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Newly recorded species of the genus *Synura* (Synurophyceae) from Korea

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Abstract

Background: Species in the heterokont genus *Synura* are colonial and have silica scales whose ultrastructural characteristics are used for classification. We examined the ultrastructure of silica scales and molecular data (nuclear SSU rDNA and LSU rDNA, and plastid *rbcl* sequences) to better understand the taxonomy and phylogeny within the section *Peterseniana* of genus *Synura*. In addition, we report the first finding of newly recorded *Synura* species from Korea.

Results: We identified all species by examination of scale ultrastructure using scanning and transmission electron microscopy (SEM and TEM). Three newly recorded species from Korea, *Synura americana*, *Synura conopea*, and *Synura truttiae* were described based on morphological characters, such as cell size, scale shape, scale size, keel shape, number of struts, distance between struts, degree of interconnections between struts, size of base plate pores, keel pores, base plate hole, and posterior rim. The scales of the newly recorded species, which belong to the section *Peterseniana*, have a well-developed keel and a characteristic number of struts on the base plate. We performed molecular phylogenetic analyses based on sequence data from three genes in 32 strains (including three outgroup species). The results provided strong statistical support that the section *Peterseniana* was monophyletic, and that all taxa within this section had well-developed keels and a defined number of struts on the base plate.

Conclusions: The phylogenetic tree based on sequence data of three genes was congruent with the data on scale ultrastructure. The resulting phylogenetic tree strongly supported the existence of the section *Peterseniana*. In addition, we propose newly recorded *Synura* species from Korea based on phylogenetic analyses and morphological characters: *S. americana*, *S. conopea*, and *S. truttiae*.

Keywords: *Synura americana*, *S. conopea*, *S. truttiae*, Morphology, Ultrastructure, Scale, Molecular phylogeny, Taxonomy

Background

Ehrenberg established the genus *Synura* in 1834 (Ehrenberg 1834), with *S. uvella* as the type species. *Synura* is the most common and widespread genus in many phytoplankton floras (Kristiansen & Preisig 2007). The species in this genus are colonial flagellates with two visible flagella and two chloroplasts, and are covered by imbricate silica scales. Several scale morphologies (apical scales, body scales, transition scales, and caudal scales) occur at different locations on the surface of the same cell. These body scales are the most important character for species identification (Kristiansen & Preisig 2007).

Early classification of *Synura* species using light microscopy (LM) was based largely on features such as cell size and shape, general outline of scales, and the spine or keel (Ehrenberg 1834). Previous taxonomical studies of *Synura* have traditionally stressed the distinguishing features of these scales.

The classification of *Synura* species using electron microscopy (EM) is based on scale ultrastructure (Korshikov 1929; Petersen & Hansen 1956; Petersen & Hansen 1958; Fott & Ludvík 1957; Asmund 1968; Balonov & Kuzmin 1974; Péterfi & Momeu 1977; Takahashi 1967; Takahashi 1972; Takahashi 1973; Takahashi 1978; Cronberg 1989; Škaloud et al. 2012; Škaloud et al. 2013; Škaloud et al. 2014). In fact, examination of the ultrastructural features of the silica scales has revolutionized *Synura* taxonomy. The first classification scheme to consider scale ultrastructure

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suggested that the genus *Synura* is divided into two sections: *Petersenianae* and *Uvellae* (Petersen & Hansen 1956). Subsequent classification schemes have made additional subgeneric distinctions (Balonov & Kuzmin 1974; Péterfi & Momeu 1977; Takahashi 1967; Takahashi 1972; Takahashi 1973; Takahashi 1978; Cronberg 1989).

The first molecular analyses investigated the genetic variability in 15 individuals of *Synura petersenii* by comparison of nuclear internal transcribed spacer (ITS) sequences (Wee et al. 2001). Subsequent molecular analyses examined ITS sequences from 21 other individuals (Kynčlová et al. 2010). Also, phylogenetic analyses investigated about 100 *S. petersenii* using seven-protein gene and confirmed the high degree of cryptic, species-level diversity within this nominal species (Boo et al. 2010). A recent taxonomic assessment of observed cryptic diversity redefined the species concept within the *S. petersenii* morphotype and recognized six cryptic lineages as separate species: *Synura americana*, *Synura conopea*, *Synura glabra*, *Synura macropora*, *Synura petersenii*, and *Synura truttiae* (Škaloud et al. 2012). Most recently, the classification of *Synura* described an additional four new species within the *S. petersenii* species complex based on scale morphology and sequence data (ITS, *rbcL*, and *cox1*) (Škaloud et al. 2014).

Several researchers have studied the genus *Synura* from different regions in Korea by the use of EM (Kim 1997). These studies described nine species and provided very short descriptions based on scale ultrastructure (Kim 1997; Kristiansen 1990). Most recently, the first molecular multigene phylogeny of a large number of *S. petersenii* confirmed the high degree of cryptic, species-level diversity (Boo et al. 2010).

The purpose of the present study was to provide a better understanding of the taxonomy and molecular phylogeny within the section *Petersenianae* of genus *Synura* by analysis of the ultrastructure of the silica scales and molecular data (nuclear SSU rDNA and LSU rDNA, and plastid *rbcL* sequences) and to describe three species of *Synura* that are new to Korea.

