

Research Article

Akira F. Peters*, Liliana A. Muñoz, Niko R. Johansson, Anastasia Rizouli, Michael D. Guiry, Ga Youn Cho and Frithjof C. Küpper

Cosmopolitan geographic distribution of *Phaeosaccion multiseriatum* (Phaeosacciaceae, Phaeosacciophyceae), and description of *P. westermeieri* sp. nov. from Chile

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Abstract: The minute marine multicellular heterokont alga originally described as “*Giraudyopsis stellifer*” by P.J.L. Dangeard, *nom. inval.*, from Atlantic France, was re-isolated by the germling emergence technique and classified according to *psaA* and *psbC* sequences. It is genetically similar (99–100 % identity) to *Phaeosaccion multiseriatum* R.A. Andersen, L. Graf *et* H.S. Yoon recently described from the NE Pacific, an ephemeral alga of wide geographical distribution. We isolated it also from substratum samples collected in Korea and the Falkland Islands, where it had

not been reported previously. Two isolates of similar morphology from the coast of Chile had the same nuclear ribosomal SSU sequence but differed from *P. multiseriatum* and *P. okellyi* R.A. Andersen, L. Graf *et* H.S. Yoon from New Zealand in *psaA* and *psbC* sequences (3–4 % genetic distance). These two isolates are here described as *Phaeosaccion westermeieri* sp. nov.. Our isolations of *P. multiseriatum* and *P. westermeieri* are a further demonstration that the germling emergence technique can reveal microscopic multicellular benthic algae that are easily overlooked in the field.

Keywords: *Antarctosaccion applanatum*; biogeography; molecular-assisted identification; *Phaeosaccion collinsii*; taxonomy

***Corresponding author: Akira F. Peters**, Bezhin Rosko, 40 rue des pêcheurs, 29250 Santec, France; and School of Biological Sciences, University of Aberdeen, Cruickshank Building, St Machar Drive, Aberdeen AB24 3UU, Scotland, UK, E-mail: akirapeters@gmail.com. <https://orcid.org/0000-0001-5332-199X>

Liliana A. Muñoz, Centro i-mar, Millenium Nucleus MASH and CeBiB, Universidad de Los Lagos, Puerto Montt, Chile. <https://orcid.org/0000-0002-6392-0985>

Niko R. Johansson, School of Biological Sciences, University of Aberdeen, Cruickshank Building, St Machar Drive, Aberdeen AB24 3UU, Scotland, UK; and Botany and Mycology Unit, Finnish Museum of Natural History LUOMUS, PL7 University of Helsinki, Helsinki, Finland. <https://orcid.org/0000-0003-4968-3845>

Anastasia Rizouli, School of Biological Sciences, University of Aberdeen, Cruickshank Building, St Machar Drive, Aberdeen AB24 3UU, Scotland, UK. <https://orcid.org/0000-0001-8724-702X>

Michael D. Guiry, AlgaeBase, Ryan Institute, University of Galway, University Road, H91 TK33, Galway, Ireland. <https://orcid.org/0000-0003-1266-857X>

Ga Youn Cho, National Institute of Biological Resources, Incheon 22689, Korea. <https://orcid.org/0009-0006-5016-3651>

Frithjof C. Küpper, School of Biological Sciences, University of Aberdeen, Cruickshank Building, St Machar Drive, Aberdeen AB24 3UU, Scotland, UK; and Department of Chemistry, Marine Biodiscovery Centre, University of Aberdeen, Aberdeen AB24 3UE, Scotland, UK. <https://orcid.org/0000-0003-1273-7109>

1 Introduction

Wynne and Furnari (2014) have pointed out that several taxa described by P.J.L. Dangeard [Father, Pierre Clement Augustin Dangeard (1862–1947) and son, Pierre Jean Louis Dangeard (1895–1970), are frequently confused by phycologists. Both described many marine and freshwater algae] were invalidly published because he did not indicate a type or include a single gathering as required by the International Code of Nomenclature after 1 January 1958 (ICN Art. 40.1; Turland *et al.* 2018). One such designation is “*Giraudyopsis stellifer*” P.J.L. Dangeard, a minute ephemeral heterokont multicellular marine alga from Atlantic France originally classified in the Phaeophyceae (Dangeard 1966a). Cytological, ultrastructural, and biochemical examinations (Billard 1974; Billard *et al.* 1990; Loiseaux 1967, 1970; O’Kelly and Floyd 1985) showed that it was not a brown alga. Loiseaux (1967) referred *Giraudyopsis* to the “filamentous chrysophytes”, but sequence data were required for its precise classification. However, “*Giraudyopsis stellifer*” and the genus designation “*Giraudyopsis*” P.J.L. Dangeard are invalid as the

protologue of “*Giraudyopsis stellifer*” included two gatherings from France (Guéthary, Pyrénées-Atlantiques and Roscoff, Bretagne), and a type was not indicated; a genus designation based on an invalid species designation is also invalid. The original, correct orthography of the species designation “*stellifer*” was generally incorrectly rendered “*stellifera*” by subsequent authors. While both are acceptable as botanical epithets, the choice of the original author has precedence.

