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Gracilaria khanjanapajiae sp. nov. (Gracilariales, Rhodophyta) from the Andaman coast of Thailand

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ABSTRACT

Taxonomy and diversity of the Gracilariaceae has been increasingly investigated by using integrated morphological and genetic approaches. The Indo-Pacific is likely a hotspot for diversity of these macroalgae. Collections of flattened *Gracilaria* samples from Natai beach, Andaman coast of Thailand, were morphologically and genetically analysed. Our results clearly indicated the presence of a new species, *G. khanjanapajiae* sp. nov., in Thailand. In comparison to other known Indo-Pacific flattened species, *G. khanjanapajiae* can be distinguished by its dentate blade margin, deep spermatangial conceptacles (*verrucosa*-type) and numerous lateral and basal nutritive filaments within mature cystocarps. This new species resembles *G. srilankia* in having similar branching pattern and male reproductive structures, but differs in blade margin features. Phylogenetically, *G. khanjanapajiae* was more closely related to *G. spinulosa* from Taiwan than other Thai and Indian Ocean species. This present study highlights the continuing discovery of *Gracilaria* diversity and distribution in the tropical Indo-Pacific.

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Agarophyte; Phylogeny; *rbcl*; Seaweed; Systematics; Taxonomy

INTRODUCTION

The family Gracilariaceae is composed of at least nine genera with approximately 250 species worldwide (Guiry & Guiry 2021). The Gracilariaceae have received attention largely because of their commercial and medical properties (Alemañ *et al.* 2019; Torres *et al.* 2019). Additionally, taxonomic and systematic research of this family have advanced greatly with the incorporation of DNA data, although the generic taxonomy remains controversial (Gurgel *et al.* 2018, 2020; Lyra *et al.* 2021b), with the newest multi-gene data suggesting that genera within *Gracilaria sensu lato* cannot be distinguished anatomically and a single genus is more appropriated (Lyra *et al.* 2021a). Recent investigations, based on combined genetic and morpho-anatomical data, have unravelled many new gracilariacean species (e.g. Muangmai *et al.* 2017; Soares *et al.* 2018; Le *et al.* 2020; Preuss *et al.* 2020; Suzuki & Terada 2021) and such discoveries have expanded our knowledge of diversity, distribution and evolution of this group.

Within the family, *Gracilaria* Greville is one of the most diverse genera with recognition of over 200 species (Guiry & Guiry 2021). *Gracilaria* thalli vary from cylindrical or slightly compressed to flattened. Flattened *Gracilaria* species are relatively common and occur along the tropical to temperate coastlines around the world, and at least 40 species are currently recognized (Gurgel *et al.* 2004; Lin *et al.* 2012; Soares *et al.* 2018; Le *et al.* 2020). In Southeast Asian (SE) region, more than 50 species of *Gracilaria* have been reported, nearly 20 of which are flattened species (Muangmai *et al.* 2014; Phang *et al.* 2016; Le *et al.* 2020). Morphologically, these

species share many features in common, for example, habit shape, size and branching pattern; however, male and female reproductive structures plus blade margin are likely to be useful to distinguish flat *Gracilaria* species in this region (Lin 2006; Lin & De Clerck 2006; Lin *et al.* 2012; Muangmai *et al.* 2017).

In Thailand, certain *Gracilaria* species are commonly cultivated along the southern and eastern coasts of the country, and mainly used for human consumption and aquatic animal feed (Terada *et al.* 2004; Chirapart 2016). The diversity of the *Gracilaria* is also continually being explored, and several new species have been discovered in the country. For example, *Gracilaria minuta* Lewmanomont; *G. lantaensis* Muangmai, Zuccarello, Noiraksa & Lewmanomont; and *G. copejansii* Muangmai, Lewmanomont, Prathep, R. Terada & Zuccarello (Lewmanomont 1994; Muangmai *et al.* 2014, 2017). Over the past few years, efforts to catalogue gracilariacean diversity in Thailand and adjacent areas has been on-going, including the collection of compressed or flattened specimens from the Andaman Sea. This present study aims to clarify the identities of these specimens based on morphology and *rbcl* sequences.

