Notes on the Marine Algae of the Bermudas. 12. A phylogenetic Assessment of *Nemastoma gelatinosum* M. Howe (Rhodophyta, Nemastomatales) from its Type Locality

Author(s): Craig W. Schneider , Daniel C. McDevit , Gary W. Saunders & Christopher E. Lane

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Notes on the marine algae of the Bermudas. 12. A phylogenetic assessment of *Nemastoma gelatinosum* M. Howe (Rhodophyta, Nemastomatales) from its type locality[1]

Craig W. SCHNEIDER[a], Daniel C. MCDEVIT[b], Gary W. SAUNDERS[b]*
& Christopher E. LANE[c]

[a]Department of Biology, Trinity College, Hartford, CT 06106, USA

[b]Centre for Environmental & Molecular Algal Research, Department of Biology, University of New Brunswick, Fredericton, NB E3B 5A3, Canada

[c]Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881, USA

Abstract – Using three genetic markers (COI-5P, LSU, *rbc*L), plants historically identified as *Platoma cyclocolpum* from Bermuda have been linked to *Nemastoma gelatinosum* from its type locality, each representing a distinct seasonal morphology in the islands. Further, the Bermuda plants are genetically related to the recently described *P. chrysymenioides* from the Gulf of Mexico. These molecular studies and morphological observations confirm the generic placement of the Bermuda plants in *Platoma*, necessitating the taxonomic change to the nomenclatural precedent as *P. gelatinosum* (M. Howe) comb. nov.

COI-5P / LSU / *Nemastoma gelatinosum* / Nemastomatales / *Platoma chrysymenioides* / *Platoma cyclocolpum* / *Platoma gelatinosum* comb. nov. / *rbc*L / Rhodophyta

Résumé – Notes sur les algues marines des Bermudes. 12. Évaluation phylogénétique de *Nemastoma gelatinosum* M. Howe (Rhodophyta, Nemastomatales) de la localité type. L'utilisation de trois marqueurs génétiques (COI-5P, LSU, *rbc*L) a permis de démontrer la conspécificité de plantes historiquement identifiées comme *Platoma cyclocolpum* aux Bermudes et un topotype de *Nemastoma gelatinosum ;* ces deux entités présentant des morphologies saisonnières distinctes dans l'archipel. De plus, les plantes des Bermudes sont génétiquement proches d'un taxon récemment décrit au Golfe du Mexique, *P. chrysymenioides.* Ces études moléculaires et ces observations morphologiques confirment le placement des plantes des Bermudes au sein du genre *Platoma*, ce qui nécessite un changement nomenclatural d'où la proposition de *P. gelatinosum* (M. Howe) comb. nov.

COI-5P / LSU / *Nemastoma gelatinosum* / Nemastomatales / *Platoma chrysymenioides* / *Platoma cyclocolpum* / *Platoma gelatinosum* comb. nov. / *rbc*L / Rhodophyta

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* Correspondence and reprints: craig.schneider.1@trincoll.edu

INTRODUCTION

In the long history of floristic studies in the islands of Bermuda only two species of the Nemastomatales have been reported. Most probably, the first of these was originally collected in 1881 by W.G. Farlow, who at the time labeled these specimens *Nemastoma cervicornis* J. Agardh in his unpublished exsiccata, '*Algae Bermudiensis*' (Fig. 1). This name was penned onto specimen labels but never validated by Agardh [see entry for *Platoma cervicornis* (J. Agardh) Bornet in *Index Nominum Algarum Bibliographia Phycologia Universalis*, http://ucjeps.berkeley.edu/INA.html]. These Farlow specimens from Bermuda are also probably those first noted in the literature by E. Bornet (1892) as *Platoma cyclocolpum* (Mont.) F. Schmitz from "Bermudes", but no specimen data are given in this early report. Separates of '*Algae Bermudiensis*' were distributed widely in Europe (Harvard University's Farlow Herbarium, http://asaweb.huh.harvard.edu:8080/databases/botanist_index.html), including the Muséum National d'Histoire Naturelle (PC) where Bornet would have had access to these unpublished specimens. Interestingly, the name *P. cyclocolpum* used by Bornet (1892) was also invalid at this time in that Schmitz (1889) initially recognized the genus *Platoma* without supplying a description. He later properly validated the genus and his chosen generitype, *P. cyclocolpum* (Schmitz, 1894). In the next century, based upon the earlier, as well as their own, collections, *P. cyclocolpum* was reported by Collins & Hervey (1917) (Fig. 2) and Howe (1918) in their Bermuda algal floras, as well as by Taylor (1960) in his comprehensive regional flora for subtropical and tropical western Atlantic waters.