Graf et al. (2020) described two strains present in an algal culture collection (CCMP1308 from the Northeast Pacific and CCMP1666 from New Zealand; Table 1) and identified originally as *Giraudyopsis stellifer* and *Giraudyopsis* sp., respectively, as *Phaeosaccion multiseriatum* R.A. Andersen, L. Graf et H.S. Yoon and *P. okellyi* R.A. Andersen, L. Graf et H.S. Yoon, respectively. Because they did not study material from Europe, they did not comment on the identity of Dangeard’s *G. stellifer*. *Phaeosaccion* and the new class Phaeosacciophyceae were based on *P. collinsii* Farlow, a macroscopic species with a sac-like habit described in 1882 from the NW Atlantic Ocean, which had likewise initially been classified in the Phaeophyceae (Farlow 1882). In addition to *P. multiseriatum* and *P. okellyi*, a further strain not yet identified to species level, designated as *Giraudyopsis* sp., was isolated from Japan and maintained as culture 1862 in the public culture collection of the National Institute for Environmental Studies, Japan (NIES, Table 1).

To clarify the identity of the alga studied by Dangeard in Europe we have re-isolated it at Roscoff, which is one of the original localities. Here we show, using the two plastid-encoded markers *psaA* and *psbC*, that this alga is identical to *Phaeosaccion multiseriatum*, and we provide new records of the species from Korea and the Falkland Islands. Additionally, we describe a morphologically similar species discovered in Chile, which genetically differs from the closely related *P. multiseriatum* and *P. okellyi*.

2 Materials and methods

Abiotic or biotic substrata from nine localities in temperate regions (Figure 1, Table 2) were incubated in the laboratory to stimulate the emergence of macroalgae from the bank of microscopic stages (“germling emergence”, Peters et al. 2015). Single clonal cultures free of other eukaryotes were obtained by sub-isolating individual germlings. They were cultivated in Petri dishes in half-strength Provasoli-enriched (Coelho et al. 2012) autoclaved natural sea water from Roscoff, 10–15 °C and natural light near a north-facing window. Micrographs were taken with a Zeiss Axiovert compound microscope equipped with a Zeiss AxioCam MRC™ camera. The most important strains were deposited in the

Table 1: Taxa and isolates of *Phaeosaccion* present in public collections, and accessions of sequences published for them; ND = no data.

Taxon	Culture accession	Origin	Year of isolation	Isolator	SSU	psaA	psaB	psbA	psbC	rbcl	CAC gene; LHCP gene
<i>Phaeosaccion collinsii</i>	A12843 ^b	Little Nahant, Massachusetts	2011	Andersen, R.A.	MT582120	MT582058	MT582026	MT581992	MT581966	ND	ND
<i>Phaeosaccion multiseriatum</i>	CCMP 1308 ^c	San Jun Island, Washington, USA	<1991	Norris, R.E.	U78034	HQ710646	ND	HQ710702	MK787194	HQ710597	Z46920 ^e
<i>Phaeosaccion okellyi</i>	CCMP 1666 ^c	Leigh, North Island, New Zealand	1985	O’Kelly, C.	HQ710557	HQ710645	MT582027	HQ710701	HQ710755	HQ710596	ND
<i>Phaeosaccion</i> sp. ^a	NIES 1862 ^d	Awaji Isl. Iwaya, Awaji Hyogo Japan	2005	Kai, A.	AB365204	ND	ND	ND	ND	AB365205	ND

^a*Giraudyopsis* sp. in the NIES strain catalog. ^bNot clear which collection; strain information from GenBank entry. ^cNational Center for Marine Algae and Microbiota, USA, ncmabigelow.org. ^dMicrobial Culture Collection at the National Institute for Environmental Studies, Tsukuba, Japan, mcc.nies.go.jp. ^eNot clear if from this isolate. Used in publication doi: 10.1007/bf00019125.