Methods

Strains and cultures

The information and accession numbers for the 32 strains (including three outgroup species) examined in this study are in Table 1. Strains were either obtained from culture collections or collected with a 20- μ m mesh plankton net (Bokyeong Co., Pusan, Korea) from small ponds in Korea. The details of the culture methods were previously published (Jo et al. 2011; Jo et al. 2013).

Morphological investigations

For field emission scanning electron microscopy (SEM), cells were filtered using nylon membrane filters (Whatman Ltd., Maidstone, UK), rinsed in distilled water, fixed in 1%

OsO₄, dehydrated, and then prepared and viewed as described previously (Jo et al. 2011). Voucher specimens were stored at the Kyungpook National University Herbarium. For field emission transmission electron microscopy (TEM), cells were prepared by air drying onto formvar coated copper grids. The grids were viewed in a JEM 1010 TEM (JEOL Ltd., Tokyo, Japan) at 80 kV. Images were recorded on Kodak EM Film 4489 (Eastman Kodak Co., Rochester, NY, USA) and scanned to digital format using an Epson Perfection V700 Photo scanner (Epson Korea Co., Ltd, Seoul, Korea). The terminology used to describe scale ultrastructure follows a previous method (Škaloud et al. 2012).

DNA extraction, amplification, sequence alignment, and phylogenetic analyses

DNA extraction, PCR amplification, PCR product purification, and sequence alignment were conducted as previously described (Jo et al. 2011; Jo et al. 2013). Phylogenetic analyses were performed using a combined dataset of 5011 characters (nr SSU rDNA = 1638, nr LSU rDNA = 2548, and pt *rbcL* = 825) by maximum likelihood (ML) and Bayesian inference (BI). Although nuclear ITS1 and ITS2 sequences were also determined, these sequences were used to examine groups of genetically identical strains and as a barcode to identify species. The sequences of three species of Chrysophyceae (*Chromulina* sp., *Ochromonas danica*, and *Ochromonas* sp.) were used as outgroups to root the tree. Primer regions and ambiguously aligned regions were removed prior to phylogenetic analyses. Prior to ML analysis, the best-fit model for individual and concatenated data sets was traced under Bayesian information criterion (BIC) using Modeltest 3.7 (Posada & Crandall 1998). GTR + I + G model for all the individual and concatenated data sets was selected. We used the GTR + I + G nucleotide model as implemented in RAxML v8 (Stamatakis 2014). Bayesian analyses were run using MrBayes 3.2 (Ronquist et al. 2012) with a random starting tree and ran for 2×10^6 generations, keeping on tree every 1000 generations. The burn-in point was identified graphically by tracking the likelihoods in Tracer v.1.6 (Rambaut et al. 2013). Trees were visualized using the FigTree v.1.4.2 program (Rambaut A. FigTree v1.4.2 2014). Each analysis was conducted as previously described (Jo et al. 2011; Jo et al. 2013).

Results and discussion

Morphological characteristics

We identified all species based on scale ultrastructure from SEM and TEM. This analysis led to identification of three species that are new to Korea: *S. americana*, *S. conopea*, and *S. truttiae* (Figs. 1, 2 and 3 and Table 2). The scales of the newly recorded species, all in the section

Table 1 List of strains used in the molecular study and GenBank accession number

Taxa/strain	Nuclear ITS	Nuclear SSU	GenBank accession	Nuclear LSU	Plastid <i>rbcl</i>
<i>S. americana</i> Kynčlová and Škaloud					
Chimu112407C	KP268712	KM590551		KM590617	KM590838
Joha010508F	KP268711	JX455151		JX455155	JX455147
CCMP862	GU338124	GU325583		—	GU325485
CCMP863	GU338125	GU325584		—	GU325486
KNUJO-CM20151226	KX610938	KX610941		KX610944	KX6109447
<i>S. asmundiae</i> (Cronberg and Kristiansen) Škaloud, Kristiansen and Škaloudová					
S90D10	KP268729	KM590553		KM590619	KM590840
S90D11	KP268730	HF549069		—	HF549079
<i>S. bjoerkii</i> (Cronberg and Kristiansen) Škaloud, Kristiansen and Škaloudová					
SC57A6	KP268731	HF549070		—	HF549080
<i>S. coropea</i> Kynčlová and Škaloud					
Sugyej041808B	KP268690	KM590557		KM590623	KM590844
Yeonseong120807E	KP268689	KM590558		KM590624	KM590845
CCMP859	GU338121	GU325580		—	GU325482
NIES1007	GU338119	GU325578		—	GU325479
KNUJO-YG20160117	KX610939	KX610942		KX610945	KX6109448
<i>S. glabra</i> Korshikov emend. Kynčlová and Škaloud					
Bonggye101407K	KP268722	KM590564		KM590630	KM590851
Cheonma041908B	KP268716	KM590565		KM590631	KM590852
Dohak111107C	KP268721	JX455149		JX455153	JX455145
Geumma020610B	KP268718	KM590568		KM590634	KM590855
Hwangsan012508A	KP268724	KM590571		KM590637	KM590858
<i>S. macracantha</i> (Petersen and Hansen) Asmund					
S90B5	KP268732	HF549064		KM590648	HF549075
<i>S. petersenii</i> Korshikov emend. Škaloud and Kynčlová					
Buje100307A	KP268710	KM590586		KM590657	KM590873
Gangak111107C	KP268707	KM590587		KM590658	KM590874
Swaeji103109I	KP268705	KM590589		KM590660	KM590876
Yongseong112407A	KP268706	KM590590		KM590661	KM590877

