

cryptogamie

Algologie

2024 • 45 • 1

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art. 45 (1) — Published on 17 January 2024
www.cryptogamie.com/algologie

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Cryptogamie, Algologie is a fast track journal published by the Museum Science Press, Paris

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ISSN (imprimé / *print*): 0181-1568 / ISSN (électronique / *electronic*): 1776-0984

Australasian *Lophothamnion* J.Agardh aligns genetically with *Pleonosporium* Nägeli (Wrangeliaceae, Spongoconlieae): new species from the western Atlantic

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Submitted on 22 August 2023 | Accepted on 27 October 2023 | Published on 17 January 2024

Schneider C. W. & Saunders G. W. 2024. — Australasian *Lophothamnion* J.Agardh aligns genetically with *Pleonosporium* Nägeli (Wrangeliaceae, Spongoconlieae): new species from the western Atlantic. *Cryptogamie, Algologie* 45 (1): 1-10. <https://doi.org/10.5252/cryptogamie-algologie2024v45a1>. <http://cryptogamie.com/algologie/45/1>

ABSTRACT

During a genetic analysis of western Atlantic Wrangeliaceae J.Agardh, specimens closely related to the generitype of *Lophothamnion* J.Agardh fell into a clade including the generitype of the earlier described *Pleonosporium* Nägeli, causing us to subsume the former genus. Two new species are described, *P. novae-angliae* G.W.Saunders & C.W.Schneider, sp. nov. for specimens from southern New England and New York, United States, formerly identified there as *P. borneri* (Smith) Nägeli, and *P. ricksearlesii* C.W.Schneider & G.W.Saunders, sp. nov. from Bermuda. The relationship of *Pleonosporium* with its sister genus *Spongoconium* Sonder is discussed with the transfer of *Spongoconium australicum* Womersley to *Pleonosporium*.

RÉSUMÉ

Le genre australasien *Lophothamnion* J.Agardh se révèle génétiquement aligné avec *Pleonosporium* Nägeli (Wrangeliaceae, Spongoconlieae): nouvelles espèces de l'Atlantique occidentale.

Au cours d'une analyse génétique des Wrangeliaceae J.Agardh de l'Atlantique occidentale, des spécimens étroitement liés au généritype de *Lophothamnion* J.Agardh sont tombés dans un clade comprenant le généritype de *Pleonosporium* Nägeli décrit précédemment, nous obligeant à englober le premier genre. Deux nouvelles espèces sont décrites, *P. novae-angliae* G.W.Saunders & C.W.Schneider, sp. nov. pour les spécimens du sud de la Nouvelle-Angleterre et de New York, États-Unis, anciennement identifiés là-bas sous le nom de *P. borneri* (Smith) Nägeli, et *P. ricksearlesii* C.W.Schneider & G.W.Saunders, sp. nov. des Bermudes. La relation entre *Pleonosporium* et son genre frère *Spongoconium* Sonder est discutée avec le transfert de *Spongoconium australicum* Womersley dans *Pleonosporium*.

KEY WORDS

Bermuda,
New England,
Lophothamnion,
Pleonosporium,
Spongoconium,
new combination,
new species.

MOTS CLÉS

Bermudes,
Nouvelle-Angleterre,
Lophothamnion,
Pleonosporium,
Spongoconium,
combinaison nouvelle,
espèces nouvelles.

INTRODUCTION

Two genetic species have been discovered in regular barcoding assessments of marine macroalgae in North American and Bermudian waters, both clustering with species of the three genera presently comprising the tribe Spongoconlieae of the family Wrangeliaceae J. Agardh (Choi *et al.* 2008), viz. *Lophothamnion* J. Agardh (1892), *Pleonosporium* Nägeli (1862), and *Spongoconium* Sonder (1855). These genera have had complicated and intertwined nomenclatural histories over the past more than 150 years based upon branching patterns, cortication of axes, and presence or absence of post-meiotic divisions in tetrasporangia (Wynne 2005: note 104). *Pleonosporium* is a widespread genus in the Wrangeliaceae presently consisting of 31 species from tropical to polar waters (Guiry & Guiry 2023). It is characterized by uniseriate, filamentous axes often with alternate distichous branching in distal regions, and with most species corticated by rhizoidal investments over lower axes but some ecorticate, and adaxial sporangia on upper branches (Schneider & Searles 1991; Maggs & Hommersand 1993).

The monotypic Australasian genus *Lophothamnion* is based upon *L. comatum* J. Agardh (1892), a species that was found a century later to be a heterotypic synonym of *L. hirtum* (Hooker f. & Harvey) Womersley from Australia, New Zealand and the subantarctic islands (Womersley & Wollaston 1998: 297). *Lophothamnion* has had a long nomenclatural connection to the genus *Pleonosporium*, and both genera share the production of polysporangia. De Toni (1903: 1309) was the first to consider, although with some hesitation, that the genotype *L. comatum* might better be placed in *Pleonosporium* as *P. ?comatum* (J. Agardh) De Toni, while Laing (1905: 393) moved *Callithamnion hirtum* Hooker f. & Harvey (Harvey & Hooker 1845: 192) to *Pleonosporium* (as *P. hirtum* (Hooker f. & Harvey) Laing) before Womersley & Wollaston (1998) created the new combination in *Lophothamnion*. In effect, Womersley & Wollaston (1998) resurrected the genus *Lophothamnion* when they moved *C. hirtum* to the genus stating that “there was no apparent difference between the Australian *L. comatum* and the earlier named *C. hirtum* from the Auckland Is...”. *Lophothamnion* is defined by basally branched lateral branchlets with long unbranched termini, rhizoidal cortication proximally, and polysporangia sessile on lower cells of lateral branches (Kyllin 1956; Womersley & Wollaston 1998).