MATERIAL AND METHODS

Collections and morphological analyses

Algal specimens were collected at low tide from Natai Beach, Phang Nga Province, southern Thailand. Entire samples were pressed and dried onto herbarium sheets and deposited at the Natural History Museum of the National Science Museum

(THNHM), Thailand. Pressed specimens were examined for morphological features, such as thallus shape, branching patterns, cell arrangement and reproductive structures. Cross sections for anatomical observation were made by hand using a razor blade, stained with 1% aniline blue, acidified with 1 N HCL and mounted in 40% Karo syrup on microscope slides. Digital images were photomicrographed with an Olympus DP20 digital camera (Olympus, Tokyo, Japan) and eventually edited using Adobe Photoshop 2021 (Adobe, San Jose, California, USA).

DNA extraction, amplification and phylogenetic analyses

DNA was extracted from small fragment of the dried tissue removed from herbarium vouchers using 5% Chelex according to Zuccarello *et al.* (1999). Sequences of *rbcL* region were amplified using PCR with two primer combinations: *rbcL*-for and R753, plus F577 and *rbcL*-rev (Freshwater & Rueness 1994; Nam *et al.* 2000). PCR amplifications and procedures followed Zuccarello *et al.* (2002), and then products were confirmed by gel electrophoresis in 1% agarose. PCR products were cleaned using

ExoSAP-IT (USB, Ohio, USA) and subsequently commercially sequenced (Macrogen Inc., Seoul, Korea).

Contig assembly and alignments were conducted in Geneious Prime 2021.2.2 (<https://www.geneious.com>), using the MUSCLE algorithm. The *rbcL* data set included 69 published sequences of the Gracilariaceae retrieved from GenBank (Table S1). The genus *Gracilariopsis* E.Y. Dawson was selected as an outgroup following Gurgel *et al.* (2004). All new sequences generated in this study were submitted to GenBank. Phylogenetic trees were constructed using maximum likelihood (ML) and Bayesian inference (BI) methods. ML analyses were carried out using the IQ-TREE web server (<http://iqtree.cibiv.univie.ac.at>) (Nguyen *et al.* 2015; Trifinopoulos *et al.* 2016). The most suitable nucleotide substitution models for each codon position were selected (TIME+I+G4 for the first codon position, K3Pu+F+I+G4 for the second and GTR+F+I+G4 for the third) using ModelFinder (Kalyaanamoorthy *et al.* 2017) in IQ-TREE. The ML tree was reconstructed under the selected model with ultrafast bootstrap (UFBoot) replications (Hoang *et al.* 2018). BI analyses were performed using MrBayes v3.2 (Ronquist *et al.* 2012) under the best-fit nucleotide model (GTR+I+G for all codon positions) selected