Table 1 List of strains used in the molecular study and GenBank accession number (*Continued*)

Youngji101407A	KP268708	JX455150	JX455154	JX455146
<i>S. truttae</i> (Siver) Škaloud and Kynčlová				
Hanjeong080611J	KP268702	KM590609	KM590680	KM590896
Jangjuk032611J	KP268703	KM590610	KM590681	KM590897
CAUP2	GU338138	GU325598	—	GU325500
CAUPD5	GU338140	GU325600	—	GU325502
KNUJJO-HJ20151222	KX610940	KX610943	KX610946	KX610949
<i>Chromulina</i> sp.				
SAG 17.97	—	EF165103	GU935638	EF165151
<i>Ochromonas danica</i> Pringsheim				
SAG 933.7	—	JQ281514	GU935636	GU935657
<i>Ochromonas</i> sp.				
SAG 933.10	—	EF165109	GU935637	GU935658

New sequences are indicated in italic type

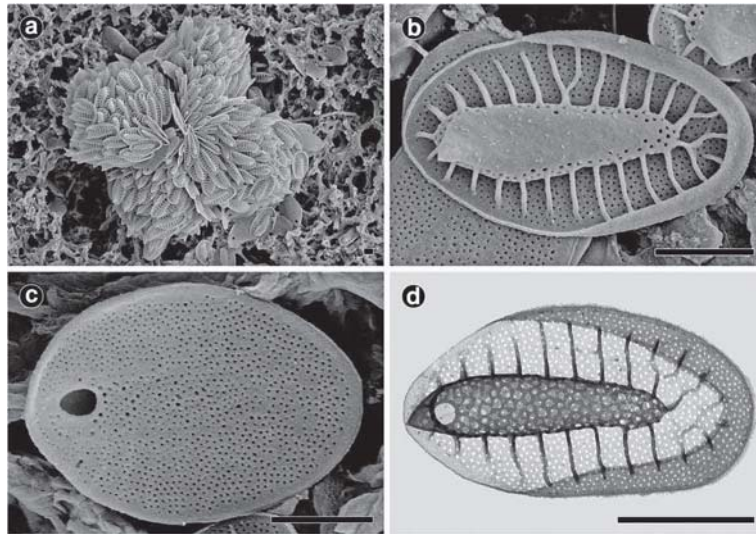


Fig. 1 Morphology of the colony and scales of *Synura americana* (a–c: SEM, d: TEM). All scale bars, 1 μm . **a** SEM image of colony forming cells. **b** Top surface of a body scale. **c** Bottom surface of a body scale. **d** TEM image of body scale

Peterseniana, have well-developed keels and a number of struts on the base plate. The terminology used to describe the ultrastructure of these scales follows a previous method (Škaloud et al. 2012). Other studies have described newly recorded species of *Synura* from Korea based on morphological characters, such as cell size, scale shape, scale size, keel shape, number of struts, distance between struts, degree of interconnections between struts, size of the base plate pores, keel pores, base plate hole, and posterior rim (Škaloud et al. 2012). Two of our species (*S. americana* and *S. conopea*) are morphologically similar to *S. petersenii*, suggesting a close relationship. *S. conopea* was most similar to

S. petersenii in terms of cell shape and transverse folds, although these species differ in keel reticulation. *S. conopea* is distinguished by its smaller scales and its large and closely arranged keel pores. *S. americana* is characterized by rounded scales, a near absence of transverse folds, an occasionally triangular keel, and long rear scales. *S. truttae* is characterized by small scale size, keel tips, large base plate hole, and short distance between struts.

Taxonomic description

S. americana Kynčlová and Škaloud 2012 (Fig. 1)

Reference: Škaloud et al. 2012, p. 320, Figs. 62–69.

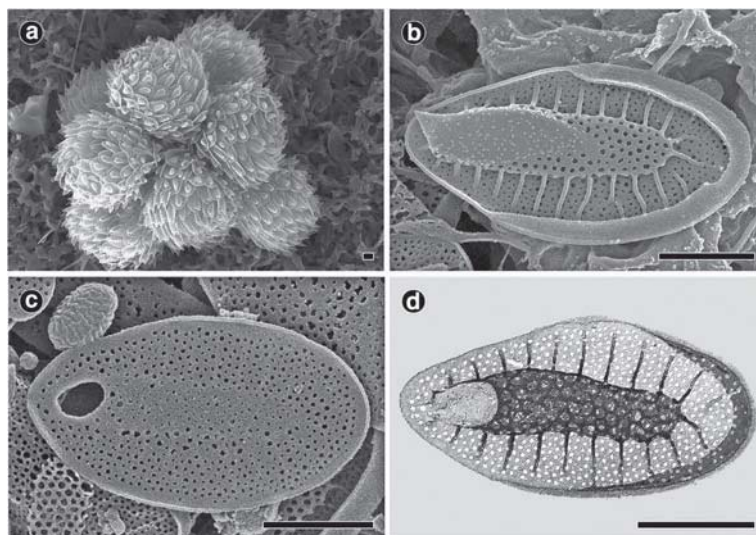


Fig. 2 Morphology of the colony and scales of *Synura conopea* (a–c: SEM, d: TEM). All scale bars, 1 μm . **a** SEM image of colony forming cells. **b** Top surface of a body scale. **c** Bottom surface of a body scale. **d** TEM image of a body scale