At present, *Spongoconium* consists of ten species (Guiry & Guiry 2023) confined to the Indo-Pacific except for one, *S. caribaeum* (Børgesen) M.J. Wynne, known from the tropical western Atlantic (Wynne 2022). The genus was described by Sonder (1855) and based upon *S. conspicuum* Sonder from Victoria, Australia, “presumably in reference to the spongy texture of the thallus” (Huisman 2018). Since the protologue, several species have been added to *Spongoconium*, most from Australia and New Zealand (Guiry & Guiry 2023), and all lacking “spongy” habits. *Spongoconium* is characterized by dense, irregular branching, thick rhizoidal cortication proximally, and tetrasporangia, rarely octosporangia (Itono 1977; Womersley & Wollaston 1998). It is noteworthy that Womersley & Wollaston (1998) loosely differentiated two groups

of species in southern Australia, those that strictly produce tetrasporangia, and those that also produce octosporangia.

In the present study, we assess the two genetic species groups from southern New England, United States, and Bermuda that align in a clade comprised of the Spongoconlieae (Fig. 1). Historically, one species of *Pleonosporium* has been reported from southern New England, *P. borneri* (Smith) Nägeli, a species with a European type locality, also known from the Mediterranean Sea, many eastern Atlantic islands, and various Indo-Pacific locations (Guiry & Guiry 2023). In North America, it is reportedly distributed from Long Island Sound to the southern side of Cape Cod, Massachusetts. No other member of the Spongoconlieae has previously been reported in this region (Mathieson & Dawes 2017), nor any in the Bermuda flora (Schneider 2003). Along with the genetic species that we have discovered from these two areas, we also consider genus-level relationships within the tribe.

MATERIAL AND METHODS

Fragments of individual specimens chosen for DNA analysis were dried on silica gel and also preserved with 4–5% formaldehyde in sea water for anatomical study. The remainder of each specimen was pressed fresh and dried on herbarium paper as archival vouchers. Wet specimen fragments were mounted permanently on microscope slides in a 20:1 solution of 30% Karo® corn syrup (ACH Food Company, Inc., Memphis, TN, United States) and 1% aniline blue. Dried specimens were scanned on an Epson ET-2650 scanner (Seiko Epson Corporation, Suwa, Nagano, Japan), and photomicrographs were taken using a Zeiss Axioskop 40 microscope (Carl Zeiss, Oberkochen, Germany) equipped with a Spot Idea 28.2-5MP digital camera (Diagnostic Instrument, Sterling Heights, MI, United States). Voucher specimens are deposited in the herbaria under each species (herbarium abbreviations follow the online Index Herbariorum (Thiers 2023) and standard author initials follow the online International Plant Names Index (IPNI, <https://www.ipni.org/index.html>). The *Phycotheca Boreali-Americana* (P.B.-A.) exsiccata cited here (Collins *et al.* 1897) is part of the personal herbarium of CWS.

DNA extractions of our silica-dried samples followed Saunders & McDevit (2012), and PCR amplification and sequencing of COI-5P, *rbcL* and SSU were as detailed in Saunders & Moore (2013). Amplification products were sent to Genome Quebec for sequencing, and all successfully generated sequences for all specimens and markers are included in Appendix 1. In addition, *rbcL* data for *Pleonosporium borneri* were downloaded from GenBank for our analyses (Appendix 1). Three single-gene alignments were generated: COI-5P (11 sequences, 664 bp [base pairs]); *rbcL* (13 sequences, 1358 bp); and SSU (7 sequences, 1750 bp). These alignments were analyzed separately in Geneious 2023.1.1 with maximum likelihood (general time reversible with invariant sites and gamma-distributed rates for the variable sites, GTR+I+G; Soares *et al.* 2019) using RAxML (Stamatakis 2014) with partitioning by codon (for the two protein coding genes) and