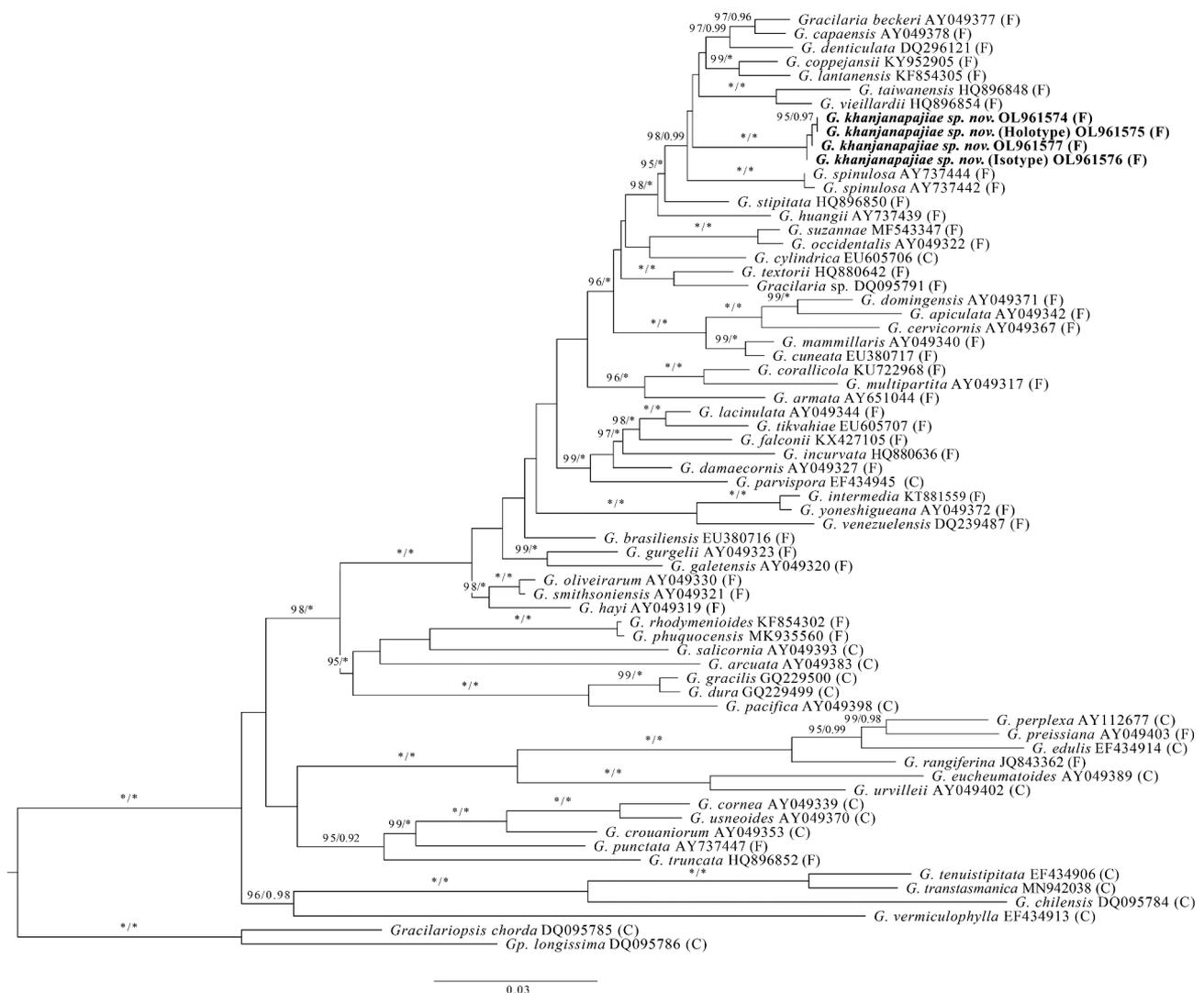
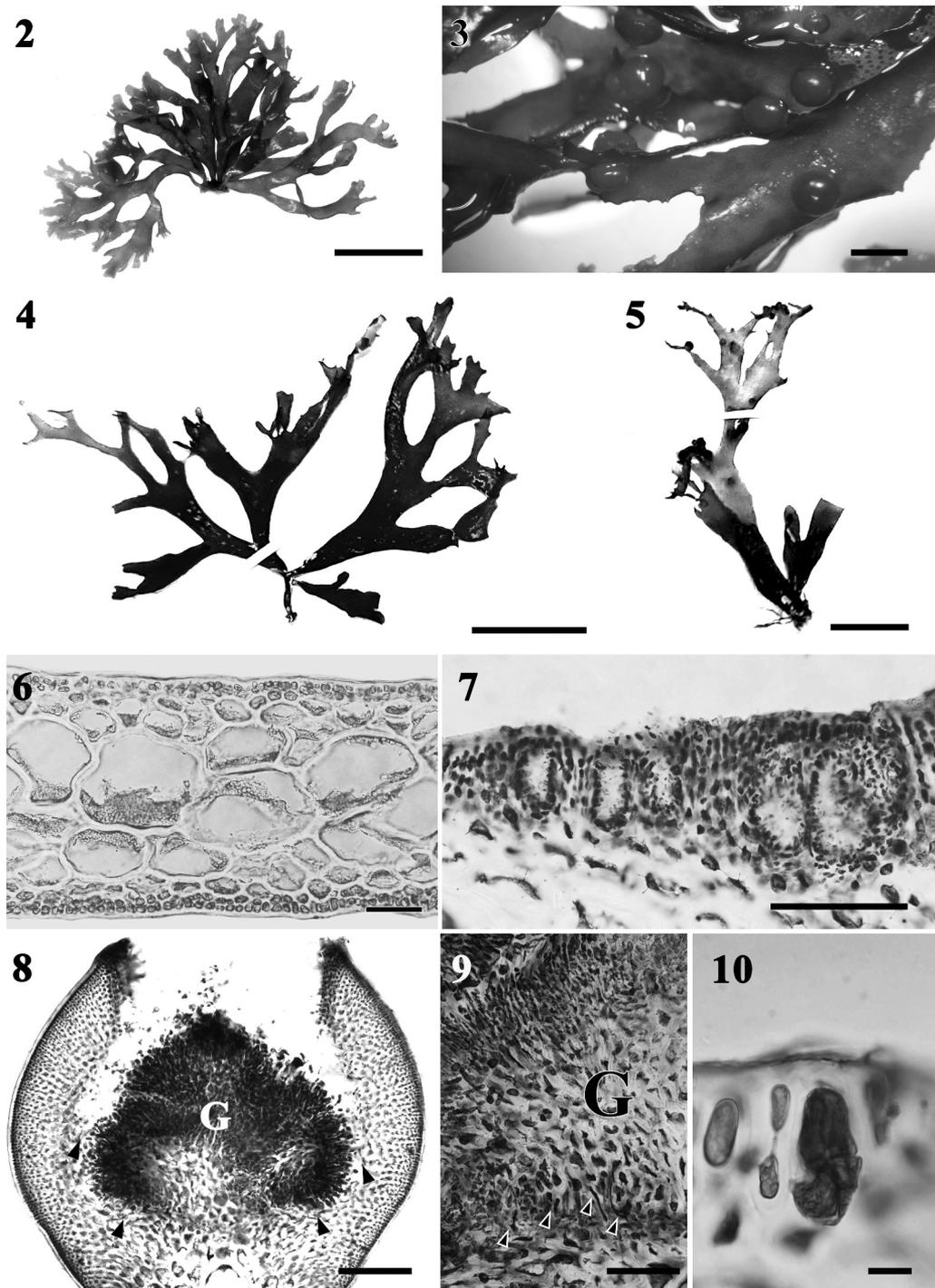