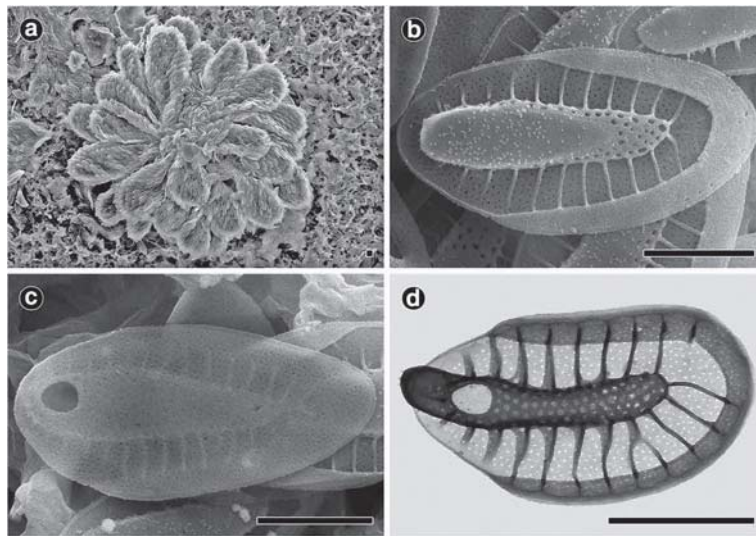


Fig. 3 Morphology of the colony and scales of *Synura truttiae* (a–c: SEM, d: TEM). All scale bars, 1 μm . **a** SEM image of colony forming cells. **b** Top surface of a body scale. **c** Bottom surface of a body scale. **d** TEM image of a body scale

Specimens examined: KNUJO-CM20151226.

Description: Colonies globular and 22–51 μm in diameter (Fig. 1a). Cells pyriform (22–28 \times 8–12 μm) and entirely covered by rounded scales (Fig. 1a). Body scales 3.0–4.2 \times 1.7–2.3 μm (Fig. 1b–d). The keel often terminates at an acute tip (Fig. 1b) and is ornamented by medium-sized pores (Fig. 1d). In some cases, the keel is wider in the anterior region, giving it a triangular shape (Fig. 1b). The basal plate, ornamented by numerous small pores, is anteriorly perforated by a rounded base plate hole that is 0.08–0.27 μm in diameter (Fig. 1b–d). Numerous struts (21–24) extend regularly from the keel to the edge of the scale but almost never interconnect the transverse folds (Fig. 1b and d). The spacing between struts is 0.27–0.30 μm (Fig. 1b and d).

Site of collection: Chimu, Daesan-myeon, Haman-gun, Gyeongsangnam-do, Korea (35°20'21"N, 128°25'47"E).

Date of collection: 26 Dec 2015.

Distribution: Widely distributed. Canada (Wee et al. 2001), Colombia (Cronberg 1989), Czech Republic (Škaloud et al. 2012; Kynčlová et al. 2010), Denmark (Kristiansen 1988), Germany (Kies & Berndt 1984), Korea (Boo et al. 2010, this study), North America (Kling & Kristiansen 1983; Kristiansen 1975; Wee 1981), and USA (Wee et al. 2001; Boo et al. 2010).

***S. conopea* Kynčlová and Škaloud 2012 (Fig. 2)**

Reference: Škaloud et al. 2012, p. 324, Figs. 78–85.

Specimens examined: KNUJO-YG20160117, NIBRFL0000131748, and NIBRFL0000131749.

Description: Colonies globular and 25–47 μm in diameter (Fig. 2a). Cells pyriform (20–28 \times 8–12 μm) and entirely covered by lanceolate scales (Fig. 2a). Body scales 3.3–4.1 \times

1.4–1.9 μm (Fig. 2b–d). The keel terminates at an acute tip (Fig. 2b) and is usually broadened apically and ornamented by medium to large-sized pores (Fig. 2d). The basal plate, ornamented by numerous medium-sized pores, is anteriorly perforated by a round to oblong base plate hole that is 0.19–0.32 μm in diameter (Fig. 2b–d). Numerous struts (24–30) extend regularly from the keel to the edge of the scale but are usually not interconnected by transverse folds (Fig. 2b and d). The spacing between struts is 0.23–0.26 μm (Fig. 2b and d).

Site of collection: Yongji, Yongchon-ri, Toseong-myeon, Goseong-gun, Gangwon-do, Korea (38°13'43"N, 128°33'49"E).

Date of collection: 17 Jan 2016.