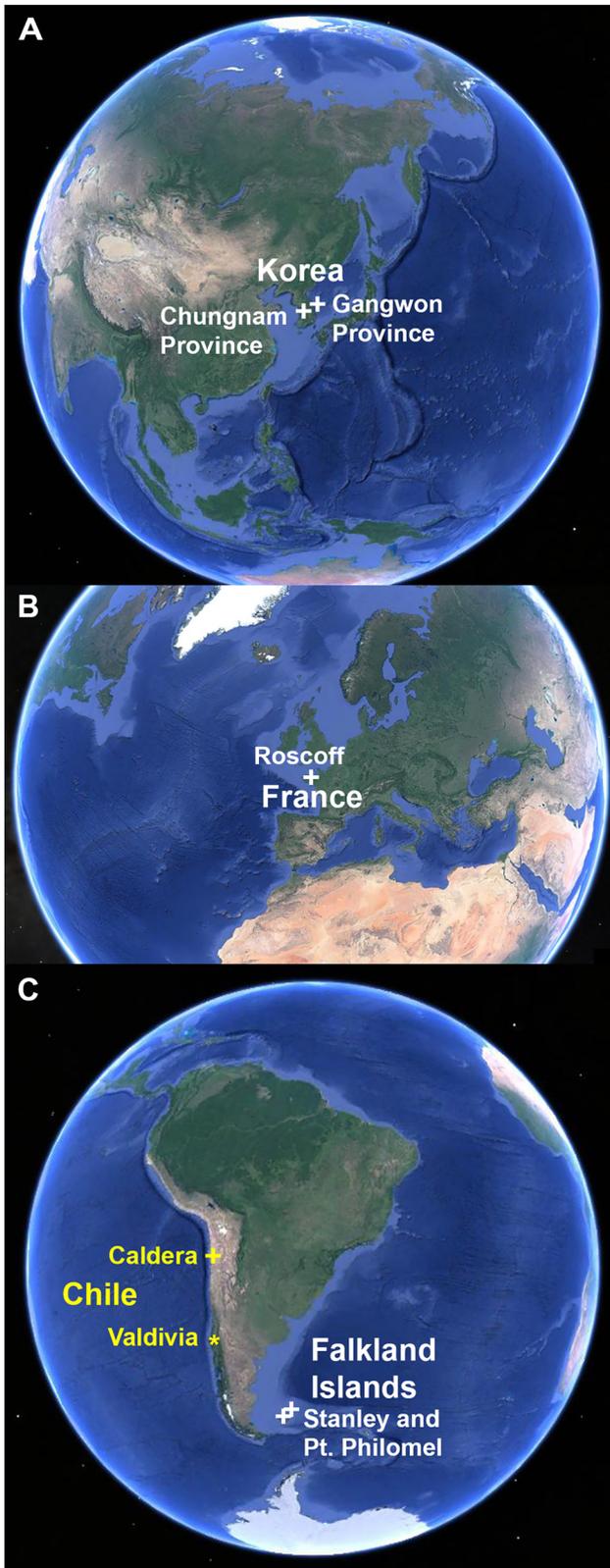


Figure 1: New collecting sites of *Phaeosaccion multiseriatum* (white text) and *P. westermeieri* sp. nov. (yellow text); asterisk indicates type locality of *P. westermeieri*.

Roscoff Culture Collection (RCC; <https://roscoff-culture-collection.org/>) and the Culture Collection of Algae and Protozoa (CCAP, Gachon et al. 2013) (Table 2).

Permanent microscopic mounts on microscope slides were prepared using acetocarmine as fixative and dye and 50 % Karo™ syrup as embedding medium (Müller and Ramírez 1994). Herbarium abbreviations follow the Index Herbariorum (<https://sweetgum.nybg.org/science/ih/>).

DNA extraction, PCR amplification and Sanger sequencing techniques were as described previously (Muñoz et al. 2018), the markers targeted being the nuclear ribosomal small subunit (18S; our sequences included 1,100 bp at the 5'-end and 523 bp at the 3'-end), the plastid-encoded *psaA* (1,566 bp) and 5'-partial *psbC* (617 bp), for which there existed previously generated sequences (Table 1) and we possessed oligonucleotide primers that worked with our isolates (Supplementary Table S1). Sequences were deposited in the public data base NCBI/GenBank (www.ncbi.nlm.gov) (Table 2).

