

First report of freshwater red alga *Compsopogon caeruleus* (Compsopogonaceae, Rhodophyta) in Korea

Eun-Young Lee^{1,†}, Soon Jeong Lee^{2,†} and Sang-Rae Lee^{3,*}

¹Species Diversity Research Division, National Institute of Biological Resources, Incheon 22689, Republic of Korea

²Tongyeong Regional Office of National Fishery Products Quality Management Service, Tongyeong, Gyeongsangnam-do 53019, Republic of Korea

³Marine Research Institute, Pusan National University, Busan 46241, Republic of Korea

[†]These authors contributed equally to this work.

*Correspondent: antithamnion@gmail.com

The filamentous freshwater red alga *Compsopogon caeruleus* (Compsopogonophyceae, Compsopogonaceae, Rhodophyta) occurs in tropical and subtropical regions of worldwide. This species has been reported from Asia, America, Africa, Europe and Oceania, and the worldwide distribution of *Compsopogon caeruleus* is in variable water habitats. Several morphospecies of the genus *Compsopogon* had been recorded, but recent molecular phylogenetic analyses with worldwide sampling identified a monospecific genus, *C. caeruleus*. In the present study, we first report a freshwater red alga *Compsopogon caeruleus* from Korea. We identified *Compsopogon caeruleus* in an urban river in Yongin City, and analyzed its morphological and genetic characteristics. Nuclear 18S rDNA, plastidal *rbcL* gene and mitochondrial *cox1* gene sequences isolated from Korean *Compsopogon caeruleus* showed high sequences similarity with *Compsopogon caeruleus* from worldwide (98.6–100% (18S rDNA), 99–100% (*rbcL*) and 97.7–100% (*cox1*)). These sequences similarities support the identification of a red alga found in Korea as *Compsopogon caeruleus*. This new geographical report provides the useful information for understanding the distribution and habitat range of *Compsopogon caeruleus* especially concerning urban freshwater environments.

Keywords: 18S rDNA, *Compsopogon caeruleus*, *cox1* gene, *rbcL* gene, species identification

© 2024 National Institute of Biological Resources
DOI:10.12651/JSR.2024.13.3.332

INTRODUCTION

Compsopogon Montagne 1846, a red macroalga, lives in freshwater habitats, including springs, lakes, ponds, and streams. Species of the genus *Compsopogon* have also been reported in brackish waters and seawater coastal lagoons (Sheath and Vis, 2015; Rybak and Woyda-Ploszczyca, 2022). *Compsopogon caeruleus* (Balbis ex C. Agardh) Montagnes, which shows a free-floating or epilithic characteristics, has macroscopic branched filaments with uniseriate axes and branches, covered by clathrate polygonal cortical cells. Its distinct features include dark red, purple, blue, and olive-green (Necchi Jr. *et al.*, 2013; Tomás *et al.*, 2013; Nan *et al.*, 2016; de Zaburlin *et al.*, 2019).

Compsopogon caeruleus has a global distribution, especially in tropical and subtropical regions, and more rarely in temperate waters with locally elevated tempera-

tures (Taylor, 1960; Krishnamurthy, 1962; Nakamura and Chihara, 1983; Necchi Jr. *et al.*, 1990, 1999; Millar and Kraft, 1993; Rintoul *et al.*, 1999; Sherwood, 2004; Tomás *et al.*, 2013; Nan *et al.*, 2016).

Compsopogon caeruleus was documented in China (Xie and Ling, 1998) and in Japan (Kitayama, 2011), but not yet been reported in Korea, which could be a taxonomic missing linker. Molecular phylogenetic studies, covering globally derived samples of *Compsopogon* species have found low genetic diversity on inter-specific relationships, and those suggested that previous species reports basing on previously species reports basing on morphological characteristics should be readdressed (Necchi Jr. *et al.*, 2013; Nan *et al.*, 2016). In this study, we first identified *Compsopogon caeruleus* in proliferating algal mats in an urban river (Yongin City, Korea) and examined its morphological and molecular taxonomic characteristics.

MATERIALS AND METHODS

Samples of *Compsopogon caeruleus* were collected from a filamentous mat in an urban stream, Seongbok Stream in Yongin-si, Gyeonggi-do, Korea (37° 19'10.35"N, 127°03'42.98"E) during early summer on the shallow area at the edge of the stream (Fig. 1). All specimens (NIBRRD0000010748–50) were deposited at the algal herbarium of the National Institute of Biological Resources (NIBR) in Incheon, Korea. Morphological observation was conducted using a light microscope (Olympus BX50, Japan) and a stereo-microscope (Nikon, Japan).

