Phylogenetic relationships of *Stenogramma* (Gigartinales, Rhodophyta) with a description of *S. coreanum* sp. nov.

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ABSTRACT: Despite the recent description of *Stenogramma guleopoense* in Korea, the issue of *S. interruptum* in the northwestern Pacific is still a matter of debate. We analyzed 24 *rbcL* sequences from specimens collected in Korea, including a longer fragment of *rbcL* (949 base pairs from the type of *S. guleopoense*, in addition to morphological observations. Phylogenetic analysis of *rbcL* sequence revealed a new distinct clade that differed from *S. guleopoense* from Korea and other species of *Stenogramma*. The morphology and anatomy of the Korean clade supported its distinct position in the genus *Stenogramma*. On the basis of these results, we describe *S. coreanum* sp. nov. from Korea. *Stenogramma coreanum* is distinguished by a combination of its large size (up to 24 cm) of dichotomous to subdichotomous branches divided up to nine times, wider blades with laciniate segments, one to two layers of cortical cells, two to three layers of medullary cells, a gradient of one to two layers of smaller cells between the cortex and medulla, and discontinuous cystocarps on the centre of the frond. *Stenogramma coreanum* occurs mostly along the south coast of Korea, whereas *S. guleopoense* occurs along the west coast. The biogeographic implications of the global diversification in *Stenogramma* are discussed.

KEY WORDS: Morphology, Phyllophoraceae, *rbcL*, *Stenogramma guleopoense*, Systematics

INTRODUCTION

*Stenogramma* Harvey is a well-defined phyllophoracean red algal genus that is distributed in the Atlantic Ocean, Australasia, and in both the Indian and Pacific Oceans. It is characterized by rose-red flattened thalli with dichotomous branching, a medial line of procarps, cystocarps resembling an interrupted midrib on female plants, and tetrasporangial nemathecia forming patches scattered over the fronds (Harvey 1849; Millar 1990; Lewis & Womersley 1994; Le Gall & Saunders 2010). Plants occur on rocks at a depth of up to 53 m and they are often cast ashore after strong winds (Lewis & Womersley 1994; Yoneshigue-Valentin & Gestinari 2000). Some species produce carrageenan, a family of linear sulfate polysaccharides (Furneaux & Miller 1985).

Harvey (1841) established *Stenogramma* using the generic type *S. californicum* Harvey from San Francisco, California, USA. Montagne (1846) described *S. interruptum* (C.Agardh) Montagne on the basis of a specimen in Bory St. Vincent’s herbarium (PC0062515), which was labelled *Delesseria interruptum* C.Agardh from Cadiz, Spain (Le Gall & Saunders 2010). Agardh (1885) described a third species from southern Australia, *S. leptophyllum* J.Agardh. However, Harvey merged *S. californicum* into *S. interruptum* in his subsequent papers on the basis of their morphological similarity (Harvey 1849, 1853, 1862). Subsequently, *S. interruptum* became one of the most widespread species of red algae, found in Oceania, the eastern Atlantic Ocean, the Mediterranean Sea, the Pacific Ocean, and the southwest Atlantic Ocean (Dawson 1961; Mikami 1965; Kang 1966; Abbott & Hollenberg 1976; Dixon & Irvine 1977; Millar 1990; Ramirez & Santelices 1991; Lewis & Womersley 1994; Yoneshigue-Valentin & Gestinari 2000; Wynne 2011). *Stenogramma rhodymenioides* Joly & Alveal from Chile was also considered conspecific with *S. interruptum* (Joly & Alveal 1969; Ramirez & Rojas 1986).

Molecular taxonomic studies, however, do not support the worldwide distribution of *Stenogramma interruptum*. For example, Lopez-Bautista et al. (2002) and Le Gall & Saunders (2010) reinstated *S. californicum* from the United States and *S. rhodymenioides* from Chile. Additional species have been described in *Stenogramma* on the basis of molecular data and morphology: *Stenogramma bamfieldiense* from Pacific Canada, *S. guleopoense* from Korea, *S. lamyi* from Madagascar, and *S. phyllophoroides* from Australia (Millar 1990; Le Gall & Saunders 2010; Calderon & Boo 2014; Le Gall et al. 2015). A total of eight species of *Stenogramma* are currently recognized in the world inventory (Guiry & Guiry 2017), and species classification by morphology does not reflect phylogenetic relationships.