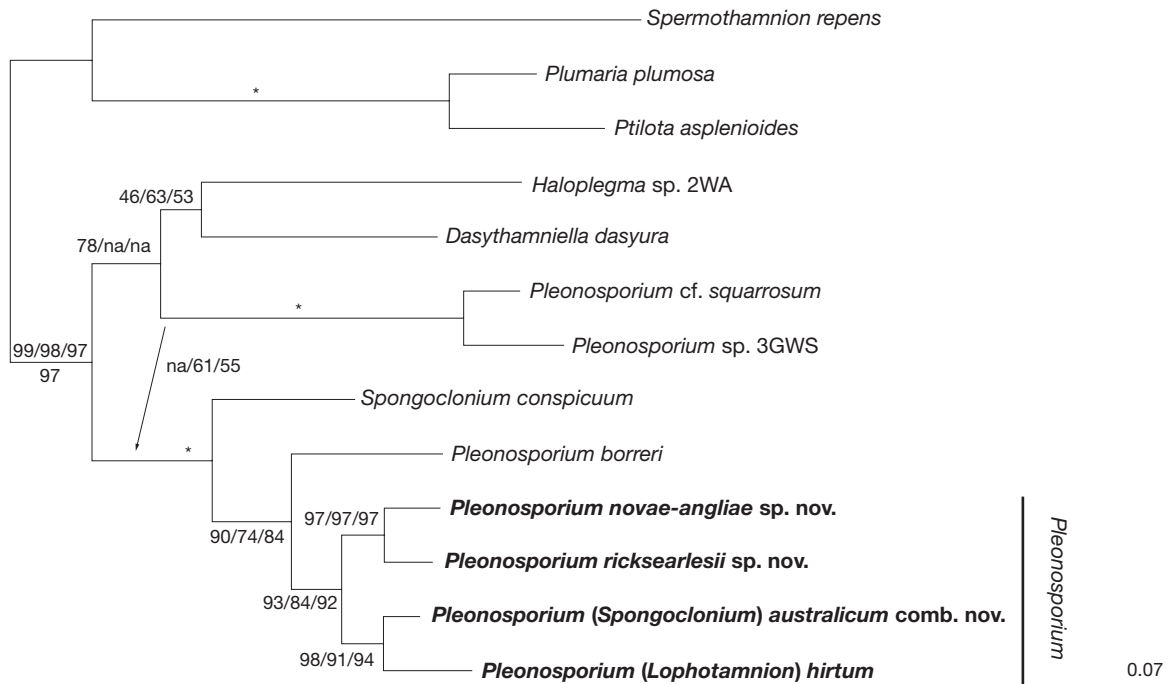


Fig. 1. — Maximum likelihood analyses of the SSU + *rbcl* + COI-5P alignment with bootstrap values for SSU + *rbcl* + COI-5P / *rbcl* + COI-5P / *rbcl* only, respectively, included. Pacific *Pleonosporium* spp. join that lineage in *rbcl* + COI-5P / *rbcl* only analyses. Asterisks (*) indicate 100% support in all three analyses. Taxa in **bold type** are new species described here, as well as those transferred to different genera. Scale: substitutions per site.

500 bootstrap replicates. Because no strong conflicts were detected, concatenated COI-5P + *rbcl* + SSU (13 sequences, 3742 bp) and COI-5P + *rbcl* (13 sequences, 1992 bp) alignments were constructed with analyses as described for the single-gene alignments, but with partitioning by gene and codon and with 1000 bootstrap replicates (Fig. 1). Phylogenetic trees were rooted with an outgroup of allied genera in the Wrangeliaceae (Choi *et al.* 2008).

RESULTS

Newly generated *rbcl* sequences for what had previously been reported as *Pleonosporium borrieri* from New England differed by 81 substitutions from a European collection of this species (Appendix 1). Indeed, our North American specimens were closer to an entry in GenBank for *Lophothamnion hirtum* (diverging by only 48 substitutions). Thus, more species of these genera were sequenced precipitating the current study. Our phylogenetic analyses resolved collections from southern New England and Bermuda as sister species (Fig. 1), these in turn allied to *Lophothamnion* (*L. hirtum* specimen from Tasmania, type locality: Auckland Island, New Zealand) and *Spongoconium australicum* (specimen from Tasmania, type locality: Kangaroo Island, SA, Australia). The previous were sister to the type species of *Pleonosporium* (*P. borrieri* specimen from Galicia in northwestern Spain, type locality: Yarmouth, England), with the type of *Spongoconium* (*S. conspicuum* specimen from Warrnambool, VIC, Australia, type locality: Victoria, Australia) a distant sister to all the previous (Fig. 1).

These presently represent all of the genera in the Spongoconieae (Guiry & Guiry 2023), but a further complication was the distant and variously unsupported alliance to the Pacific species (*P. cf. squarrosum* and sp. 3GWS; as well as other species not included in the current study) currently assigned to *Pleonosporium* (Fig. 1). As a result of our analyses, we return *L. hirtum* to *Pleonosporium* where it had been earlier moved by Laing (1905), designate here a new combination for *S. australicum* in the same genus, and recognize two new species for the western Atlantic.

Family WRANGELIACEAE J. Agardh Genus *Pleonosporium* Nägeli

Pleonosporium hirtum (Hooker f. & Harvey)

Transactions and Proceedings of the New Zealand Institute 37: 393, pl. 27, fig. 1 (Laing 1905). — *Callithamnion hirtum* Hooker f. & Harvey, *Flora Antarctica*: 192, pl. 78, fig. 2 (Harvey & Hooker 1845).

TYPE LOCALITY. — New Zealand, Auckland Island.

Pleonosporium australicum (Womersley) G.W. Saunders & C.W. Schneider, comb. nov.

Spongoconium australicum Womersley in Womersley & Wollaston, *The Marine Benthic Flora of Southern Australia*: 293, 296, 297, figs 139, 141A, B (Womersley & Wollaston 1998).

TYPE LOCALITY. — Australia, South Australia, Kangaroo Island.

Pleonosporium novae-angliae

G.W.Saunders & C.W.Schneider, sp. nov.
(Fig. 2)

HOLOTYPE (DESIGNATED HERE). — **United States**. Rhode Island, Fort Wetherill, 41°28'44.8"N, 71°21'36.2"W, subtidal (6 m) on other algae, 10.VIII.2007, G.W. Saunders & B. Clarkston, *GWS005733* (holo-, UNB), GenBank: [OQ561797](#) (COI-5P), [OQ561894](#) (*rbcl*), [OQ561850](#) (SSU).

PARATYPE. — **United States**. Massachusetts, Woods Hole, Garbage Beach Breakwater, 41°31'30.7"N, 70°40'21.2"W, subtidal (3 m) on *Sargassum* C.Agardh, 14.IV.2010, B. Clarkston, D. McDevitt, M. Bruce, A. Savoie & C. Longtin, *GWS017847* (para-, UNB), GenBank: [OR336111](#) (*rbcl*-3P).

ADDITIONAL MATERIAL STUDIED. — **United States**. Massachusetts, Martha's Vineyard, Edgartown, 5.VII.1897, M. Jernegan, *P.B.-A. 342b* (Herb. CWS); Connecticut, Bridgeport, Black Rock Beach (Seabright Beach), 26.VIII.1894, I. Holden 1031 (Herb. CWS); Fairfield, Penfield Reef, 19.VII.1896, I. Holden 1203 (Herb. CWS); Penfield Reef near Bridgeport, VII-VIII.1897, I. Holden, *P.B.-A. 342a* (Herb. CWS); Waterford, Millstone Point, Fox Island South, 12.X.1976, C. Schneider 1310 (Herb. CWS); Waterford, Goshen Point, 5.XI.1977, C. Schneider 1874 (Herb. CWS); Groton, Bluff Point State Park, 12.IX.1978, C. Schneider 78-16-3 (Herb. CWS).

