interpretation of the origin of the auxiliary cells, supporting cell, and involucral filaments (=nutritive filaments) have contributed to confusion (Chiang 1970; Gargiulo et al. 2013; Lin et al. 2008; Rodríguez-Prieto et al. 2022). Given the monophyly of the Grateloupiaceae, further examination of the internal genetic relationships within family is required, necessitating comprehensive collections and multi-gene analyses. However, it is crucial that these analyses encompass all recognized taxa within the group to avoid misinterpretation (Kim et al. 2023).

Compared to other related genera, members of *Pachymeniopsis* are primarily distributed in Asia, particularly in Korea, Japan, and China (Guiry and Guiry 2024). Korea and Japan share the distribution of most *Pachymeniopsis* species, though several species such as “*G.* chiangii”, “*G.* cornea”, and “*G.* crispata” have been identified only in Japan, based on molecular evidence (Yang and Kim 2015). In Korea, the taxonomy of Grateloupiaceae has been extensively explored using molecular data (Kim et al. 2021, 2023; Lee et al. 2009, Yang and Kim 2015), as they are significant component of the macroalgal ecosystem, with 15 species confirmed to occur (Yang and Kim 2015). The discovery of *Pa. shinchorai* sp. nov. in Korea is remarkable, as this species is restricted to a narrow intertidal zone in Shinchor, Jeju Island, despite its abundant populations. Given its confined habitat, ongoing monitoring is essential to protect *Pa. shinchorai* sp. nov. from potential threats of habitat destruction.

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Bionotes



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