Fig. 1. Maximum-likelihood tree ($-\ln L = 10,170.617$) of partial *rbcL* sequences. Support values of ML ultrafast bootstrap higher than 95% (left) and Bayesian posterior probabilities higher than 0.9 (right) are depicted at each node. Asterisk (*) indicates full support (100%, 1.0) in both analyses. Taxa in bold correspond to new sequences from this study. The letters in parentheses after the names of taxa refer to cylindrical (C) and flattened (F) thallus.



Figs 2–10. Habit and detailed morphological features of *Gracilaria khanjanapajiae* sp. nov.

Fig. 2. Habit of fresh specimens. Scale bar = 2 cm.

Fig. 3. Close-up of female gametophyte, showing the dentate margin of the blade and mature cystocarps. Scale bar = 2 mm.

Fig. 4. Holotype, male gametophyte (THNHM-P-2021-0001). Scale bar = 2 cm.

Fig. 5. Isotype, female gametophyte (THNHM-P-2021-0002). Scale bar = 3 cm.

Fig. 6. Cross-section of vegetative plant, showing medullary cells and cell size transition. Scale bar = 150 μm.

Fig. 7. Cross-section of male gametophyte, showing deep pit-shaped spermatangial conceptacles (*verrucosa*-type). Scale bar = 100 μm.

Fig. 8. Cross-section of mature cystocarp, showing gonimoblasts (G) and lateral and basal nutritive filaments (arrowheads). Scale bar = 200 μm.

Fig. 9. Close-up of lateral nutritive filaments (arrowheads). Scale bar = 40 μm.

Fig. 10. Cross-section of tetrasporophyte, showing cruciately divided tetrasporangium surrounded by modified cortical cells. Scale bar = 10 μm.

by Kakusan 4 (Tanabe 2011). Two parallel runs of four Markov chains were performed for two million generations. We sampled one tree every 1,000 generations, with the first 25% discarded as burn-in, and then determined a consensus topology and posterior probabilities (PP). Both ML and BI trees were visualized with the program FigTree v1.4.3 (Rambaut 2016).

RESULTS

A total of four *rbcL* sequences were newly generated and produced an alignment of 1,112 bp. The ML and BI analyses produced nearly identical tree topologies, and only ML tree is presented in Fig. 1. Our *Gracilaria* samples formed a distinct clade with high support (UFBoot = 100%, PP = 1.0), in a group consisting of *G. spinulosa* (Okamura) C.F. Chang & B.M. Xia and other flattened *Gracilaria* species (Fig. 1). Genetic distance within our samples ranged between 0.0% and 0.17%, while the distance between our samples and the next closest species, *G. spinulosa*, was greater than 2.5%. Our *rbcL* gene analyses clearly showed that our *Gracilaria* samples were genetically distinct from all other *Gracilaria* species and thus can be recognized as a new species. Accordingly, we describe our *Gracilaria* samples as the following new species:

***Gracilaria khanjanapajiae* Saengkaew, Muangmai & Zuccarello
sp. nov.
Figs 2–10**

DESCRIPTION: Thalli flattened, erect, 1.5–5.0 cm high and 1–5 mm wide. One to three blades borne on a stipe, up to 1 cm long. Blade with dentate margins, three or four times regularly di- or trichotomously branched. Thallus in cross section consisting of 1–2 layers of cortical cells, 1–2 layers of subcortical cells and 3–4 layers of medullary cells. Cell transition from cortex to medulla abrupt. Spermatangia formed in solitary or confluent deep pits. Mature cystocarps hemispherical, pericarps rather thick. Lateral and basal nutritive filaments numerous. Tetrasporangia scattered, borne in modified cortex.