ETYMOLOGY. — *Novae-angliae* (Latin, genitive), for “of New England”, its present distribution in northeastern North America.

DISTRIBUTION. — From southern Cape Cod, Massachusetts to Connecticut and New York in Long Island Sound, United States.

DESCRIPTION

Plants epiphytic, bushy, erect to 2-6 cm tall (Fig. 2A), Redwood red (Graf1x 2023) to purplish-red in colour, attached by basal cells and rhizoids; relatively common descending rhizoids simple or branched and variously adherent to, or free of, main axes and typically produced from basal cells of branches (Fig. 2B); axes throughout uniseriate and essentially ecorticate, indeterminate axes with slightly overtopping branches in a weak sigmoidal pattern, branching regularly alternate in a single plane in upper portions, appearing pyramidal in outline (Fig. 2C); upper axial cells of indeterminate axes 16-20 µm diam. and 18-25 µm long, middle portions with relatively regular and alternate (slightly spiralled) branches, mid-axial cells prominent, 35-50 µm diam. and 112-154 µm long; indeterminate axial cells in lower portions 125-260 µm diam. and 550-860 µm long, the axes held together by a tangle of free rhizoids; non-sequenced plants with tetrasporangia and octosporangia adaxially sessile on upper branches (Fig. 2D, E), borne singly or on a series of successive cells (Fig. 2F); subglobose to obovoidal, 35-50 µm diam. and 50-60 µm long, including a thick wall; spermatangia in oblong masses (Taylor 1957), cystocarps unknown.

Pleonosporium ricksearlesii

C.W.Schneider & G.W.Saunders, sp. nov.
(Fig. 3)

HOLOTYPE (DESIGNATED HERE). — **Bermuda**. Somerset Island, 32°16.783'N, 64°52.788'W, on wooden dock in Ely's Harbour,

depth 0-1 m, 30.VI.2015, C.W. Schneider & T.R. Popolizio 15-21-3 (holo-, MICH[1210917]), dried silica sample: BDA1944, GenBank: [OR336107](#) (COI-5P), [OR336112](#) (*rbcl*).

ISOTYPES. — Same data as holotype (iso-, NY, UNB, Herb. CWS).

ETYMOLOGY. — Named for Prof. Richard Brownlee Searles, the first author's graduate mentor, collaborator and friend, on the occasion of his 87th birthday. Joint cruises with the first author to study mesophotic seaweeds off Bermuda aboard the R/V *Seahawk* in the early 1980s initiated four decades of investigation on the macroalgal flora of this Atlantic archipelago.

DISTRIBUTION. — Endemic to Bermuda as currently known.

DESCRIPTION

Delicate plants lignicolous or on mud-saturated wood, bushy, erect to 5.0 cm tall, Persian red in colour (Graf1x 2023) and ecorticate (Fig. 3A); indeterminate axes fine with alternately irregular branching above with corymbose and narrowly-angled branches at apices, some with some branches overtopping the apex (Fig. 3B); most branches simple of 15 with fewer cells or once branched, indeterminate branches irregularly replacing these branches; in lower portions of indeterminate axes, the lateral branches markedly smaller than the axis that produced them (Fig. 3C), and with most lateral branches losing all but a few of their most proximal cells; in distal portions the axes only slightly larger in diam. than the branches they produce; indeterminate axial cells cylindrical and usually flared at their proximal ends in basal portions of main axes (Fig. 3C, F, G), 95-150 µm diam. and 370-530 µm long, gradually tapering distally to cells 20-30 µm diam. and 85-250 µm long several segments below the apices; upper branches incurved, apical cells slightly tapering but obtuse (Fig. 3D); tetrasporangia adaxially sessile on upper incurved branches, borne singly or in a series of successive cells or every other branch cell (Fig. 3E), subglobose to obovoidal, 33-36 µm diam. and 36-48 µm long, including a thick wall, sporangia also forming laterally or terminally, at times clustered or in second series, on broken lower and regenerating lateral branches (Fig. 3F, G), some appearing to have single-celled stalks; gametangia unknown.

DISCUSSION

When Harvey (1853: 233) first reported the “variable” *Callithamnion borrieri* for North America, he stated that his specimens were “more slender and softer than the European form...”, and he could “possibly have described them as a new distinct species”. Three decades later, Farlow (1881: 125) also noted that New England specimens were “always more slender than European forms of the species”, but wrote that “there can be almost no doubt that we have true *C. borrieri*.” Following suit, Taylor (1957) reported that the American material of *Pleonosporium borrieri* was “much more slender than that from Europe”. Two recent collections made in southern New England, one each from Massachusetts and Rhode Island, morphologically appeared to be the species identified by these and other earlier workers in the region as *P. borrieri*. Using *rbcl*, we unequivocally establish that the