Distribution: Widely distributed. Argentina (Vigna & Munari 2001), Brazil (Couté & Franceschini 1988), Czech Republic (Škaloud et al. 2012; Kynčlová et al. 2010), Greenland (Jacobsen 1985), Ireland (Řezáčová & Škaloud 2005), Japan (Boo et al. 2010), and Korea (Boo et al. 2010, this study).

***S. truttiae* (Siver 1987) Škaloud and Kynčlová 2012 (Fig. 3)**

Basionym: *S. petersenii* f. *truttiae* (Siver 1987), p. 111, Figs. 12–14.

Reference: Škaloud et al. 2012, p. 318, Figs. 52–61.

Specimens examined: KNUJO-HJ20151222.

Description: Colonies globular and 35–48 μm in diameter (Fig. 3a). Cells pyriform (22–31 \times 11–13 μm) and entirely covered by lanceolate scales (Fig. 3a). Body scales elongated and 3.3–3.8 \times 1.5–1.8 μm (Fig. 3a–d). The keel of the body scales has no apparent tip or a much reduced tip and is ornamented by small pores (Fig. 3b). The keel tip frequently has several (two to

Table 2 Summary of the major characteristic features observable with EM used in this study to distinguish between taxa of the section *Peterseniinae*

Taxon	Cell size (μm)	Scale size (μm)	Base plate hole size (μm)	Number of struts	Distance of struts (μm)	Interconnection of struts by transverse folds	Other
<i>S. americana</i> Kynčlová & Škaloud	22–28 × 8–12	*3.0–4.2 × 1.7–2.3	0.08–0.27	21–24	0.27–0.30	Almost never interconnected	Occasional triangular shape of the keel
<i>S. conopea</i> Kynčlová & Škaloud	20–28 × 8–12	*3.3–4.1 × 1.4–1.9	0.19–0.32	24–30	0.23–0.26	Usually not interconnected	Large and closely arranged keel pores
<i>S. glabra</i> Korshikov emend. Kynčlová & Škaloud	19–28 × 10–14	*2.4–3.4 × 1.5–2.4	0.14–0.32	17–22	0.25–0.29	Never interconnected	With a small, narrow and sometimes bent keel
<i>S. petersenii</i> Korshikov emend. Škaloud & Kynčlová	20–31 × 8–12	*3.6–4.6 × 1.8–2.3	0.24–0.36	26–34	0.24–0.28	Mainly interconnected	Large scale dimensions, common presence of transverse folds
<i>S. truttiae</i> (Siver) Škaloud & Kynčlová	22–31 × 11–13	*3.3–3.8 × 1.5–1.8	0.32–0.56	27–33	0.19–0.24	Mainly interconnected	Keel tip has several (two to four) very short teeth on its top end and large base plate hole

*The dimensions of body scales

four) very short teeth on its top (Fig. 3d) and is covered by a number of small bumps. The basal plate, ornamented by numerous small pores, is anteriorly perforated by a large, round to oblong base plate hole that is 0.32–0.56 μm in diameter (Fig. 3b–d). Numerous struts (27–33), which are often interconnected, regularly extend from the keel to the edge of the scale (Fig. 3b and d). Scales with nearly absent transverse folds (Fig. 3b–d). The spacing between struts is 0.19–0.24 μm (Fig. 3b and d).

Site of collection: Hanjeong, Girin-ri, Soseong-myeon, Jeongeup-si, Jeollabuk-do, Korea (35°33'55"N, 126°46'30"E).

Date of collection: 22 Dec 2015.

Distribution: Widely distributed. Czech Republic (Škaloud et al. 2012; Kynčlová et al. 2010), Korea (This study), and USA (Siver 1987; Siver & Wujek 1993; Siver & Lott 2004).