The newly generated DNA sequences were assembled, manually aligned, and examined with Se-AL™ v2.0a11 (Sequencing Alignment Editor Version 2.0 alpha 11; Rambaut 2002), checked for correctness by inspecting the chromatograms, and compared to published sequences by means of the Basic Local Alignment Search Tool (BLAST) housed at the United States National Center of Biotechnology Information (NCBI; Zhang et al. 2000). Phylogenetic trees were calculated from the plastid-encoded sequences using Maximum Likelihood (ML) and Bayesian Inference (BI). ML was executed in RAXML version 8.2.11 with 1,000 bootstrap replications (BP) and GTR GAMMA as evolutionary model. RAXML only implements GTR-based models because GTR is the most common and general model for real-world DNA analysis (Stamatakis 2014). BI was implemented in MrBayes version 3.2.6, using default settings four MCMC chains, with a chain length of 1,000,000, subsample frequency of 1,000, and a burn-in of 10 %. (Huelsenbeck and Ronquist 2001). Both plugins were developed to be executed in Geneious® 11.1.5 (<https://www.geneious.com>). Analyses were made for each gene separately, and for an alignment of concatenated sequences of the two genes combined.

3 Results

3.1 New isolates of *Phaeosaccion multiseriatum*

Phaeosaccion multiseriatum thalli were not directly observed in field material but appeared in our laboratory cultures after incubation of abiotic or biotic substrata (Table 2). Our isolates of

Table 2: Collecting sites, isolated strains and sequence accessions. See also Figure 1.

No.	Locality	Country	Coordinates	Substratum and site details	Date	Species isolated	Identification based on	Strain code	Culture collection and strain accession	Sequence accessions
1	Perharidy, Roscoff, Brittany (type locality of Dangeard's <i>G. stellifer</i>)	France	48° 72584 N 4° 01753 W	Dead shell of <i>Loripes lucinalis</i> (Lamarck, 1818) in lowermost intertidal pool, within <i>Zostera marina</i> Linnaeus meadow	31-01-14	<i>Phaeosaccion multiseriatum</i>	Morphology, sequences	PmulPH14-1	RCC7275, CCAP2111/1	PP216034 and PP216038 (SSU) PP230472 (<i>psaA</i>) PP230480 (<i>psbC</i>) PP216035 and PP216039 (SSU) PP230473 (<i>psaA</i>) PP230481 (<i>psbC</i>) PP216036 (SSU) PP230474 (<i>psaA</i>) PP230482 (<i>psbC</i>)
2	Sodol, Jumunjin, Gangneung, Gangwon Province	Korea	37° 90582 N 128° 83023 E	Small pebble in tide pool	27-10-15	<i>Phaeosaccion multiseriatum</i>	Morphology, sequences	KR15-001-1 KR15-002-3	Strains not deposited	PP216041 (SSU) PP230475 (<i>psaA</i>) PP230483 (<i>psbC</i>) PP216042 (SSU) PP230476 (<i>psaA</i>) PP230484 (<i>psbC</i>) PP216036 and PP216043 (SSU) PP230478 (<i>psaA</i>) PP230486 (<i>psbC</i>)
3	Padori Beach, Taeon, Chungnam Province	Korea	36° 73981 N 126° 13217 E	Old shell fragment in uppermost subtidal	29-10-15	<i>Phaeosaccion multiseriatum</i>	Morphology, sequences	KR15-157-1, KR15-161-1	Strains not deposited	PP216041 (SSU) PP230475 (<i>psaA</i>) PP230483 (<i>psbC</i>) PP216042 (SSU) PP230476 (<i>psaA</i>) PP230484 (<i>psbC</i>) PP216036 and PP216043 (SSU) PP230478 (<i>psaA</i>) PP230486 (<i>psbC</i>)
4	Bahía Salada, Caldera	Chile	27° 63182 S 70° 90857 W	<i>Heterozostera chilensis</i> J. Kuo, drift	14-11-13	<i>P. westermeyeri</i> sp. nov.	Sequences	CH13-259A	Strain not deposited	PP216037 and PP216044 (SSU) PP230479 (<i>psaA</i>) PP230487 (<i>psbC</i>) Not sequenced
5	Pilolcura, Valdivia (type locality of <i>Phaeosaccion westermeyeri</i>)	Chile	39° 67290 S 73° 35326 W	<i>Scytosiphon</i> sp., mid intertidal pool	26-11-13	<i>P. westermeyeri</i> sp. nov.	Sequences	CH13-637	CCAP2111/2	PP216037 and PP216044 (SSU) PP230479 (<i>psaA</i>) PP230487 (<i>psbC</i>) Not sequenced
6	Top Island, Port William, East Falkland (Stanley area)	Falkland Islands	51° 67328 S 57° 72347 W	Small pebble, 15 m depth	18-01-17	<i>Phaeosaccion multiseriatum</i>	Morphology	FAL17-034-01	Strain not deposited	Not sequenced
7	North West Bay, Port Philomel	Falkland Islands	51° 71475 S 60° 37765 W	Unidentified brown alga, intertidal pool	20-01-17	<i>Phaeosaccion multiseriatum</i>	Morphology	FAL17-045-02	Strain not deposited	Not sequenced
8	Hooker's Point, East Falkland (Stanley area)	Falkland Islands	51° 69937 S 57° 77520 W	<i>Halopteris</i> sp., lower intertidal pool	28-01-17	<i>Phaeosaccion multiseriatum</i>	Morphology	FAL17-223-04	Strain not deposited	Not sequenced
9	Port Williams, Yorke Point, East Falkland (Stanley area)	Falkland Islands	51° 64852 S 57° 75960 W	<i>Wildemanina amplissima</i> (Kjellman) Foslie, 10 m depth	28-01-17	<i>Phaeosaccion multiseriatum</i>	Morphology, sequences	FAL17-244-03	Strain not deposited	PP230477 (<i>psaA</i>) PP230485 (<i>psbC</i>)