For species identification via DNA analysis, we isolated a small piece (<0.5 cm) of a single-filament specimen for DNA extraction. Total genomic DNA was extracted using a DNeasy Plant Mini Kit (Qiagen, Germantown, MD, USA) according to previously described protocols with some modifications (Lee and Lee, 2018). Multiple molecular markers including the nuclear small subunit ribosomal RNA coding gene (18S rDNA), plastidial *rbcL* and mitochondrial *cox1* gene sequences, were used for DNA barcoding of *Compsopogon* species (Necchi Jr. *et al.*, 2013). New primers were designed to amplify the *rbcL* region using the plastid genome of *Compsopogon caeruleus* (GenBank accession number: NC_035350): forward primer (*rbcL*-comp-190F; 5'-GAATCTTCTACAGCAACTTGGAC-3') and reverse primer (*rbcL*-comp-1352R; 5'-GCATCTCTTATTATTTGAGGACC-3'). Forward primer GazF1 and reverse primer GazR1 were used to amplify the *cox1* gene (Saunders, 2005). The 18S rDNA region was amplified using primers A/SSU-inR1 (Lee *et al.*, 2010).

PCR was performed with an initial denaturation step at 94°C for 3 min followed by 40 cycles at 94°C for 30 s, 50°C for 30 s, and 72°C for 1 min, and a final extension step at 72°C for 7 min. The AmfiXp PCR Master Mix (GenDEPOT, Katy, TX, USA) was used for the PCR, and the products were sequenced using a commercial sequencing service (Macrogen, Seoul, Korea). Chromatograms were assembled using Sequencher 5.4.6 (Gene Codes, Ann Arbor, MI, USA). The 18S rDNA, *rbcL* and *cox1* gene sequences were compared to a public database using a BLAST search in GenBank at the National Center for Biotechnology Information (NCBI). For molecular phylogenetic analyses, reference sequences for *rbcL* gene were obtained from GenBank at NCBI (Fig. 2). Phylogenetic analyses were performed using MEGA version 6 (Tamura *et al.*, 2013), employing the neighbor-joining method with 2,000 bootstrap replicates. Pairwise distances were calculated using Kimura's two-parameter method. *Boldia* species were selected as the outgroup.



Fig. 1. Collection site of *Compsopogon caeruleus* from Korea. A. Location of urban stream in Yongin City. B. Sampling location and habitat of *C. caeruleus* (arrowhead).

RESULT

1. Species identification using 18S rDNA, *rbcL* and *cox1* gene sequences

DNA sequences of 18S rDNA, *rbcL* and *cox1* were amplified from red algal specimen collected in Yongin, Korea. The sequences identified were 485 bp for 18S rDNA (GenBank accession number PP471840), 1103 bp for *rbcL* (GenBank accession number; PP477321), and 664 bp for the *cox1* gene (GenBank accession number; PP477322). The Korean red algae sample collected from Yongin showed high sequence identity with *Compsopogon caeruleus* in the database of GenBank (NCBI) reported from worldwide basing on 18S rDNA, *rbcL* and *cox1* gene sequence analyses. From the BLAST search, the 18S rDNA sequence showed high sequence similarity (98.6–100%) with 12 individuals of *Compsopogon caeruleus*. Some 18S rDNA sequences under different species names of Compsopogonaceae also showed 100% identity including *Compsopogon hookeri* (AJ880416) and *Compsopogonopsis leptoclados* (AF087123, AF087125) with Korean *Compsopogon caeruleus*. *Boldia erythro-*

siphon (Compsopogonales; Boldiaceae) showed 90.5% (AF055299) and 95.4% (AF168631) sequence identity with the isolates (Table 1).

The *rbcL* gene sequence also showed high sequence identity with many individuals of *Compsopogon caeruleus* (99–100%, Fig. 2). The *rbcL* sequence of Korean *Compsopogon caeruleus* showed 99.6% and 99.2% sequence identity with *Compsopogonopsis leptoclados* (AF087115, AF087120). *Boldia erythrosiphon* (AF087121, AF087122, NC_034776) and *Pulvinaster venetus* (NC_062387) were more distantly related to *Compsopogon* species, with sequence identities of 83.9–84.6% and 88.1%, respectively. The *cox1* gene sequences showed 97.7–100% identity with 19 reported *cox1* sequences of *Compsopogon caeruleus*. *Compsopogon hookeri* (OP747576) also had 100% identity. *Pulvinaster venetus* (NC_062399) was distantly related to *Compsopogon caeruleus* with 79% sequence

identity.