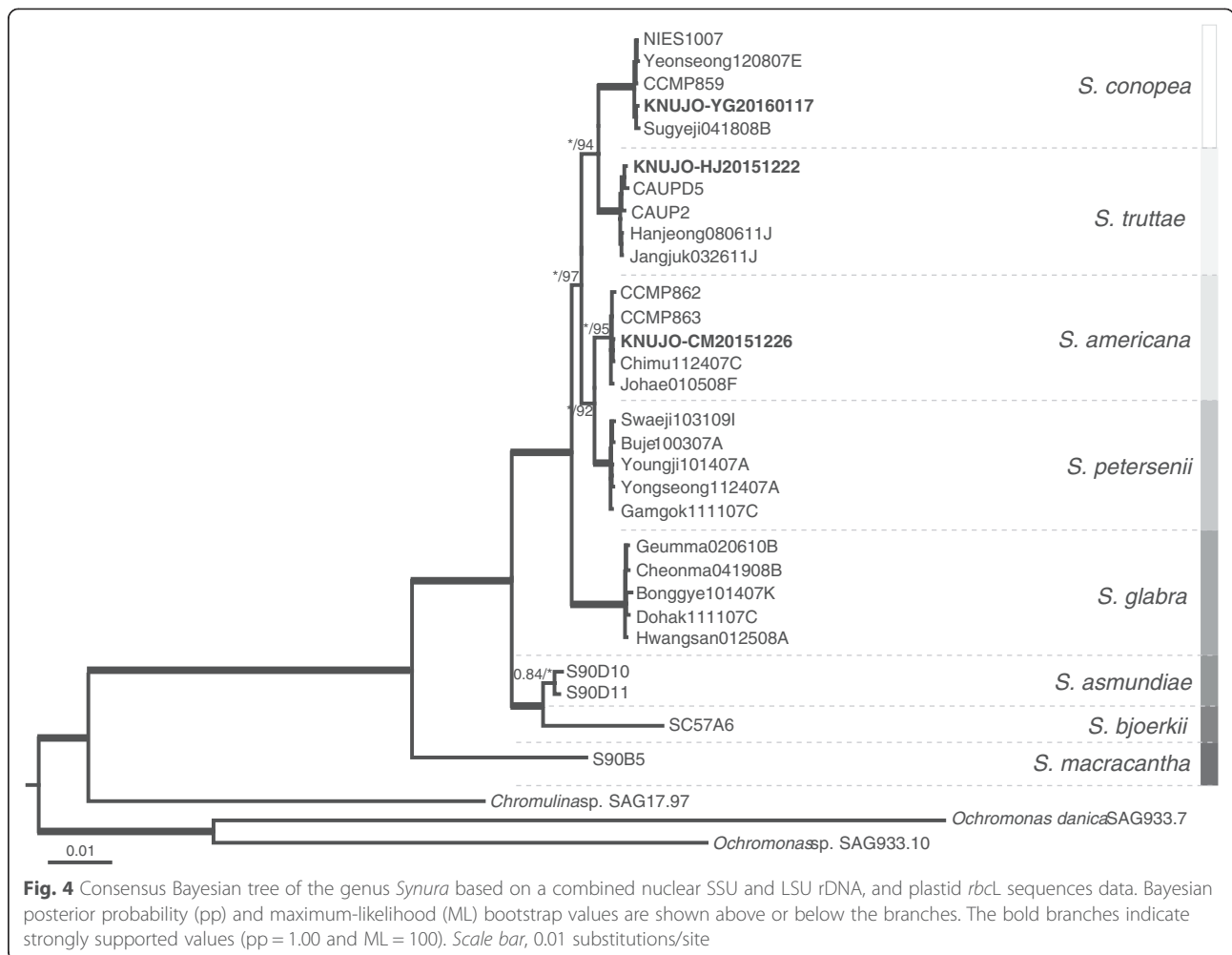
Molecular data

The 5011 nucleotides of the combined data set (nuclear SSU and LSU rDNA, and plastid *rbcL*) were determined

for 32 strains (Table 1). Although the nuclear ITS1, 5.8S, and ITS2 sequences were also determined, these sequences were only used for to confirm identification, not to assess phylogenetic relationships. The combined sequences had 5011 nucleotides, 4039 variable sites, and 725 parsimoniously informative sites. The molecular data contained 12 new sequences (3 new nr SSU rDNA sequences, 3 new nr LSU rDNA sequences, 3 new nr ITS sequences, and 3 new pt *rbcL* sequences) and 102 published sequences (29 nr SSU rDNA sequences, 20 nr LSU rDNA sequences, 25 nr ITS sequences, and 28 pt *rbcL* sequences).

Phylogenetic analyses

We analyzed nr SSU and LSU rDNA, and pt *rbcL* sequences from 32 strains (including three outgroup species). The phylogenetic tree based on the Bayesian analysis was rooted with three species of Chromulinaceae serving as outgroups. The Bayesian and ML analyses recovered a tree with identical topologies (Fig. 4). The phylogenetic tree consisted of species of the section *Peterseniana*, each of which has a well-developed keel and a number of struts on



the base plate. The section *Petersenianae* formed a strongly supported monophyletic lineage (pp = 1.00 and ML = 100). The single strain of *Synura macracantha* diverged at the base of the tree, followed by *Synura bjoerkii* and *Synura asmundiae*. The single strain of *S. bjoerkii* was closely related to *S. asmundiae*, which included two strains (pp = 1.00 and ML = 100). *Synura glabra* formed a sister group with *S. americana*, *S. conopea*, *S. petersenii*, and *S. truttiae* (pp = 1.00 and ML = 100), and *S. americana* and *S. petersenii* diverged at the next *S. glabra*. The five strains of *S. petersenii* formed a strongly supported monophyletic lineage (pp = 1.00 and ML = 100) and was a sister group to the five strains of *S. americana*, which included KNUJO-CM20151226 (pp = 1.00 and ML = 92). The five strains of *S. americana* were monophyletic group (pp = 1.00 and ML = 95), and the intraspecific similarity based on nuclear ITS rDNA sequence data ranged from 99.9% to 100.0%. The five strains of *S. truttiae* (including KNUJO-HJ20151222) were a sister group to the five strains of *S. conopea*, which included KNUJO-YG20160117 (pp = 1.00 and ML = 94). The five strains of *S. conopea* formed a monophyletic lineage with strong support values (pp = 1.00 and ML = 100), and the intraspecific similarity based on nuclear ITS rDNA sequence data ranged from 98.5% to 100.0%. The five strains of *S. truttiae* formed a monophyletic lineage with strong support values (pp = 1.00 and ML = 100), and the intraspecific similarity based on nuclear ITS rDNA sequence data was 100.0%.