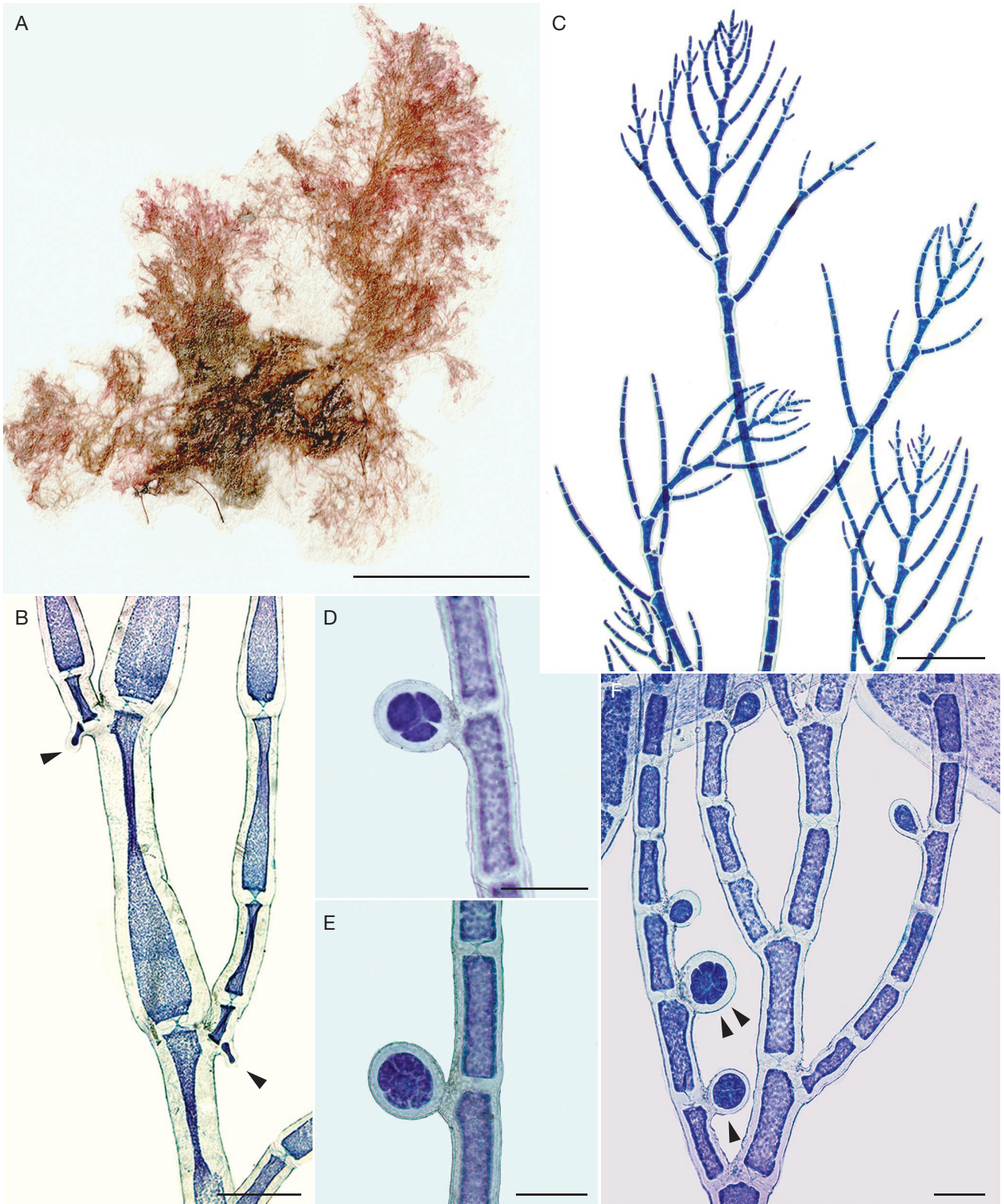


FIG. 2. — *Pleonosporium novae-angliae* G.W.Saunders & C.W.Schneider, sp. nov., holotype specimen (GWS005733): **A**, habit of type specimen; **B**, origins of rhizoids (**arrowheads**) that will eventually loosely envelop proximal axial cells (CWS 78-16-3); **C**, apices of axes and branches with distichous, triangular patterns (CWS 1310); **D**, tetrasporangium (CWS 78-16-3); **E**, octosporangium (CWS 78-16-3); **F**, adaxial tetrasporangium (**arrowhead**) and octosporangium (**double arrowheads**) developing singly and in a series on upper lateral branches (CWS 78-16-3). Scale bars: A, 2 cm; B, C, 250 μ m; D-F, 50 μ m.

North American populations are distinct from a collection of *P. borrieri* from Europe for which this marker has been sequenced (Fig. 1). Indeed, the two New England specimens were identical in their *rbcL* sequences but were much closer to Bermudian *P. ricksearlesii* C.W.Schneider & G.W.Saunders, sp. nov. (15 substitution, thus representing distinct species) than they were to the European *P. borrieri* (81 substitutions). The New England and Bermudian populations also differed by 62 substitutions in the COI-5P gene, again indicating their unique status. Both species were closer to Australian species in our phylogenetic analyses than they were to the genotype, *P. borrieri*, the name formerly used for the southern New England/New York taxon (Fig. 1). Therefore, on the basis of its genetic sequences and morphological comparisons, we describe *P. novae-angliae* G.W.Saunders & C.W.Schneider, sp. nov. for our cold-temperate North American collections, as well as those specimens historically known as *P. borrieri* in the western Atlantic (Harvey 1853, as *Callithamnion borrieri* (Smith) C.Agardh; Farlow 1881, as *C. borrieri*; Taylor 1957; Mathieson & Dawes 2017).

Indeterminate axes of both *Pleonosporium borrieri* and *P. novae-angliae* G.W.Saunders & C.W.Schneider, sp. nov. produce alternately distichous branches from the distal ends of axial cells. Near their apices, the alternately pinnate branching pattern suggests a pyramidal outline (Fig. 2C), a pattern that can be found in other members of the Wrangeliaceae (e.g. *Compsothamnion*), as well as some in the related Callithamniaceae (e.g. *Aglaothamnion*, *Callithamnion*, *Gaillona*). Both *P. borrieri* and *P. novae-angliae* G.W.Saunders & C.W.Schneider, sp. nov. produce entangling rhizoids issued from basal cells of lower branches that attach to other axes as well as other plants and substrata. As noted by early workers on the New England flora, the axes of *P. novae-angliae* G.W.Saunders & C.W.Schneider, sp. nov. are on average much finer than those of European *P. borrieri*. Maggs & Hommersand (1993) reported that the rhizoids of *P. borrieri* descend and intertwine loosely around the lowermost axial cells causing the lower axes to be as large as 500 µm in diameter, whereas in *P. novae-angliae* G.W.Saunders & C.W.Schneider, sp. nov. only a few loose rhizoids are produced exposing the axial cells that are maximally c. 260 µm wide (Fig. 2B).