Our recent collection from Korea included specimens of *Stenogramma*, but the morphology of some specimens did not agree with *S. guleopoense* and other species in the genus,
with the new Korean collections being rather similar to S. interruptum from Europe. To identify our specimens and reconfirm S. guleopoense by molecular tools, we analyzed plastid rbcL DNA sequences, commonly used in the taxonomy of the Phyllophoraceae (Lopez-Bautista et al. 2002; Le Gall & Saunders 2010; Calderon & Boo 2014; Le Gall et al. 2015). We amplified a 949-base pair (bp) fragment of rbcL from the type specimen of S. guleopoense that was previously analyzed only for 124 bp of rbcL (Calderon & Boo 2014). On the basis of morphological observations and phylogenetic analyses of rbcL sequences, we concluded that our Korean specimens represent a new species of phyllophoraceous red algae, which we hereby describe.

MATERIAL AND METHODS

A total of 24 specimens of Stenogramma were collected along the Korean coast (see supplementary data Table S1). They were dried in silica gel and then pressed on herbarium sheets. Of these, nine were tetrasporophytes, five were females with cystocarps, and one was vegetative. Microscopic observations were made by sectioning with a razor blade and staining with 1% aqueous aniline blue acidified with 1% HCl and mounted in 70% glycerine. Photomicrographs were taken with a DP-71 Olympus camera (Nikon Corp., Tokyo, Japan) attached to a BX51 Olympus microscope (Japan and Olympus Corp., Tokyo, Japan). Voucher specimens have been deposited in the Algal Biomass Center in Chungnam National University (CNUK), Daejeon and the Institute of Korean Biological Resources, Incheon, Korea.

DNA extraction, polymerase chain reaction amplification, and sequencing from our collections were performed as described in Boo et al. (2013). The primers used for amplifying and sequencing were F7, F645, R753, and RrbcS start for rbcL (Freshwater & Rueness 1994; Lin et al. 2001). To amplify a larger fragment of rbcL, DNA from a type fragment of Stenogramma guleopoense was amplified following the procedures described by Lindstrom et al. (2011). Because the type specimen was soaked in formalin–seawater before mounting, we followed the guidelines and precautionary methods of Hughey & Gabrielson (2012). Three primer sets were used to amplify rbcL from the type fragment F492–R898, F645–R1150, and F993–R1442 (Freshwater & Rueness 1994; Lin et al. 2001; Kim et al. 2010). Sequencing was performed using both forward and reverse primers provided by Genotech (Daejeon, Korea). Electropherograms were edited using the program Chromas v1.45 (Conor McCarthy, Griffith University, Australia; http://www.technelysium.com.au/chromas.html). Sequences were compiled and aligned using the MUSCLE algorithm in MEGA5 v5.2 (Tamura et al. 2011). Twenty-four newly determined sequences (including the 949 bp of S. guleopoense) were deposited in GenBank (see supplementary data Table S1).

Phylogenies of rbcL sequences were inferred using maximum likelihood (ML) and Bayesian inference (BI). PartitionFinder v.1.1.0 (Lanfear et al. 2012) was used to select the best-fitting partitioning schemes and models of molecular evolution using the greedy algorithm with unlinked branch lengths. The ML analysis was performed using the Pthreads version of RAxML v8.0.X under the GTRGAMMA model (Stamatakis 2014). A rapid bootstrap analysis and search for the best-scoring ML tree were performed with 1000 bootstrap replicates. BI was performed using MrBayes v3.2.1 with the Metropolis-coupled Markov chain Monte Carlo under the GTR + G + I model (Ronquist et al. 2012). Two million generations of two independent runs were performed with four chains and sampling trees every 100 generations. The burn-in period was identified graphically by tracking the likelihoods at each generation to determine whether they reached a plateau. Twenty-five percent of saved trees were removed, and the remaining trees were used to infer Bayesian posterior probabilities (BPPs).

RESULTS

Stenogramma coreanum G.Y.Cho, I.K.Hwang, M.S.Calderon & S.M.Boo sp. nov.
Figs 1–16

DIAGNOSIS: Thalli 13 to 24 cm high, rose-red to darker red in colour, and dichotomous or subdichotomous branches divided up to nine times; thalli with wide and parallel-sided segments, terminal branches basally constricted (Figs 1–3); surface cells (Fig. 4) angular with dimensions of 7.5–8 × 7–13.5 μm; structure multiaxial, branches in the middle 209–253 μm thick, cortex one to two cells thick, medulla two to three cells thick, with one to two layers of smaller cells present between the cortex and medulla (Fig. 5); tetrasporophytes and female gametophytes isomorphic; tetrasporic thalli forming elliptic nemathecia scattered as wartlike blotches over both surfaces, formed by divisions of outer cortical cells (Fig. 6), giving rows of cruciately divided tetrasporangia, 22–30 μm long and 14–16 μm wide (Figs 7–9); cystocarps developing inwardly (Figs 10–14), forming an interrupted median thickened line containing masses of carpospores, 407.5 ± 22.3 μm in diameter, surrounded by a multilayered cortex (Figs 15, 16). Male thalli not observed.