2. Morphological description of *Compsopogon caeruleus*

Compsopogonophyceae G.W. Saunders & Hommersand,
2004 붉은털홍조강
Compsopogonales Skuja, 1939 보라털목 (국명 신칭)

Table 1. Intra/interspecific DNA sequences similarity among *Compsopogon caeruleus* and related species.

	<i>C. caeruleus</i>	<i>Boldia erythrosiphon</i>	<i>Pulvinaster venetus</i>
18S rDNA	98.6–100%	90.5–95.4%	–
<i>rbcL</i>	99–100%	83.9–84.6%	88.1%
<i>cox1</i>	97.7–100%	–	79%

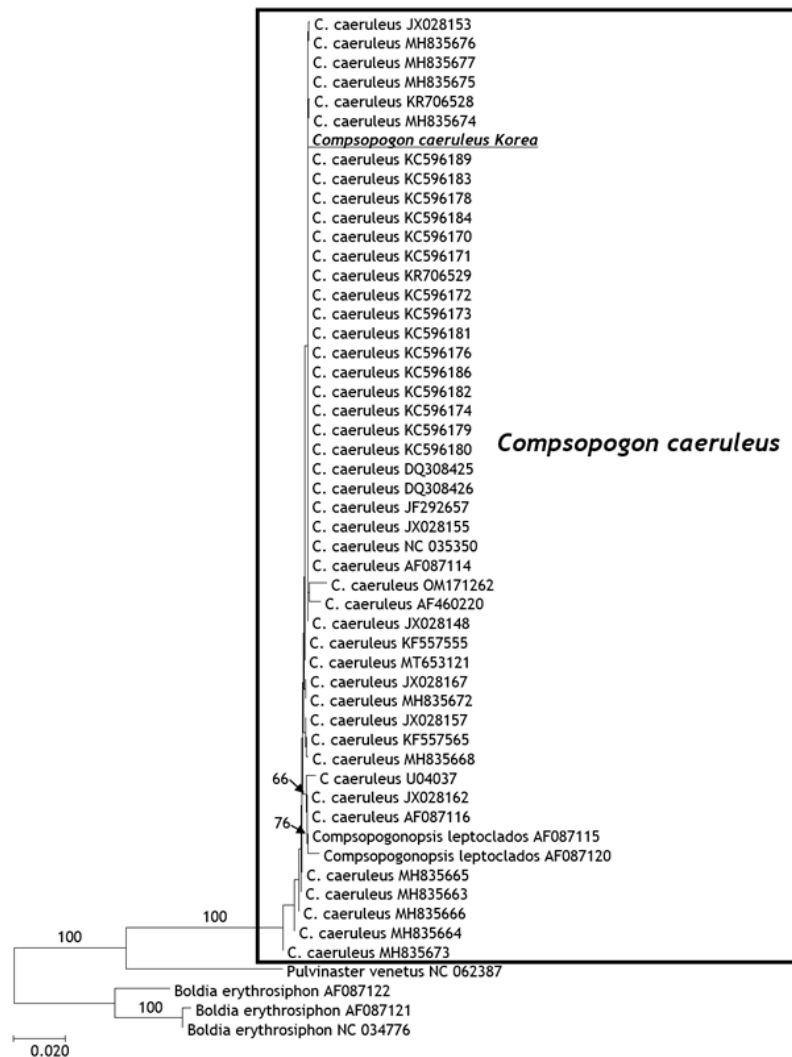


Fig. 2. Phylogenetic relationship of Korean *Compsopogon caeruleus* as first reported in this study. The neighbor-joining tree is constructed and the bootstrap value percentages (>50%) are indicated on the branches.