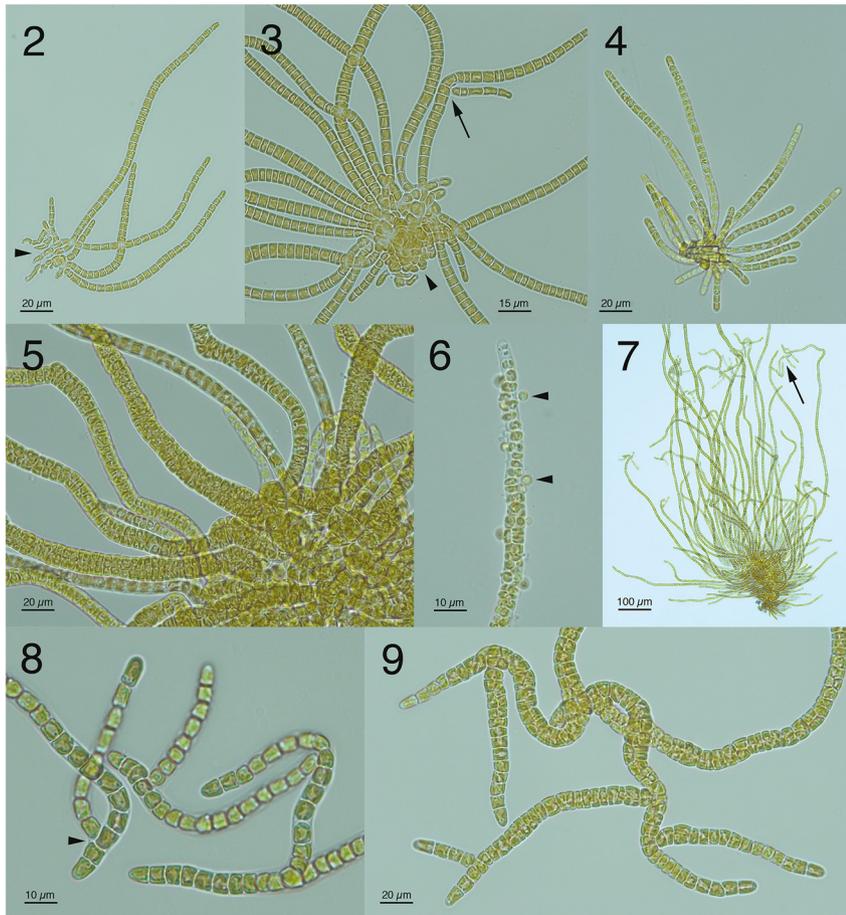
P. multiseriatum from Roscoff and Korea first developed a prostrate base, on which erect, initially monosiphonous filaments were formed, consisting of cylindrical cells of 6–8 µm diameter and the same length (Figures 2–4). Rarely, the uprights were branched distally (Figure 3). At maturity, the basal portions of the erect filaments became wider and multiseriate (Figure 5), and the cells of the filaments were transformed into zooids (Figure 6). The zooids developed into thalli showing the same morphology as their parents. Isolates from the Falkland Islands had the same morphology except for the more frequent occurrence of false ramifications (Figures 7–9).

3.2 *Phaeosaccion westermeieri* A.F. Peters, sp. nov.