HOLOTYPE: THNHM-P-2021-0001, male gametophyte (Fig. 4), collected 4 October 2011 by Narongrit Muangmai, deposited in the Natural History Museum of the National Science Museum, Thailand. GenBank Accession number for *rbcL*: OL961575.

ISOTYPE: THNHM-P-2021-0002, female gametophyte (Fig. 5), collected 4 October 2011 by Narongrit Muangmai, deposited in the Natural History Museum of the National Science Museum, Thailand. GenBank Accession number for *rbcL*: OL961576.

TYPE LOCALITY: 8°17.232'N, 98°16.378'E; Natai Beach, Phang Nga Province, Thailand.

ETYMOLOGY: This species is named in honour of Prof. Khanjanapaj Lewmanomont, Kasetsart University, for her diverse and pioneering contributions to Gracilariaceae research in Thailand.

Algae were flattened throughout and erect, growing in tufts from a fused disclike holdfast, 1.5–5.0 cm high and 1–5 mm wide (Fig. 2). Plants were pinkish red to dark red. Blades had dentate edges (Fig. 3), and were borne on a stipe up to 1 cm long and usually 2 mm in diameter (Fig. 4). The short stipes were cylindrical to compressed, up to 1 mm long (Fig. 4). Branching was dichotomous, but sometimes trichotomous, and usually with three or four orders (Figs 2, 4). Damaged blades produced several blades from their cut margins (Fig. 5). Blades were up to 0.9 mm

thick, consisting of 1–2 cortical cells and 3–4 medullary cells (Fig. 6). Transition of cell size from cortex to medulla was abrupt throughout the thallus (Fig. 6).

The gametophytes were dioecious. Spermatangia were formed in lower to middle parts of thalli and occurred in oval-shaped deep (*verrucosa*-type) cavities, up to 75 µm deep (Fig. 7). Spermatangial conceptacles were either found individually or confluent (Fig. 7). Mature cystocarps were hemispherical without a beak, 0.9–1.5 mm in diameter, and slightly constricted at the base (Figs 3, 8), and mostly occurred in the upper parts of thalli. Gonimoblast tissue was dense, consisting of medium-sized, round to oval cells, and tubular nutritive filaments were numerous in the lateral and basal regions of the cystocarp (Figs 8, 9). Pericarps were thick, 75–125 µm deep, and comprised 13–17 cell layers (Fig. 8). Tetrasporangia were cruciately divided and ovoid, *c.* 18 by 29 µm, embedded in anticlinally elongate cortical cells, and scattered throughout the thallus (Fig. 10).

DISCUSSION

Our morphological and molecular data clearly confirm the discovery of a new flattened species of *Gracilaria*, *G. khanjanapajiae* *sp. nov.*, from the Andaman coast (Indian Ocean) of Thailand. The *rbcL* sequence analyses revealed that *G. khanjanapajiae* was distinct from any described *Gracilaria* species. Our phylogenetic analyses also indicated that this new species is closely related to *G. spinulosa* from Taiwan and to a clade comprised of other flattened species from the Indo-Pacific and South Africa, but this relationship did not receive statistical support. *Gracilaria khanjanapajiae* and *G. spinulosa* share the same gross morphology, for example, thallus with dentate margins and dichotomous branching pattern. However, *G. khanjanapajiae* differs from *G. spinulosa* by having deep spermatangial conceptacles of the *verrucosa*-type vs superficial spermatangia (*textorii*-type), a greater number of medullary cells (3–4 vs 2–3) and lateral nutritive filaments within cystocarps in upper regions (Table 1; Lin 2006). Additionally, in comparison with other Indo-Pacific flattened species with dentate margins, *G. khanjanapajiae* has a superficial similarity to *G. vieillardii* P.C. Silva. The differences that separate these two species are the features of spermatangial conceptacle (*verrucosa*-type in *G. khanjanapajiae* and *textorii*-type in *G. vieillardii*) and nutritive filament placement within cystocarp (in lateral and basal portions in *G. khanjanapajiae*, but only basal in *G. vieillardii*) (Table 1; Lin 2006; Lin *et al.* 2012).