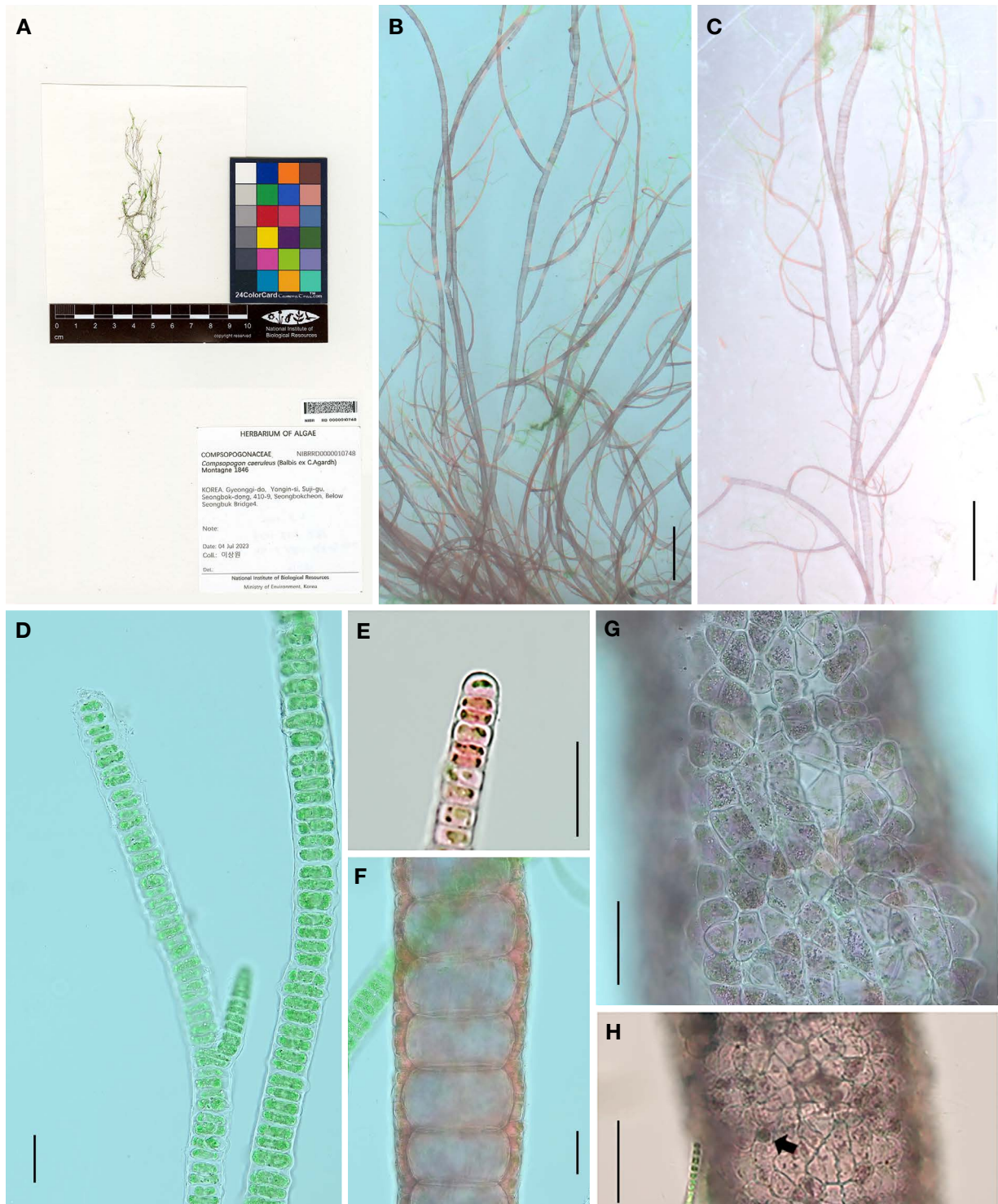


Fig. 3. Morphology of *Compsopogon caeruleus*. A. Dried specimen (NIBRRD00000010748). B. Tufted filamentous features. C. One individual body branching. D. The non-corticated young part of body. E. Apical cell of filament. F. Uniseriate part surrounded by cortical layer. G-H. Polygonal cortical cells (arrowhead indicates monosporangia). Scale bar: B. 500 μ m, C. 2 mm, D-G. 50 μ m, H. 100 μ m.

Compsopogonaceae F. Schmitz, 1896
 보라털과 (국명 신칭)
Compsopogon Montagne, 1846 보라털속 (국명 신칭)

Compsopogon caeruleus (Balbis ex C. Agardh)
 Montagne, 1846 보라털 (국명 신칭)

Fronds are minute, densely tufted, purple to red, green in color (Fig. 3A). Thalli are branched filaments, with the main axis and primary or secondary laterals, up to 8 cm in length (Fig. 3B).