Measurements collected from the two genetic specimens of *Pleonosporium novae-angliae* G.W.Saunders & C.W.Schneider, sp. nov. reported here are consistent with those retrieved from archival New England/New York specimens from the 1800s to 2000 identified at the time as *P. borrieri*. These specimens include *P.B.-A. no. 342* listed as *P. borrieri* with 1897 collections from both Connecticut and Massachusetts (Collins *et al.* 1897). As we have yet to sequence recent tetrasporangial or octosporangial specimens, these all being collected prior to our regular specimen processing for molecular analysis, we tentatively assigned sporangial measurements from archival specimens to the above description. *Pleonosporium borrieri* was reported from the warmer, more southern waters of North Carolina (Williams 1951), but Schneider & Searles (1991) were unable to locate Williams' vouchers of this species. Because of its similarity to *P. boergesenii* (A.B.Joly) R.E.Norris (Schneider

1975, as *Mesothamnion boergesenii* Joly), Schneider & Searles (1991) excluded *P. borrieri* from the southeastern U.S. flora, although Mateo-Cid *et al.* (2018) recently reported it from the Atlantic coast of Mexico.

Sequences from collections of a fine, bushy filamentous species from a wooden dock in Bermuda (field identified as *Aglaothamnion* sp.) also nested the clade with *P. borrieri* and congeners. Prior to this study, the genus *Pleonosporium* was unknown in Bermuda, but comparison with known species in the genus showed these isolates to represent *P. ricksearlesii* C.W.Schneider & G.W.Saunders, sp. nov. from the warm temperate western Atlantic. The specimens from Somerset, Bermuda, aligned with *P. borrieri*, *P. hirtum* and *P. australicum* (Womersley) G.W.Saunders & C.W.Schneider, comb. nov., and directly with its sister species, *P. novae-angliae* G.W.Saunders & C.W.Schneider, sp. nov. (Fig. 1). *Pleonosporium ricksearlesii* C.W.Schneider & G.W.Saunders, sp. nov. differs from *P. novae-angliae* G.W.Saunders & C.W.Schneider, sp. nov. by not developing a pronounced alternately pinnate branching pattern with a pyramidal outline in distal portions. The apices of *P. ricksearlesii* C.W.Schneider & G.W.Saunders, sp. nov. develop alternate branches, but these are issued irregularly, appearing congested and not pinnately displayed (Fig. 3B, D). The Bermuda species also has much smaller axial cells in lower portions of the indeterminate axes than *P. novae-angliae* G.W.Saunders & C.W.Schneider, sp. nov. (95–150 µm diam. × 370–530 µm long vs 125–260 µm diam. × 550–860 µm long) and longer upper axial cells (85–250 µm vs 18–25 µm long). Among the known members of the genus, *P. ricksearlesii* C.W.Schneider & G.W.Saunders, sp. nov. is morphologically most similar to *P. boergesenii* from North Carolina to Brazil through the Caribbean Sea (Guiry & Guiry 2023), a species yet to be sequenced. *Pleonosporium ricksearlesii* C.W.Schneider & G.W.Saunders, sp. nov. differs in having finer cells near their bases, 95–150 µm diam. and 370–530 µm long, as compared to those of *P. boergesenii*, 210–325 µm diam. and 600–900 µm long (Schneider & Searles 1991; Littler *et al.* 2008). Tetrasporangia of both species develop in similar positions, but those of *P. ricksearlesii* C.W.Schneider & G.W.Saunders, sp. nov. are smaller than those of *P. boergesenii*, 33–36 µm diam. by 36–48 µm long vs 40–75 µm diam. by 85–160 µm long (Joly 1957, as *Mesothamnion boergesenii* A.B.Joly; Littler *et al.* 2008). *Pleonosporium ricksearlesii* C.W.Schneider & G.W.Saunders, sp. nov. has some similarity to the habit of *P. mexicana* E.Y.Dawson from Pacific Mexico and Brazil (Dawson 1962; Oliveira Filho 1969), but that species is strictly distichous and also has much larger axial cells and sporangial dimensions than the new species.

The genus *Pleonosporium* is characterized as producing mitotic divisions beyond the normal meiotic division in sporangia (Maggs & Hommersand 1993). Species of the Spongocloniae producing sporangia would first produce meiotic tetrasporangia before dividing sequentially again to eight (octosporangia), 16 or 32 spores (polysporangia). Unlike the great majority of species presently in the genus, *P. ricksearlesii* C.W.Schneider & G.W.Saunders, sp. nov. is one of just three species found to produce only tetrasporangia,