HOLOTYPE: CNU071484 (female gametophyte, Fig. 1), cast ashore, Hoedong (34°25’17”N, 126°20’41”E), Jindo, Korea; 23 March 2016 (S.M.Boo, J.I.Lee & J.Y.Kim, collection number not given). CNUK.

ISOTYPES: CNU071480 in the University Herbarium, University of California at Berkeley (UC), USA and CNU071481-2 in CNUK.

ETYMOLOGY: The specific epithet refers to the Latin name of Korea.

Morphological characteristics of Stenogramma guleopoense

Specimens of Stenogramma guleopoense were collected in Daecheon on the west coast and Chujado Isles, Jeju, Korea. Thalli were up to 8 cm long, with complanate, dichotomously divided branches (Fig. 17) and had notched apices (Fig. 18). Segments were slender and parallel sided. Cortex consisted of two-celled layers and medulla included two- to three-celled layers (Fig. 19). Nemathecia arose on one surface of fronds (Fig. 20). Tetrasporangia were elliptical (Fig. 21). Cystocarps had an obscure ostiole with the mass of carposporangia surrounded by a multilayered cortex (Fig. 22).
Molecular identification and phylogeny

Twenty-four rbcL sequences from Korean *Stenogramma* were generated in the present study. All 15 specimens of *S. coreanum* from different locations had identical rbcL. We amplified 949 bp of rbcL from the type specimen of *S. guleopoense* after repeated attempts using three primer sets. Three other specimens from Jeju and Daecheon were identical with the type of *S. guleopoense* in the rbcL sequence. Phylogeny of rbcL sequences revealed genetic distinctness of all species of *Stenogramma* except *S. leptophyllum* from southern Australia, which was unavailable for rbcL sequence. *Stenogramma* was resolved into three groups: (1) Australia/Madagascar, (2) North Atlantic, and (3) Pacific Ocean regions (Fig. 23). The Australia/Madagascar group included *S. lamyi*, *S. phyllophoroides*, and *Stenogramma* sp. (78% for ML and 0.89 for BPP). *Stenogramma lamyi* from Madagascar was basal to the subgroup of two Australian species, *S. phyllophoroides* and *Stenogramma* sp. The North Atlantic group contained only *S. interruptum*, and all three specimens from France, Spain, and UK had identical rbcL sequences. The Pacific group included *S. bamfieldiense*, *S. californicum*, *S. coreanum*, *S. guleopoense*, and *S. rhodymenioides* (87% for ML and 1.0 for BPP). Of interest, three east Pacific species, *S. bamfieldiense*, *S. californicum*, and *S. rhodymenioides* formed a closely related subgroup (76% for ML and 1.0 for BPP). The pairwise divergence between *S. coreanum* and *S. guleopoense* from Korea was about 2.5% (31 bp) in rbcL.
DISCUSSION

Our analyses of rbcL sequences clearly confirmed the occurrence of Stenogramma guleopoense as well as a new species, S. coreanum, in Korea. Stenogramma coreanum was distinguished mostly by a combination of its larger size (up to 24 cm) of dichotomous to subdichotomous branches divided up to nine times, wider blades with wide and laciniate segments, retuse apices, one to two layers of cortical cells, two to three layers of medullary cells, and a gradient of one to two layers of smaller cells between the cortex and medulla, and discontinuous cystocarps in the frond center. The habitat of S. coreanum is considered subtidal, and it can be found cast ashore on the south coast of Korea. This species was misidentified as S. interruptum in a previous list of Korean marine algae (Kang 1966; Boo & Ko 2012; Kim et al. 2013). Either coxl or rbcL sequences should be analyzed from the Japanese taxon to verify the currently reported range of S. interruptum.