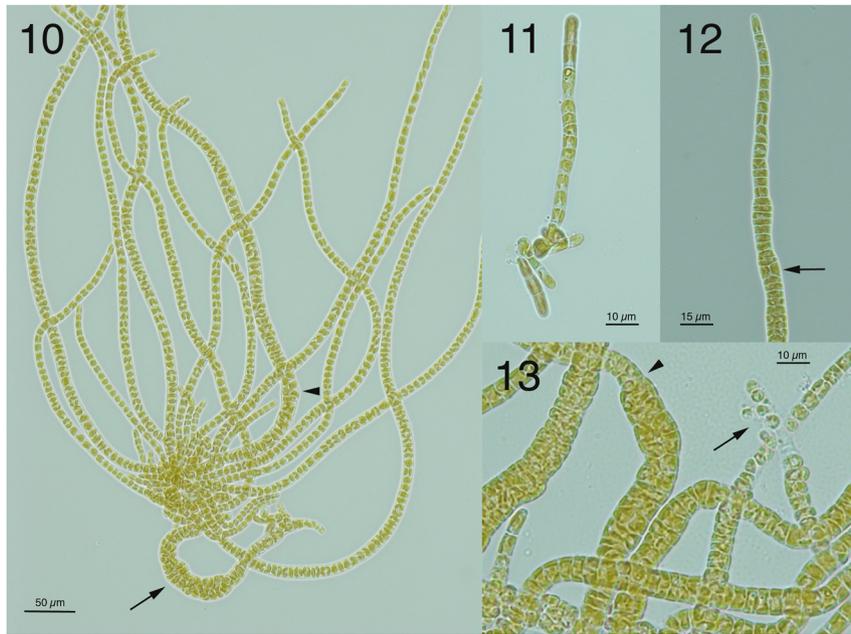
Type locality: CHILE, Valdivia, Pilolcura, Roca Hueca (39° 67,290 S 73° 35,326 W), leg. A.F. Peters, A. Montecinos and M.-L. Guillemín, 26 November 2013 (holotype PC0677387, isotype PC0677388). Sequence accessions: SSU PP216037 and PP216044, *psaA* PP230479, *psbC* PP230487. Authentic strain CH13-637 deposited as CCAP 2111/2.

Etymology: The specific epithet honours Renato Westmeier, Professor Emeritus of Universidad Austral de Chile, for his contributions to the knowledge of macroalgae and their mariculture in Chile.

Description: Minute multicellular alga (Figure 10) attached to the substratum by basal creeping filaments (Figure 11). Erect filaments unbranched, flexible, tapering, initially monosiphonous, subsequently showing longitudinal divisions and becoming wide and multiseriate (Figures 10–12). The transition between the thinner distal and the thicker basal parts of the uprights is occasionally abrupt (Figure 13). Vegetative cells cylindrical, from distally 6–8 µm in diameter to basally 20 µm, and 6–10 µm in length. All cells may be transformed into heterokont zooids 4 × 6 µm in size, containing a plastid with a red stigma. They are released each through an individual pore in the cell wall of the loculus (Figure 13). Settled zooids develop into the same kind of thallus as the parents. The two isolates of *P. westermeieri* from Chile showed the same overall morphology, which is similar to that of *P. multiseriatum*, however, we have not observed branching of the erect filaments.



Figures 2–9: *Phaeosaccion multiseriatum*, laboratory culture. (2–3) Strain from Roscoff: (2) creeping filaments adhering to substratum (arrowhead) and monosiphonous uprights; (3) basal filaments forming a small disk (arrowhead). One of the uprights shows branching (arrow). (4–6) Germlings from Korea: (5) reproductive thallus, showing thicker basal portions of uprights; (6) terminal part of upright filament transformed into zooids, two of them released and attached to empty loculus (arrowheads). (7–9) Thalli from the Falkland Islands: (7) general habit with more frequent branching of upright filaments (arrow); (8) detail of branching, note continuous pectin layer (arrowhead); (9) another example of branching, showing that it can also occur in multiseriate parts of the thallus.



Figures 10–13: *Phaeosaccion westermeieri* sp. nov. from Chile, laboratory culture. (10) Overall morphology of immature thallus from the type locality near Valdivia. Incipient (arrowhead) and more advanced (arrow) multiseriate thallus parts. (11–13) Strain from Caldera: (11) group of very young germlings; (12) distal part of upright, with first longitudinal division (arrow); (13) mature thallus. Arrowhead shows rather abrupt transition from thinner to thicker parts of an erect filament. Zoids are being released distally in another part (arrow).