The main axial filaments are uniseriate and composed of nodal cells. The branches are thinner than the main axis and become thinner toward the tip. The laterals are occasionally constricted abruptly at the base attached to the node (Fig. 3C). The size of the cell is up to 83–120 µm in length, 208–280 µm in width in axial part, and the 38–42 µm in length, 111–173 µm in width in primary branches, 13–24 µm in length, 44–48 µm in width in secondary branches.

The young part of each branch is composed of only axis cells without any cortex and is round at the apex (Fig. 3D, E). The main axis is surrounded by a 1–2 row cortical layer in the mature part (Fig. 3F). Cortex is composed of polygonal cells, 22–28 µm in diameter (Fig. 3G). Monosporangia are spherical with dense contents, solitary, which are located in cortical layer (Fig. 3H).

Specimens examined: NIBRRD0000010748, NIBRRD0000010749, and NIBRRD0000010750; Gyeonggi-do Yongin-si, Seongbok-dong 410-9; 04 July 2023.

Accession numbers: PP471840 (18S rDNA), PP477321 (*rbcL*), and PP477322 (*cox1*) (sequences derived from NIBRRD0000010748).

Basionym: *Conferva caerulea* Balbis ex C. Agardh 1824.

Synonyms:

Compsopogon aegyptiacus Aleem 1981; *Compsopogon aeruginosus* (J. Agardh) Kützing, 1849: 433; *Compsopogon chalybeus* Kützing 1849; *Compsopogon corticrassus* Chihara and Nakamura 1980: 136; *Compsopogon hoohri* Montagne 1846: 157; *Compsopogon iyengarii* Krishnamurthy 1958: 402; *Compsopogon lusitanicus* Reis 1977: 91; *Compsopogon minutus* Jao 1941: 5; *Compsopogon oishii* Okamura 1915: 128; *Compsopogon prolificus* Yadava and Kumano 1985; *Compsopogon sparsus* Xie and Ling 1998: 1; *Compsopogon tenellus* Xie and Ling 1998: 1; *Compsopogonopsis leptoclados* (Montagne) Krishnamurthy 1962: 219; *Compsopogonopsis japonica* Chihara 1976: 289 (Vis *et al.*, 1992; Necchi and Dip, 1992; Rintoul *et al.*, 1999; Sheath and Sherwood, 2002; Kitayama, 2011; Necchi *et al.*, 2013).

According to Necchi *et al.* (2013), only *Compsopogon caeruleus* is a correct name and other previously published species names under *Compsopogon* and *Compsopogonopsis* are synonyms.

Distribution and habit: Cosmopolitan, epilithic and epiphytic,

Africa: Algeria (Montagne, 1846); Asia: China (Hu and Wei, 2006; Nan *et al.*, 2016), Japan (Kitayama, 2011), Indonesia (Johnston *et al.*, 2014), Vietnam (Nguyen *et al.*, 2013); Europe: Britain (Sheath and Sherwood, 2011), Germany (Täuscher, 2011); America: Florida (Taylor,

1960), Louisiana (Taylor, 1960), Brazil (Nan *et al.*, 2016); Australia: Australia (Eloranta *et al.*, 2011); Pacific Islands: Hawaiian Islands (Sherwood, 2006).

DISCUSSION

The freshwater red algal specimens collected from Yongin, Korea was identified as *Compsopogon caeruleus* through DNA sequences analyses of the 18S rDNA, *rbcL* and *cox1* genes. This is the first report of *Compsopogon caeruleus* being identified in Korea. A BLAST search in GenBank (NCBI) revealed that DNA sequences under different species names of *Compsopogon* and *Compsopogonopsis* showed high sequence identity with the Korean specimen. Specifically, the 18S rDNA gene sequences of *Compsopogon hookeri* (AJ880416) and *Compsopogonopsis leptoclados* (AF087123, AF087125) are 100% identity, *rbcL* gene sequences of *Compsopogonopsis leptoclados* (AF087115, AF087120) showed 99.6% and 99.2% identity and *cox1* of *Compsopogon hookeri* (OP747576) had 100% identity with Korean *Compsopogon caeruleus*.