Currently, there are four species of flattened *Gracilaria* reported in Thailand: *G. coppejansii*, *G. lantaensis*, *G. rhodymenioides* A. Millar and *G. textorii* (Suringar) Hariot (Lewmanomont 1994; Muangmai *et al.* 2017). Our findings of a new species, *G. khanjanapajiae*, increases the diversity of flat *Gracilaria* in the country. Morphological comparisons of these five flattened *Gracilaria* species in Thailand are presented in Table 1. Useful characters to distinguish *G. khanjanapajiae* from any other Thai species are the dentate blade margin and the disposition of spermatangial conceptacles (Table 1).

In the Indo-Pacific Ocean, flattened *Gracilaria* species possessing *verrucosa*-type spermatangial conceptacles are few. Among these species, *Gracilaria srilankia* (C.F. Chang & B.M. Xia) Withell, A. Millar & Kraft closely resembles *G. khanjanapajiae*

Table 1. Comparison of *Gracilaria khanjanapajiae* sp. nov. with other similar flattened *Gracilaria* species from the Indo-Pacific region.

Character	<i>G. khanjanapajiae</i> ¹	<i>G. copejansii</i> ²	<i>G. lantaensis</i> ³	<i>G. rhodymenioides</i> ^{3,4}	<i>G. spinulosa</i> ⁵	<i>G. srilankia</i> ⁷	<i>G. textorii</i> ^{4,8}	<i>G. viellardii</i> ^{5,6}
Thallus habit	erect, 1.5–5 cm high	erect, 4–12 cm high	erect, 2–11 cm high	erect or slightly prostrate, 2–5 cm high	erect, 3–9 cm high	erect, 3–4 cm high	erect, 4–20 cm high	erect or slightly prostrate, 5–10 cm high
Blade margin	dentate	smooth, with proliferation	smooth	smooth	dentate	smooth	smooth	dentate
Branching pattern	regularly di- or trichotomous	regularly dichotomous	irregularly di- or trichotomous	irregularly di- or trichotomous	irregularly dichotomous	regularly sub- to dichotomous	flabellately dichotomous to subdichotomous	irregularly dichotomous
Medulla layers	3–4	1–3	2–3	3–4	2–3	unknown	2–4	2–3
Spermatangia	<i>verrucosa</i> -type	<i>textorii</i> -type	<i>textorii</i> -type	<i>textorii</i> -type	<i>textorii</i> -type	<i>verrucosa</i> -type	<i>textorii</i> -type	<i>textorii</i> -type
Tubular nutritive cells	lateral and basal portions	upper and lateral portions	lateral and basal portions	lateral and basal portions	upper and basal portions	unknown	upper and lateral portions	basal portions
Distribution	Thailand	Thailand	Thailand	Indian Ocean and Western Pacific	Taiwan	Indo-Pacific Ocean	Indo-Pacific Ocean	Indo-Pacific Ocean

¹This study²Muangmai et al. (2017)³Muangmai et al. (2014)⁴Lewmanomont & Chirapart (2004)⁵Lin (2006)⁶Lin et al. (2012)⁷Withell et al. (1994)⁸Lewmanomont (1994)

by having similar thallus size, branching pattern and male reproductive structure (Table 1; Withell et al. 1994). However, the blade margins separate these two species (smooth in *G. srilankia* and dentate in *G. khanjanapajiae*). Unfortunately, female reproductive features and genetic data of *G. srilankia* is not available. Additional studies on *G. srilankia* specimens will be useful for tracing morphological and phylogenetic relationships among flattened *Gracilaria* taxa with deep spermatangial pits.

Among flat *Gracilaria* species from South Africa, *Gracilaria denticulata* F. Schmitz ex Mazza is morphologically quite similar to *G. khanjanapajiae* by having dentate blade margins. However, blades of *G. denticulata* are thicker, comprising up to seven layers of medullary cells (Iyer et al. 2004; Lin & De Clerck 2006), than those of *G. khanjanapajiae*, which consist of 3–4 medullary layers. Spermatangia of *G. denticulata* are borne in shallow pits (*textorii*-type), whereas *G. khanjanapajiae* forms spermatangia in deep pits (*verrucosa*-type) (Lin & De Clerck 2006). Additionally, our phylogenetic data clearly show that the two species are distinct.

Our results increase our knowledge of the diversity of flattened tropical species of *Gracilaria* and show a very high diversity along the Thailand coasts. Continued work on these potentially commercially valuable algae will continue to uncover their diversity and evolutionary patterns.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

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