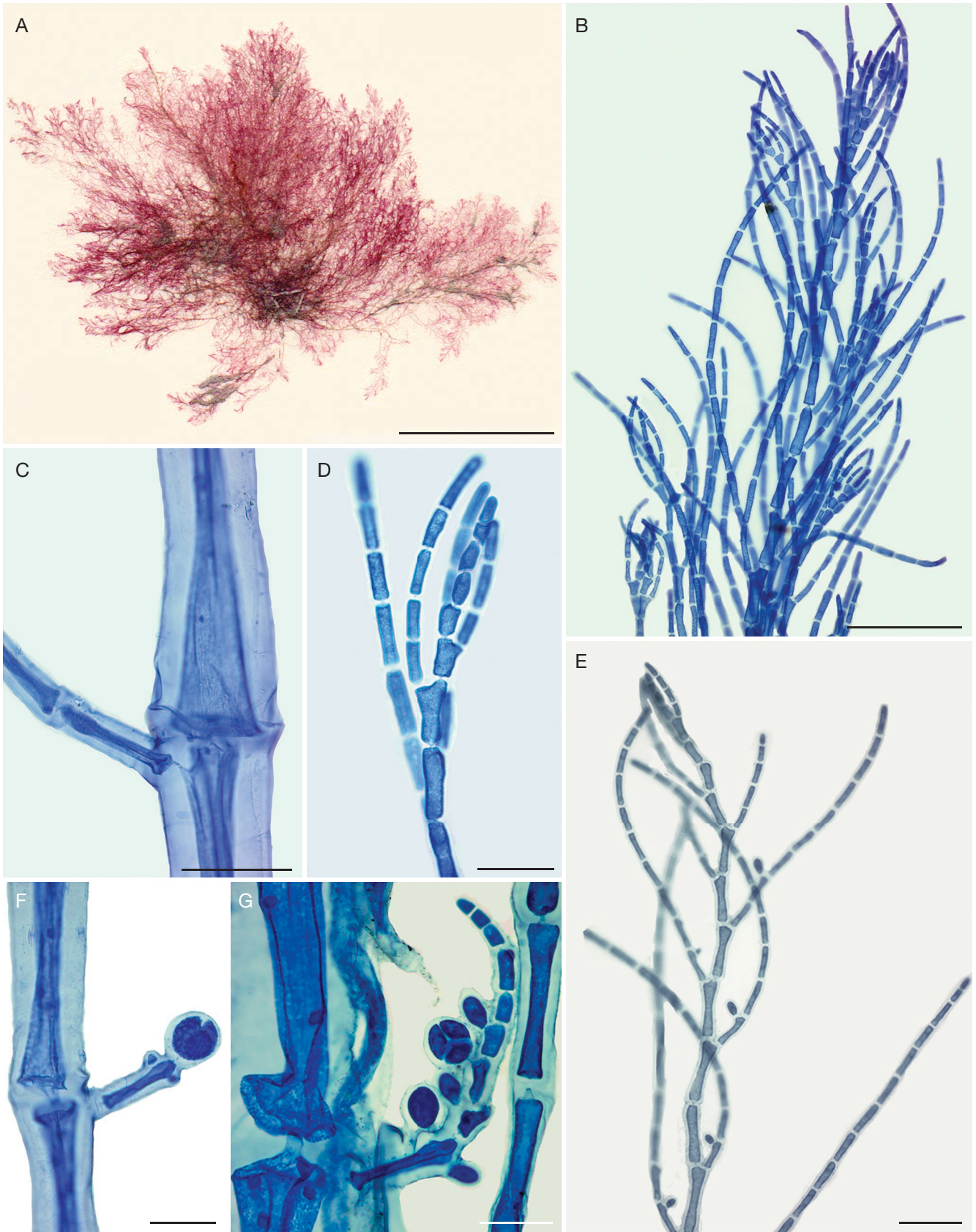


FIG. 3. — *Pleonosporium ricksearsesii* C.W.Schneider & G.W.Saunders, sp. nov., holotype specimen (CWS/TRP 15-21-3, BDA1944): **A**, habit of type specimen; **B**, apex of indeterminate axis; **C**, lateral branch origin from basal portion of axis; **D**, apex of lateral branch; **E**, apical portion of axis with adaxial tetrasporangia; **F**, terminal tetrasporangium on lateral off lower main axis with subtending branchlet or sporangial initials; **G**, regenerating lateral on lower axis producing a series of tetrasporangia. Scale bars: A, 2 cm; B, D, E, 100 µm; C, F, G, 50 µm.

not octosporangia or polysporangia. *Pleonosporium intricatum* R.E.Norris (Norris 1994) from Hawaii and *P. mageshimense* (Itono) R.E.Norris from Japan (Itono 1977) are also known to produce only tetrasporangia among the 31 currently recognized species prior to this report (Guiry & Guiry 2023). The lack of polysporangia in *P. ricksearlesii* C.W.Schneider & G.W.Saunders, sp. nov. could, however, be a collecting artifact; thus, additional collections are needed to substantiate this claim. Some species such as *P. borrieri* (Newton 1931), *P. kobayashii* Okamura (Okamura 1933) and *P. novae-angliae* G.W.Saunders & C.W.Schneider, sp. nov. have plants bearing both tetrasporangia as well as octosporangia on the same individuals. Although the recent sequenced specimens used to genetically separate *P. novae-angliae* G.W.Saunders & C.W.Schneider, sp. nov. from *P. borrieri* lacked sporangia on their branches, archival specimens from southern New England showed both tetrasporangia and octosporangia on the same individuals (Fig. 2F). As early collectors cited polysporangia for this species (Harvey 1853, as *C. borrieri*; Farlow 1881, as *C. borrieri*; Taylor 1957, as *P. borrieri*; Mathieson & Dawes 2017, as *P. borrieri*), it is possible that they used the term polysporangia for sporangia with any divisions post meiosis. Furthermore, it could be that specimens other than those we have seen may indeed produce them as well. Further collections of both of the new western Atlantic species will hopefully clarify whether these species produce any mitotic divisions beyond meiosis, and how many spores are found in the sporangia.

The genotype of *Spongoconium*, *S. conspicuum*, produces only tetrasporangia on sporophytes (Wollaston 1990). Likewise, some other species remaining in the genus produce only tetrasporangia (e.g. *S. fasciculatum* J.Agardh, *S. pastorale* Laing), while others develop tetrasporangia as well as occasional to rare octosporangia (e.g. *S. brownianum* (Harvey) J.Agardh, *S. caribaeum*, *S. yagii* (Yamada) H.-S.Kim & I.K.Lee). Each of the species varies as to the presence of (and levels of) cortication on axial cells in lower portions of indeterminate axes. Whether the number of cell divisions in sporangia becomes a useful generic distinction for *Pleonosporium* and *Spongoconium* remains to be seen after additional samples of both become available and more species are genetically tested and phylogenetically sorted. We are thus reluctant at this time to declare that *Pleonosporium* (Nägeli 1862) is a junior synonym of *Spongoconium* (Sonder 1855). Despite their sister association in our phylogenies (Fig. 1), they are relatively distantly related, and the possibility that these should remain as distinct genera in Spongoconieae requires analysis of other Australasian species in *Spongoconium*, as well as *Pleonosporium* spp. that exclusively produce tetrasporangia. Nevertheless, we are assured that *L. hirtum* is solidly aligned in the clade with *Pleonosporium* and thus subsume *Lophothamnion* (Agardh 1892) under it.