Species within the genera *Compsopogon* and *Compsopogonopsis* (*Compsopogonopsis leptoclados* (Montagne) V.K. Krishnamurthy 1962, *Compsopogon hookeri* Montagne 1846) are regarded as synonyms of *Compsopogon caeruleus* (Necchi Jr. *et al.*, 2013; Guiry and Guiry, 2022). Necchi Jr. *et al.* (2013) described the genus *Compsopogon* as a monospecific genus worldwide with *Compsopogon caeruleus* as the type species. Therefore, the sequence variation among species within the genus *Compsopogon* and *Compsopogonopsis* can be attributed to intraspecific variations of *Compsopogon caeruleus* (98.6–100% for 18S rDNA, 99–100% for *rbcL* and 97.7–100% for *cox1*). The genetic information provides robust evidence for to identify the of Korean red algae found in this study as *Compsopogon caeruleus*. Genetic analysis of samples from 24 locations worldwide, including Atlantic and Mediterranean specimens, confirmed very low genetic diversity (Nan *et al.*, 2016).

Montagne first discovered this species in Algeria in 1846, and it was later found in French Guinea. The discovery of the freshwater red alga *Compsopogon caeruleus* from an urban stream within the Yongin (Korea) provides new distribution information for this species in the East Asian region. The fronds of Korean *Compsopogon caeruleus* exhibited distinct morphological features such as green or blue-purple to red color, free floating tufted filaments, and a few mixed filaments coexisting with the dominant filamentous green algae community. Under an optical microscope, various green algae are found in a mixed state with *Compsopogon caeruleus*, so classification and ecological research on them are needed in the

further study.

Morphological examination of *Compsopogon caeruleus* revealed consistent traits, including frond color, branch pattern, and the shape of the main axis and cortex. These features align with previous reports (Xie and Ling, 1998; Kitayama, 2011; Nan et al., 2016; de Zaburlín, 2019).

The characteristics observed in our samples were within species boundaries, except for sparse branching and smaller individuals compared to the Japanese species (up to 40 cm in length) (Zhixin et al., 2006; Kitayama, 2011). Our samples did not show the short spine-like branches that develop from the cortical layer, found in the Argentinian species (de Zaburlín, 2019).

Our findings, supported by molecular and morphological evidence enhance the understanding of the global distribution of *Compsopogon caeruleus* and its presence in urban riverine ecosystems. Hypothesized spore dispersal mechanisms include migratory birds and anthropogenic activities such as shipping, aquatic plant harvesting, ship ballast water, aquarium algae and fishing (Necchi et al., 2013). Continuous monitoring of the domestic distribution of *Compsopogon caeruleus* is essential for identifying the possibility of anthropogenic introduced species and the resulting impact on the ecosystem.

CONFLICTS OF INTEREST

The author of this paper has no affiliation with any interests and is solely responsible for the paper.

ACKNOWLEDGEMENTS

We thank for collecting the sample to Mr. Lee, Sang Won, Yongin City officer and for developing the map to Dr. Kim, Taekyu, NIER researcher. This work was supported by a grant from the National Institute of Biological Resources (NIBR) (NIBR202402104), funded by Korea Ministry of Environment (MOE) and by the National Fishery Products Quality Management Service (Development & Management of Disease Control Program for Aquatic Life, NFQS2024001), Republic of Korea.