3.3 DNA sequence analyses (Supplementary Tables S2, S3)

The 3'-partial SSU sequences (ca. 500 bp) of our five isolates of *P. multiseriatum* from France and Korea, the two isolates of *P. westermeieri*, as well as the published sequences of *P. multiseriatum*, *P. okellyi* and the strain NIES-1862 were identical. They differed by five nucleotides from those of *P. collinsii* and by seven from *Antarctosaccion applanatum* (Gain) Delépine. The 5'-partial SSU sequences (ca. 1,000 bp) were identical in our *P. multiseriatum* isolate from Roscoff, one from Korea (the other isolates were not sequenced), and the authentic strain of *P. multiseriatum*. They differed by two bp from the homologous sequence of *P. okellyi*, and by three bp plus four indels from that of strain NIES-1862. The two strains of *P. westermeieri* had identical 5'-partial SSU sequences, differed by one bp from *P. okellyi*, by three bp from *P. multiseriatum*, and by four indels from strain NIES-1862. *Antarctosaccion applanatum* was more different (94.5 % identity). The *P. collinsii* SSU sequence did overlap only in a short part (426 bp) with that available for our strains. In that part it had the same sequence as *P. multiseriatum*. The SSU of our isolates from the Falkland Islands was not sequenced.

The plastid markers were more variable, the intraspecific genetic differences were 0–0.1 % in *P. multiseriatum* and 0.5–0.6 % in *P. westermeieri* (Supplementary Tables S2, S3). In *psaA*, our isolates of *P. multiseriatum* from France, Korea and the Falklands (only one from the Falklands sequenced) were identical, except for strain KR15-001-1, which differed by a single substitution. They had 1–2 substitutions compared to the authentic strain of *P. multiseriatum* from the

NE Pacific Ocean (corresponding to 99.93 and 99.86 % identity, respectively). The genetic identities with *P. okellyi*, *P. collinsii* and *Antarctosaccion applanatum* were 95.58 (95.5), 93.72 (93.79) and 86.85 (86.85) %, respectively. In *psbC*, our isolates of *P. multiseriatum* from France, Korea and the Falklands (only one from the Falklands sequenced) were identical but differed by three bp from the authentic strain (99.32 % identity). The two *P. westermeieri* strains showed a genetic distance of about 4 % from *P. multiseriatum* in both markers. Sequences of *psaA* and *psbC* of *P. okellyi* (CCMP1666) differed from strains of *P. multiseriatum*, by 4.1–4.6 % in *psaA* and 3.8–4.3 % in *psbC*; the difference from *P. westermeieri* was 3.8–4.1 % in *psaA* and 2.7 % in *psbC* (Supplementary Table S3).

Phylogenetic analyses using alignments of *psaA*, *psbC*, or of the two concatenated markers, with *Antarctosaccion* as outgroup, placed our isolates of *Phaeosaccion multiseriatum* in a highly supported clade together with the authentic strain, and *P. westermeieri* in another clade, which also contained *P. okellyi*. A further branch was formed by *P. collinsii*. Except for the grouping of *P. westermeieri* with *P. okellyi*, the topology among the species of *Phaeosaccion* was unresolved. Figure 14 and Supplementary Figures S1–S2 show the trees calculated by BI; the trees from ML analyses were similar in the essential features.

4 Discussion

DNA sequences from a newly isolated strain from France corresponding to the marine alga named *Giraudyopsis*

Our collections of *Phaeosaccion multiseriatum* in France and Korea were from low intertidal pools and the upper subtidal, but the isolates from the Falkland Islands show that the alga may occur from low intertidal pools down to at least 15 m depth (Table 1). We have not seen *P. multiseriatum* in crude cultures from substratum samples from the Mediterranean (Peters et al. 2015; Rizouli et al. 2020), subtropical Kuwait (Hasan et al. 2023) or tropical Ascension Island (Tsiamis et al. 2017), which suggests that the species may be restricted to colder waters, but it is less confined than the type species *P. collinsii*, which occurs only in Arctic waters and the cold-temperate North Atlantic (Guiry and Guiry 2023). However, we did not obtain *P. multiseriatum* from substratum samples collected in the high Canadian Arctic (Küpper et al. 2016). *Phaeosaccion westermeieri* is distributed along the coast of Chile from cold- to warm-temperate regions. The species *P. okellyi*, by contrast, is from subtropical northern New Zealand, and the strain NIES-1862, which still must be identified to species level, originates from the warm-temperate Japanese Inland Sea.