Conclusions

In summary, we used molecular analysis of three genes and data on the scale ultrastructure to investigate the phylogenetic relationships within *Synura*, with a focus on the section *Petersenianae*. The phylogenetic tree based on a combined dataset was well congruent with the ultrastructural characteristics of scales. The phylogenetic tree was comprised of members of the section *Petersenianae*. The section *Petersenianae* was monophyletic with strong support values and characterized by a well-developed keel and a number of struts on the base plate. In addition, our morphological observations and molecular analyses confirmed unambiguously that this is the first report of *S. americana*, *S. conopea*, and *S. truttiae* in Korea.

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Availability of data and materials

The sequence data from this study were deposited in GenBank with the accession codes KX610938–KX610949.

Authors' contributions

Both authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

Consent for publication

Not applicable.

Ethics approval and consent to participate

Not applicable.

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References

- Asmund, B. (1968). Studies on Chrysophyceae from some ponds and lakes in Alaska. VI. Occurrence of *Synura* species. *Hydrobiologia*, 31, 497–515.
- Balonov, I. M., & Kuzmin, G. V. (1974). Vidy roda *Synura* Ehrenberg (Chrysophyta) v vodokhranilischchakh Volzhskogo Kaskada. *Botanicheskii Zhurnal*, 59, 1675–1686.
- Boo, S. M., Kim, H. S., Shin, W., Boo, G. H., Cho, S. M., Jo, B. Y., Kim, J. H., Kim, J. H., Yang, E. C., Siver, P. A., Wolfe, A. P., Bhattacharya, D., Andersen, R. A., & Yoon, H. S. (2010). Complex phylogeographic patterns in the freshwater alga *Synura* provide new insights into ubiquity vs. endemism in microbial eukaryotes. *Molecular Ecology*, 19, 4328–4338. doi:10.1111/j.1365-294X.2010.04813.x.
- Couté, A., & Franceschini, I. M. (1988). Scale-bearing chrysophytes from acid waters of Florianópolis, Santa Catarina Island, South Brazil. *Algological Studies*, 88(Suppl 123), 37–66.
- Cronberg, G. (1989). Scaled chrysophytes from the tropics. *Nova Hedwigia Beiheft*, 95, 191–232.
- Ehrenber, C. G. (1834). Dritter Beitrag zur Erkenntnis grosser Organisation in der Richtung des kleinsten Raumes. *Abhandlungen der Königlichen Akademie der Wissenschaften Berlin*, 1833, 145–336.
- Fott, B., & Ludvík, J. (1957). Die submikroskopische Struktur der Kieselschuppen bei *Synura* und ihre Bedeutung für die Taxonomie der Gattung. *Preslia*, 29, 5–16.
- Jacobsen, B. A. (1985). Scale-bearing Chrysophyceae (Mallomonadaceae and Paraphysomonadaceae) from West Greenland. *Nordic Journal of Botany*, 5, 381–398.
- Jo, B. Y., Shin, W., Boo, S. M., Kim, H. S., & Siver, P. A. (2011). Studies on ultrastructure and three-gene phylogeny of the genus *Mallomonas* (Synurophyceae). *Journal of Phycology*, 47, 415–425. doi:10.1111/j.1529-8817.2010.00953.x.
- Jo, B. Y., Shin, W., Kim, H. S., Siver, P. A., & Andersen, R. A. (2013). Phylogeny of the genus *Mallomonas* (Synurophyceae) and descriptions of five new species on the basis of morphological evidence. *Phycologia*, 52, 266–278. doi:10.2216/12-107.1.
- Kies, L., & Berndt, H. (1984). Die *Synura*-Arten (Chrysophyceae) Hamburgs und seiner nordöstlichen Umgebung. *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg*, 19, 99–122.
- Kim, H. S. (1997). Silica-scaled chrysophytes (Synurophyceae) in several reservoirs, swamps, and a highland pond from Changnyong County, Korea. *Algae*, 12, 1–10.
- Kling, H. J., & Kristiansen, J. (1983). Scale-bearing Chrysophyceae (Mallomonadaceae) from Central and Northern Canada. *Nordic Journal of Botany*, 3, 269–290.
- Korshikov, A. (1929). Studies on the chrysomonads I. *Archiv für Protistenkunde*, 67, 253–290.
- Kristiansen, J. (1975). Chrysophyceae from Alberta and British Columbia. *Syysis*, 8, 97–108.
- Kristiansen, J. (1988). Seasonal occurrence of silica-scaled chrysophytes under eutrophic conditions. *Hydrobiologia*, 161, 171–184.
- Kristiansen, J. (1990). Studies on silica-scaled chrysophytes from Central Asia. *Archiv für Protistenkunde*, 138, 298–303.
- Kristiansen, J., & Preisig, H. R. (2007). Chrysophyte and Haptophyte algae. 2. Teil/ Part 2: synurophyceae. In B. Büdel, G. Gärtner, L. Krienitz, H. R. Preisig, & M. Schagerl (Eds.), *Süßwasserflora von Mitteleuropa* (p. 252). Berlin, Heidelberg: Spektrum Akademischer Verlag.
- Kynčlová, A., Škaloud, P., & Škaloudová, M. (2010). Unveiling hidden diversity in the *Synura petersenii* species complex (Synurophyceae, Heterokontophyta). *Nova Hedwigia Beiheft*, 136, 283–298. doi:10.1127/1438-9134/2010/0136-0283.
- Péteri, L. S., & Momeu, L. (1977). Remarks on the taxonomy of some *Synura* species based on the fine structure of scales. *Muzeul Brukenthal Studii si Comunicări-Stiințe Naturale*, 21, 15–23.
- Petersen, J. B., & Hansen, J. B. (1956). On the scales of some *Synura* species. *Biol Medd Kgl. Danske Videnskaberne Selskab*, 23(2), 3–27.