REFERENCES

- Agardh, C.A. 1824. Systema algarum. pp. [i]-xxxvii, [1]-312. Lundae [Lund]: Literis Berlingianis. Berlin.
- Aleem, A.A. 1981. *Compsopogon aegyptiacus* nov. sp., red alga from Lake Manzala, Egypt, with notes on the taxonomy of the genus. Bulletin of the Faculty of Science King Abdul Aziz University 5:59-68, 1 fig., 1 table.
- Chihara, M. 1976. *Compsopogonopsis japonica*, a new species of fresh water red algae. Japanese Journal of Botany 51:289-294.
- Chihara, M. and T. Nakamura. 1980. *Compsopogon corticrassus*, a new species of fresh water red algae (*Compsopogonaceae*, Rhodophyta). Japanese Journal of Botany 55:136-144.
- de Zaburlín, N.R.M., L.B. Guzmán, M.C. Escalada, V.M. Llano and R.E. Vogler. 2019. First record of the red alga *Compsopogon caeruleus* (Balbis ex C. Agardh) Montagne 1846 in the High Paraná River, Argentina-Paraguay. Bio-Invasions Records 8:753-763.
- Eloranta, P., J. Kwandrans and E. Kusel-Fetzmann. 2011. Rhodophyceae and Phaeophyceae. In: M. Schagerl (ed.), Süßwasserflora von Mitteleuropa Band 7. Freshwater flora of Central Europe. Volume 7, Heidelberg: Spectrum Akademischer Verlag. pp. [i]-x, [1]-155.
- Guiry, M.D. and G.M. Guiry. 2022. AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. <https://www.algaebase.org>; searched on 02 April 2024.
- Hu, H. and Y. Wei. 2006. The freshwater algae of China. Systematics, taxonomy and ecology. pp. [4 pls of 16 figs], [i-iv], i-xv, 1-1023.
- Jao, C.-C. 1941. Studies on the freshwater algae of China VIII. A preliminary account of the Chinese freshwater Rhodophyceae. Sinensia 12:245-289.
- Johnston, E.T., P-E. Lim, N. Buhari and E.J. Keil, M.I. Djawad and M.L. Vis. 2014. Diversity of freshwater red algae (Rhodophyta) in Malaysia and Indonesia from morphological and molecular data. Phycologia 53:329-341.
- Kitayama, T. 2011. First Record of *Compsopogon caeruleus* (Balbis ex C. Agardh) Montagne (*Compsopogonophyceae*, Rhodophyta) from Ogasawara Islands, Japan. Bull. Natl. Mus. Nat. Sci. Ser. B, 37(4):169-174.
- Krishnamurthy, V. 1958. The early stages of development in four species of *Compsopogon*. Phytomorphology 7:398-403.
- Krishnamurthy, V. 1962. The morphology and taxonomy of the genus *Compsopogon* Montagne. Journal of the Linnean Society of London, Botany 58:207-222.
- Kützing, F.T. 1849. Species Algarum, F. A. Brockhaus, Leipzig. vi_922 pp.
- Lee, S.-R. and E.-Y. Lee. 2018. Utility of taxon-specific molecular markers for the species identification of herbarium specimens: An example from *Desmarestia japonica* (Phaeophyceae, Desmarestiales) in Korea. Fisheries and Aquatic Sciences 21:8.
- Lee, S.-R., J.H. Oak, I.K. Chung and J.A. Lee. 2010. Effective molecular examination of eukaryotic plankton species diversity in environmental seawater using environmental PCR, PCR-RFLP, and sequencing. Journal of Applied Phycology 22:699-707.