Minute multicellular benthic algae are usually overlooked when examining field material, but they may appear in crude cultures, particularly if the species show massive replication from spores. P.J.L. Dangeard, who studied many such algae in laboratory cultures, detected *P. multiseriatum* in crude cultures of different marine algae (Dangeard 1966a, as “*Giraudyopsis stellifer*”); as did Asensi, but on one occasion he observed it in microscopically examined field material (1976). Dangeard also described other small green and brown algae from isolates that appeared in culture (e.g., Dangeard 1966c, 1970). Subsequently, other colleagues have used incubation of substratum (“germling emergence”; Peters et al. 2015) to isolate cultures of macroalgae from their microscopic stages (Müller and Ramírez 1994; Ramírez and Müller 1991). With the availability of molecular-assisted identification, algae isolated by germling emergence have become more amenable to identification and classification (e.g., Hasan et al. 2023; Kawai et al. 2003; Küpper et al. 2016; Muñoz et al. 2018; Peters et al. 2015; Rizouli et al. 2020; Robuchon et al. 2014; West et al. 2008). It is not surprising that inconspicuous algae are new records in remote localities like the Falkland Islands. The fact that *P. multiseriatum* is a new record in Korea, and *P. westermeieri* new for Chile, shows that the germling emergence technique has a potential for discoveries also in well-studied benthic marine floras. Similarly, in the intensely studied algal floras of Helgoland and the British Isles, putative *P. multiseriatum* was found rather late; in both cases, it appeared in crude cultures (Kornmann and Sahling 1983; Pedersen 1980).

The genome of the strain of *P. multiseriatum* from Roscoff has recently been sequenced (Mc Cartney et al. 2024).

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Author contributions: Conceptualization, A.F.P.; methodology, A.F.P.; software, A.F.P., N.J. and L.A.M.; validation, A.F.P.; formal analysis, L.A.M., A.F.P.; investigation, A.F.P., G.Y.C., A.R. and N.J.; resources, A.F.P, G.Y.C. and F.C.K.; data curation, A.F.P.; writing – original draft preparation, A.F.P.; writing – review and editing, A.F.P., M.D.G and all co-authors; visualization, A.F.P.; supervision, A.F.P.; project administration, A.F.P.; funding acquisition, A.F.P, G.Y.C. and F.C.K. The authors have accepted responsibility for the entire content of this manuscript and approved its submission.

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Data availability: DNA sequences were submitted to the public database (Genbank/ENA/DBJ).

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Bionotes



Akira F. Peters

Bezhin Rosko, 40 rue des pêcheurs, 29250 Santec, France
 School of Biological Sciences, University of Aberdeen, Cruickshank Building, St Machar Drive, Aberdeen AB24 3UU, Scotland, UK
akirapeters@gmail.com
<https://orcid.org/0000-0001-5332-199X>

Akira F. Peters is a retired scientist. Since the beginning of his scientific career in 1980 he has worked on life histories, taxonomy, phylogenetics, ecology, pathology, genetics, development, cultivation and utilisation of

marine algae. He has a PhD from Konstanz University, Germany, directs the enterprise Bezhin Rosko and lives near Roscoff in Brittany, NW France. His main techniques are isolation, purification and laboratory cultivation of seaweed microstages.



Liliana A. Muñoz

Centro i-mar, Millenium Nucleus MASH and CeBiB, Universidad de Los Lagos, Puerto Montt, Chile
<https://orcid.org/0000-0002-6392-0985>

Liliana A. Muñoz is a postdoctoral researcher at the i-mar center, Universidad de Los Lagos, Puerto Montt, Chile. Her MSc (2016; molecular characterization of the marine flora of Easter Island) and PhD (2022; fungal parasites affecting aquaculture facilities in South Africa) are from the University of Aberdeen, Scotland, UK. In her current research, she works on the seaweed holobiont by including fungal species inhabiting macroalgae and exploring their potential roles within their host, as well as their biotechnological application in seaweed aquaculture.



Niko R. Johansson

School of Biological Sciences, University of Aberdeen, Cruickshank Building, St Machar Drive, Aberdeen AB24 3UU, Scotland, UK
 Botany and Mycology Unit, Finnish Museum of Natural History LUOMUS, PL7 University of Helsinki, Helsinki, Finland
<https://orcid.org/0000-0003-4968-3845>

Niko R. Johansson is a doctoral researcher in the Finnish Museum of Natural History (Luomus), Helsinki, Finland, working on fungal dispersal ecology. His interests include the biodiversity, ecology, evolution and systematics of algae, fungi and lichens.



Michael D. Guiry

AlgaeBase, Ryan Institute, University of Galway, University Road, H91 TK33, Galway, Ireland
<https://orcid.org/0000-0003-1266-857X>

Michael D. Guiry is Emeritus professor of Botany at the University of Galway, Ireland. He is founder and director of AlgaeBase.



Ga Youn Cho

National Institute of Biological Resources, Incheon 22689, Korea
<https://orcid.org/0009-0006-5016-3651>

Ga Youn Cho is a senior researcher at the National Institute of Biological Resources, Korea. She was awarded a PhD at Chungnam National University for the phylogeny of Laminariales. Her research interests are biodiversity, phylogeography, and phylogeny of seaweeds.