Stenogramma guleopoense (type locality, Guleopdo Isle, Dukjeodo Islands, Korea) is characterized mostly by its small size (up to 8 cm), slender thallus with narrow and parallel-sided segments, basally constricted terminal branches, two layers of cortical cells, two to three layers of medullary cells, and a gradient of one to two layers of small cells between the cortex and medulla (Calderon & Boo 2014). The distribution of S. guleopoense is extended to Chujado Isles, Jeju from the middle of the west coast of Korea. Stenogramma interruptum (type locality, Cadiz, Spain) is distinguished by its large thalli (up to 20 cm), dichotomously and palmately divided branches, with segments about 10 mm wide (Harvey 1849; Schottet 1968; Dixon & Irvine 1977). The occurrence of S. interruptum in Europe was confirmed using rbcL sequences in France, Spain, and UK (Le Gall & Saunders 2010; Calderon & Boo 2016). Stenogramma bamefieldiense (type locality, Vancouver Island, Canada) is distinguished by its small, straplike thalli with adventitious proliferations, two dichotomies, inner structure comprising one layer of small cortical cells, and a layer of large medullary cells (Le Gall & Saunders 2010). Stenogramma californicum (type locality, San Francisco Harbour, USA) has a long (up to 20 cm) and wide (5–18 mm) thallus (Smith 1944; Abbott & Hollenberg 1976 as S. interruptum). Stenogramma rhodymenioides (type locality, Valparaíso, Chile) is distinguished by five to nine dichotomies and thallus size (Joly & Alveal 1969). The pairwise divergence of S. rhodymenioides between Canada and Chile was 0.4% (5 bp), although the two locations from the Northern and Southern hemispheres are too distant for both taxa to share the same gene pool. Additional study may be needed of the Canadian specimen of S. rhodymenioides. Stenogramma leptophyllum (type locality, Victoria, Australia) is characterized by its linear thalli and three to nine dichotomous branches.
Lewis & Womersley (1994) reported the occurrence of both *S. interruptum* and *S. leptophyllum* from southern Australia, but analyses of rbcL sequences from these two species are needed, with a morphological comparison of these two taxa with *Stenogramma* sp. collected near Kangaroo Island, Adelaide (Calderon & Boo 2014). *Stenogramma phyllophoroides* (type locality, New South Wales, Australia) has spirally twisted segments and finely dentate margins (Millar 1990).

Postfertilization and diploidization events in *Stenogramma* were reported in previous studies (Fritsch 1945; Kylin 1956; Calderon & Boo 2014). We observed female plants and the anatomy of cystocarpic development in *S. coreanum*, but we did not observe any carpogonial branches. Three-celled carpogonial branches occur in *S. guleopoense* and *S. interruptum* (Kylin 1956; Schotter 1968; Calderon & Boo 2014). Three- to four-celled carpogonial branches were reported in Australian *S. interruptum* and *S. leptophyllum* (Lewis & Womersley 1994). Further research is needed to determine whether or not cell number in carpogonial branches is related to species divergence.

Le Gall *et al.* (2015) proposed a scenario of two centres of origin for *Stenogramma* on the basis of its biogeographic structure in the rbcL phylogeny. However, our rbcL phylogeny of *S. guleopoense* and *S. coreanum* revealed three groups of species that corresponded to their distributions in the Pacific, Australia/Madagascar, and the North Atlantic. The Pacific group comprised the east and west Pacific subgroups, suggesting that their ancestor likely occurred widely in the Pacific Ocean region, as in the brown alga *Ishige* (Lee *et al.* 2009). The east Pacific ancestor of *Stenogramma* likely occurred along the Pacific American coast and diversified into *S. bamfieldiense* from Canada, *S. californica* from the United States, and *S. rhodymenioides* from Canada and Chile (Le Gall *et al.* 2015). Le Gall *et al.* (2015) suggested a key role of kelp in conveying the ancestor of these species along the Pacific Coast of the American continent. However, the wide distribution of *S. rhodymenioides* from Canada to Chile will necessitate a re-examination of morphologies of this material. The west Pacific ancestor might have occurred in Korea and likely Japan (as *S. interruptum*, Mikami 1965) and diverged into *S. coreanum* and *S. guleopoense*. The Australia/Madagascar ancestor likely occurred in the South Indian Ocean region and diversified into Madagascan *S. lamyi* and Australian *S. phyllophoroides* and *Stenogramma* sp. (KM262208). The ancestor of the North Atlantic *S. interruptum* likely dispersed through the Arctic route (Le Gall *et al.* 2015). A molecular clock of *Stenogramma* is needed to support the above phylogeographic inference; however, a lack of fossil evidence limits our ability to estimate the divergence time of *Stenogramma* species.