- Millar, A.J.K. and G.T. Kraft. 1993. Catalogue of marine and freshwater red algae (Rhodophyta) of New South Wales, including Lord Howe Island, South-western Pacific. *Australian Systematic Botany* 6:1-90.
- Montagne, C. 1846. Flore d'Algérie. Ordo I. Phyceae Fries. In: M.C. Durieu De Maisonneuve (ed.), *Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842...Sciences physiques. Botanique. Cryptogamie. Vol. 1*, Paris: Imprimerie Royale, publiée par ordre du Gouvernement et avec le concours d'une Commission Académique. pp. 1-197.
- Montagne, J.F.C. 1846. Flore d'Algérie. Ordo I. Phyceae Fries. In: M.C. Durieu De Maisonneuve (ed.), *Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842...Sciences physiques. Botanique. Cryptogamie. Vol. 1*, Paris: Imprimerie Royale, publiée par ordre du Gouvernement et avec le concours d'une Commission Académique. pp. 1-197.
- Nakamura T and M. Chihara. 1983. *Compsopogon aeruginosus* and *C. hookeri* (Compsopogonaceae, Rhodophyta) newly found in Japan. *Journal of Japanese Botany* 58:54-61.
- Nan, F., J. Feng, J. Lv, Q. Liu and S. Xie. 2016. Evolutionary history of the monospecific *Compsopogon* genus (Compsopogonales, Rhodophyta). *Algae* 31:303-315.
- Necchi, Jr. O. and M.R. Dip. 1992. The family Compsopogonaceae (Rhodophyta) in Brazil. *Algological Studies* 66:105-118.
- Necchi, Jr. O., A.S.G. Fo, D. Salomaki, J.A. West, M. Aboal and M.L. Vis. 2013. Global sampling reveals low genetic diversity within *Compsopogon* (Compsopogonales, Rhodophyta). *European Journal of Phycology* 48:152-162.
- Necchi, Jr. O., C.C.Z. Branco and RRV. Gomes. 1999. Microhabitat and plant structure of *Compsopogon caeruleus* (Compsopogonaceae, Rhodophyta) populations in streams from São Paulo State, southeastern Brazil. *Cryptogamie Algologie* 20:75-87.
- Necchi, Jr. O., R.M. Goes and M.R. Dip. 1990. Phenology of *Compsopogon caeruleus* (Balbis) Montagne (Compsopogonaceae, Rhodophyta) and evaluation of taxonomic characters of the genus. *Japanese Journal of Phycology* 38:1-10.
- Nguyen, T.V., N.H. Le, S.-M. Lin, F. Steen and O.D. Clerck. 2013. Checklist of the marine macroalgae of Vietnam. *Botanica Marina*. 56:207-227.
- Okamura, K. 1915. Icones of Japanese algae 3:123-218.
- Reis, M.P. 1977. Novidade ficológicas para a ria de Aveiro. *Boletim da Sociedade Broteriana, II série* 51:91-106.
- Rintoul, T.L., R.G. Sheath and M.L. Vis. 1999. Systematics and biogeography of the Compsopogonales (Rhodophyta) with emphasis on the freshwater families in North America. *Phycologia* 38:517-527.
- Rybak, A.S. and A.M. Woyda-Ploszczyca. 2022. Tropical red alga *Compsopogon caeruleus*: an indicator of thermally polluted waters of Europe in the context of temperature and oxygen requirements. *Algae* 37:301-316.
- Saunders, G.W. 2005. Applying DNA barcoding to red macroalgae: a preliminary appraisal holds promise for future applications. *Philos. Trans. R. Soc. B* 360:1879-2188.
- Saunders, G.W. and M.H. Hommersand. 2004. Assessing red algal supraordinal diversity and taxonomy in the context of contemporary systematic data. *American Journal of Botany* 91:1494-1507.
- Schmitz, F. 1896. Compsopogonaceae. In: A. Engler and K. Prantl (eds.), *Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten insbesondere den Nutzpflanzen unter Mitwirkung zahlreicher hervorragender Fachgelehrten, Teil 1, Abteilung 2*. Leipzig: verlag von Wilhelm Engelmann. pp. 318-320.
- Sheath, R.G. and A.R. Sherwood. 2011. Phylum Rhodophyta (Red Algae). In: D.M. John, B.A. Whitton and A.J. Brook (eds.), *The freshwater algal flora of the British Isles. An identification guide to freshwater and terrestrial algae. Second edition*. Cambridge: Cambridge University Press. pp. 159-180.
- Sheath, R.G. and M.L. Vis. 2015. Red algae. In: Wehr, H., R. Sheath and J.P. Kociolek (eds.), *Freshwater Algae of North America: Ecology and Classification*. 2nd ed. Academic Press, Amsterdam. pp. 237-264.
- Sherwood, A.R. 2004. Bibliographic checklist of the non-marine algae of the Hawaiian Islands. *Records of the Hawaii Biological survey for 2003. Bishop Museum Occasional Papers* 80:1-26.
- Sherwood, A.R. 2006. Stream Macroalgae of the Hawaiian Islands: A Floristic Survey. *Pacific Science* 60:191-205.
- Skuja, H. 1939. Versuch einer systematischen Einteilung der Bangioideen oder Protofloridae. *Acta Horti Botanici Universitatis Latviensis*. 11/12:23-38.
- Tamura, K., G. Stecher, D. Peterson, A. Filipiński and S. Kumar. 2013. MEGA6: Molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution* 30:2725-2729.
- Täuscher, L. 2011. *Compsopogon* Montagne in Bory et Durieux 1846. pp. [2]. Germany (Unpublished report)
- Taylor, W.R. 1960. *Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas*. The University of Michigan Press, Ann Arbor. xi-870 pp., 14 figs, 80 pls.
- Tomás, P., J.L. Moreno, M. Aboal, J. Oscoz, C. Durán, P. Navarro and A. Elbaile. 2013. Distribución y ecología de algunas especies de rodófitos (Rhodophyta) en la cuenca del río Ebro. *Limnetica* 32:61-70.
- Vis, M.L., R.G. Sheath and K.M. Cole. 1992. Systematics of the freshwater red algal family Compsopogonaceae in North America. *Phycologia* 31:564-575.
- Xie, S.-L. and Y.-J. Ling. 1998. Two new species of *Com-*

- psopogon* (Rhodophyta) from Shanxi and Guangxi, China. *Acta Phytotaxonomica Sinica* 36:81-83.
- Yadava, R.N. and S. Kumano. 1985. *Compsopogon prolificus* sp. nov. (Compsopogonaceae, Rhodophyta) from Allahabad, Uttar Pradesh in India. *Japanese Journal of Phycology* 33:13-30.
- Zhixin, S., S. Xie and D. Hua. 2006. *Aquae dulcis*. Tomus XIII. Science press. Beijing.

Submitted: April 4, 2024

Revised: May 14, 2024

Accepted: July 1, 2024