- Petersen, J. B., & Hansen, J. B. (1958). On the scales of some *Synura* species. II. *Biol Medd Kgl Danske Videnskabernes Selskab*, 23(7), 1–13.
- Posada, D., & Crandall, K. A. (1998). MODELTEST: testing the model of DNA substitution. *Bioinformatics*, 14(9), 817–8. doi:10.1093/bioinformatics/14.9.817.
- Rambaut A. FigTree v1.4.2. 2014. Available online at: <http://tree.bio.ed.ac.uk/software/figtree/>
- Rambaut A, Suchard MA, Drummond AJ. Tracer v1.6. 2013. Available online at: <http://tree.bio.ed.ac.uk/software/tracer/>.
- Řezáčová, M., & Škaloud, P. (2005). Silica-scaled chrysophytes of Ireland. With an appendix: geographic variation of scale shape of *Mallomonas caudata*. *Nova Hedwigia Beiheft*, 128, 101–124.
- Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A., & Huelsenbeck, J. P. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61(3), 539–42. doi:10.1093/sysbio/sys029.
- Siver, P. A. (1987). The distribution and variation of *Synura* species (Chrysophyceae) in Connecticut, USA. *Nordic Journal of Botany*, 7, 107–116. doi:10.1111/j.1756-1051.1987.tb00922.x.
- Siver, P. A., & Lott, A. M. (2004). Further observations on the scaled Chrysophyceae and Synurophyceae flora of the Ocala National Forest, Florida, USA. *Nordic Journal of Botany*, 24, 211–233. doi:10.1111/j.1756-1051.2004.tb00835.x.
- Siver, P. A., & Wujek, D. E. (1993). Scaled Chrysophyceae and Synurophyceae from Florida, USA. IV. The flora of Lower Lake Myakka and Lake Tarpon. *Florida Scientist (USA)*, 56, 109–117.
- Škaloud, P., Kristiansen, J., & Škaloudová, M. (2013). Developments in the taxonomy of silica-scaled chrysophytes from morphological and ultrastructural to molecular approaches. *Nordic Journal of Botany*, 31, 385–402. doi:10.1111/j.1756-1051.2013.00119.x.
- Škaloud, P., Kynčlová, A., Benada, O., Kofroňová, O., & Škaloudová, M. (2012). Toward a revision of the genus *Synura*, section Petersenianae (Synurophyceae, Heterokontophyta): morphological characterization of six pseudo-cryptic species. *Phycologia*, 51, 303–329. <http://dx.doi.org/10.2216/11-20.1>.
- Škaloud, P., Škaloudová, M., Procházková, A., & Němcová, Y. (2014). Morphological delineation and distribution patterns of four newly described species within the *Synura petersenii* species complex (Chrysophyceae, Stramenopiles). *European Journal of Phycology*, 49, 213–229. doi:10.1080/09670262.2014.905710.
- Stamatakis, A. (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30(9), 1312–3. doi:10.1093/bioinformatics/btu033.
- Takahashi, E. (1967). Studies on genera *Mallomonas*, *Synura* and other plankton in fresh-water with the electron microscope. VI. Morphological and ecological observations on genus *Synura* in ponds and lakes in Yamagata Prefecture. *Bulletin Yamagata University Agricultural Science*, 5, 99–118.
- Takahashi, E. (1972). Studies on genera *Mallomonas* and *Synura*, and other plankton in freshwater with electron microscope. VIII. On three new species of Chrysophyceae. *The botanical magazine= Shokubutsu-gaku-zasshi*, 85, 293–302.
- Takahashi, E. (1973). Studies on genera *Mallomonas* and *Synura*, and other plankton in fresh water with the electron microscope VII. New genus *Spiniferomonas* of the Synuraceae (Chrysophyceae). *The botanical magazine= Shokubutsu-gaku-zasshi*, 86, 75–88.
- Takahashi, E. (1978). *Electron microscopical studies of the Synuraceae (Chrysophyceae) in Japan: taxonomy and ecology*. Tokyo: Tokai University Press.
- Vigna, M. S., & Munari, C. (2001). Seasonal occurrence of silica scales chrysophytes in a Buenos Aires lake. *Nova Hedwigia Beiheft*, 122, 195–209.
- Wee, J. L. (1981). Studies on silica-scaled chrysophytes from Iowa. II. Common *Synura* species. *Proceedings of the Iowa Academy of Sciences*, 88, 70–73.
- Wee, J. L., Fasone, L. D., Sattler, A., Starks, W. W., & Hurley, D. L. (2001). ITS/5.8S DNA sequence variation in 15 isolates of *Synura petersenii* Korshikov (Synurophyceae). *Nova Hedwigia Beiheft*, 122, 245–258.

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