In conclusion, we have described a new species, *S. coreanum*, cast ashore along the south coast of Korea, and

(Figs 17–22. Habit, vegetative, tetrasporangial, and female structures of *Stenogramma guleopoense*.

Fig. 17. Habit of fan-shaped thallus with subdichotomous branches from Chujado Isles, Korea. Scale bar = 5 cm.
Fig. 18. Slightly notched apical part of thallus. Scale bar = 500 μm.
Fig. 19. Cross-section of thallus showing cortex (c), medulla (m), and small cells between cortex and medulla (arrowhead). Scale bar = 50 μm.
Fig. 20. Cross-section of a nemathecium (arrowhead) containing undivided tetrasporocytes cut off from cortical cells, arising from frond surface. Scale bar = 50 μm.
Fig. 21. Close-up of cruciately divided tetrasporangia with longitudinal arrangement. Scale bar = 20 μm.
Fig. 22. Close-up of cystocarp (arrowhead) showing mass of carposporangia and an ostiole. Scale bar = 50 μm.)
Fig. 23. Maximum likelihood tree of *rbcL* sequences from *Stenogramma*. The numbers above or below nodes are RAxML bootstrap values and Bayesian posterior probabilities. Only bootstrap values ≥ 50% and Bayesian posterior probabilities ≥ 0.90 are shown in the tree.
confirmed the extension of *S. guleopoense* to Jeju Island from the middle of the west coast of Korea. Nine species are now recognized in the genus *Stenogramma*. The limited geographic ranges and concomitant endemism in *Stenogramma* support localized divergence of its species, as in *Millerella G.H. Boo & S.M. Boo* and *Portieria Zanardini* (Payo et al. 2013; Boo et al. 2016), and contradict the wide distribution of marine organisms due to dispersal by ocean currents.

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**SUPPLEMENTARY DATA**

Supplementary data associated with this article can be found online at http://dx.doi.org/10.2216/17-53.1.s1.

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Table 1. Morphological comparison of *Stenogramma coreanum* with congeneric species. Important characters are in bold.

| Habit | Height (cm) | Segment width (mm) | Number of dichotomies | Layers of cortical cells | Layers of medullary cells | Transition layer of cells | Type locality | Reference |
|-------|-------------|--------------------|-----------------------|------------------------|--------------------------|--------------------------|--------------|----------|
| laciniate segments | 13–24 | 7–8 | 7–9 | 1 | 2–3 | 1–2 | Jindo, Korea | present study |
| parallel-sided segments | 5–6 | 3–5 | 2 | 1 | 2–3 | 1–2 | Guleopdo Isle, Korea | Calderon & Boo (2014) present study |
| broad segments, gradually broader at tips | 6–12 | 5–10 | 3–5 | 1 | 2–3 | 1–2 | Bamfield, Canada | Le Gall et al. (2010) |
| sparse branching linear segments | 6-10 | 5–10 | 3–5 | 2–3 | 1–2 | 1–2 | San Francisco, USA | Harvey (1849), Smith (1944), Abbott & Hollenberg (1976) (as *S. interruptum*). |
| gradually expanded, margin finely dentate | up to 8 | up to 5 | 1–2 | 1 | 1–2 | 1–2 | New South Wales, Australia | Lewis & Womersley (1994) |
| broad segments, small, sparse, linear segments, gradually broader at tips | up to 8 | up to 5 | 3–5 | 1–2 | 1–2 | 1–2 | Valparaiso, Chile | Harvey (1849), Smith (1944), Abbott & Hollenberg (1976) (as *S. interruptum*). |
| broad segments, small, sparse, linear segments, gradually broader at tips | up to 8 | up to 5 | 3–5 | 1–2 | 1–2 | 1–2 | Victoria, Australia | Harvey (1849), Smith (1944), Abbott & Hollenberg (1976) (as *S. interruptum*). |
| broad segments, small, sparse, linear segments, gradually broader at tips | up to 8 | up to 5 | 3–5 | 1–2 | 1–2 | 1–2 | Madagascar | Lewis & Womersley (1994) |
| broad segments, small, sparse, linear segments, gradually broader at tips | up to 8 | up to 5 | 3–5 | 1–2 | 1–2 | 1–2 | New South Wales, Australia | Lewis & Womersley (1994) |
| broad segments, small, sparse, linear segments, gradually broader at tips | up to 8 | up to 5 | 3–5 | 1–2 | 1–2 | 1–2 | Valparaiso, Chile | Harvey (1849), Smith (1944), Abbott & Hollenberg (1976) (as *S. interruptum*). |

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