We have uncovered six species of *Pleonosporium* in the Northeast Pacific, two included in our phylogeny here (Fig. 1), which fall well outside the nested *Pleonosporium*/*Spongoconium* clade. They require further taxonomic work to clarify their current ‘orphaned’ status, as well as to assign specific epithets to the genetic groups.

Acknowledgements

We acknowledge Discovery Grants from the Natural Sciences and Engineering Research Council of Canada with infrastructure support from the Canada Foundation for Innovation and the New Brunswick Innovation Foundation that funded the molecular work at UNB. Field support for GWS was provided in part through the Australian Biological Resources Study. GWS thanks the many individuals in his lab for field assistance, and Cody Brooks, Dan McDevit and Tanya Moore for generating the new sequence data used in this study. For the field work in Bermuda, we acknowledge National Science Foundation DEB grant 1120688 to CWS, and thank Thea Popolizio for her assistance in collecting and Roger Simmons of the Bermuda Aquarium who provided logistical support in Bermuda. This is contribution no. 296 to the Bermuda Biodiversity Project (BBP) of the Bermuda Natural History Museum, Department of Environment and Natural Resources.

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Submitted on 22 August 2023;
accepted on 27 October 2023;
published on 17 January 2024.

APPENDIX

APPENDIX 1. — Collection details and GenBank accession numbers for specimens included in this study.

Name	Voucher	Collection	SSU	COI-5P	rbcL
<i>Dasythamniella dasyura</i> (Harvey) Womersley	GWS000335 GWS015175	Australia, VIC, Warrnambool, 15.XI.1997, G. Kraft Australia, TAS, Burying Ground Point, 21.I.2010, G. Saunders & K. Dixon	EU718686 –	– HM917616	– KU381976
<i>Haloplegma</i> sp. 2WA	GWS025420	Australia, WA, Pt. Peron, 13.XI.2010, G. Saunders & K. Dixon	–	KU381919	KU381989
<i>Pleonosporium australicum</i> (Womersley) G.W.Saunders & C.W.Schneider, comb. nov.	GWS015077 GWS015200	Australia, TAS, George Town, Windmill Point, 19.I.2010, G. Saunders & K. Dixon Australia, TAS, Burying Ground Point, 21.I.2010, G. Saunders & K. Dixon	– –	OR336105 OR336106	OR336109 –
<i>Pleonosporium borrieri</i> (Smith) Nägeli	PD2941	Spain, Galicia, P. Díaz-Tapia, sourced from GenBank	–	–	MK814701
<i>Pleonosporium hirtum</i> (Hooker f. & Harvey) Laing	GWS001468	Australia, TAS, Bicheno, 25.XI.2002, G. Saunders	–	HM915913	KU381977
<i>Pleonosporium novae-angliae</i> G.W.Saunders & C.W.Schneider, sp. nov. (holotype)	GWS005733 GWS017847	United States of America, RI, Fort Wetherill, 10.VIII.2007, G. Saunders & B. Clarkston United States of America, MA, Woods Hole, Garbage Beach Breakwater, 14.IV.2010, B. Clarkston, D. McDevit, M. Bruce, A. Savoie & C. Longtin	OQ561850 –	OQ561797 –	OQ561894 OR336111 (rbcL-3P only)
<i>Pleonosporium ricksearlesii</i> C.W.Schneider & G.W.Saunders, sp. nov. (holotype)	CWS/TRP 15-21-3 (BDA1944)	Bermuda, Somerset Island, Ely's Harbour, 30.VI.2015, C. Schneider & T. Popolizio	–	OR336107	OR336112
<i>Pleonosporium</i> sp. 3GWS	GWS021133	Canada, BC, Haida Gwaii, Masset Inlet, Cowley Islands, 9.VI.2010, G. Saunders & K. Dixon	–	HQ919416	KU381986
<i>Pleonosporium</i> cf. <i>squarrosus</i> Kylin	GWS031006	Canada, BC, Gwaii Haanas, Tanu Island, Tanu, 14.VI.2012, G. Saunders & K. Dixon	OQ561854	KU381855	KU381982
<i>Plumaria plumosa</i> (Hudson) Kuntze	CH029 GWS009779	France, Cap Gris-Nez, 21.VIII.1997, H-G. Choi Canada, NS, Brier Island Western Light (exposed rocky site), 29.V.2008, H. Kucera & S. Hamsher	AF488382 –	– HM917150	– KU381993
<i>Ptilota asplenioides</i> (Esper) C.Agardh	CH801 GWS035795	Japan, Nemuro, 30.VI.1995, H-G. Choi Canada, BC, Gwaii Haanas, SGang Gwaay (rocks to NW), 18.VIII.2013, G. Saunders & K. Dixon	EU718696 –	– KU381943	– KU381991
<i>Spermothamnion repens</i> (Dillwyn) Magnus	GWS014712	United States of America, MA, Plymouth, White Horse Beach, 12.IV.2010, B. Clarkston, D. McDevit, M. Bruce, A. Savoie & C. Longtin	OQ561858	HM919017	OQ561899
<i>Spongoclonium conspicuum</i> Sonder	GWS000303	Australia, VIC, Warrnambool, 13.IX.1997, G. Kraft	EU718705	–	OR336110