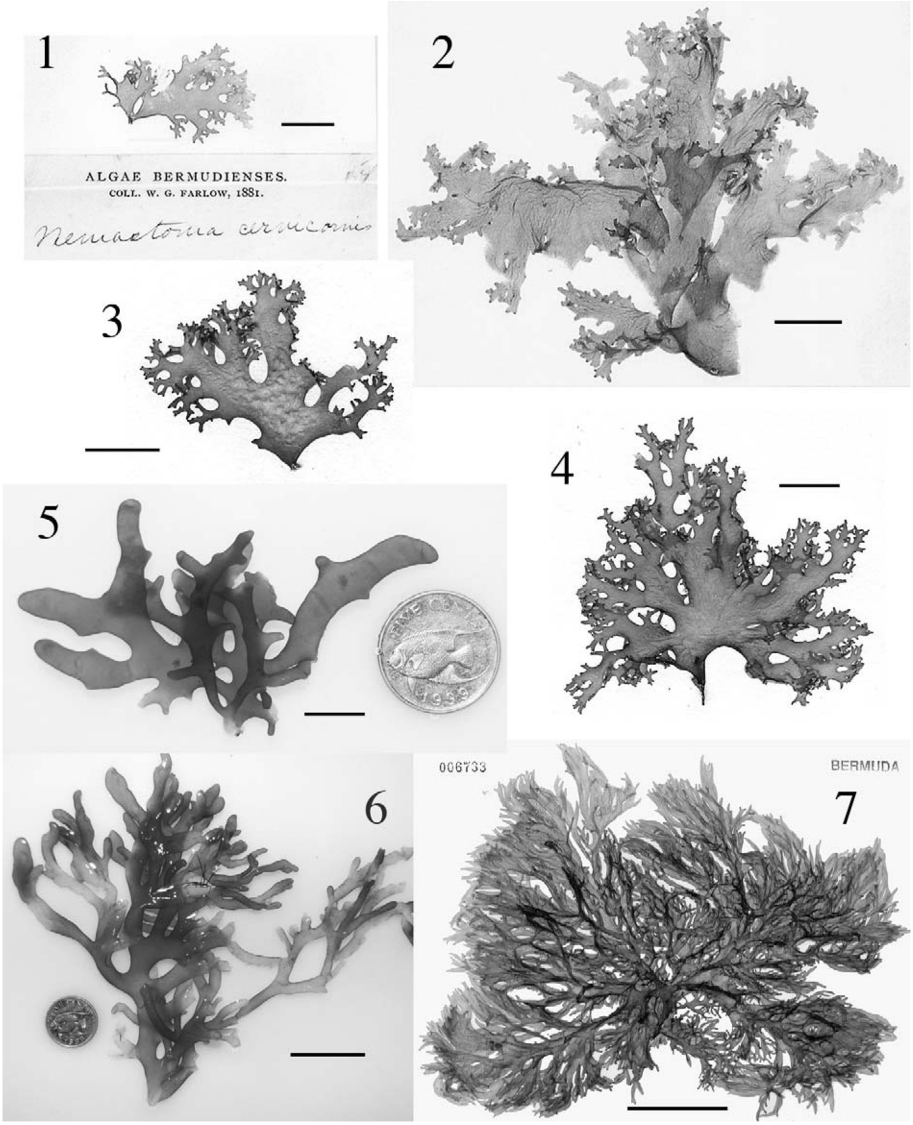
In the same publication where he listed *Platoma cyclocolpum* for the islands, Howe (1918) described a robust new species from Tucker's Town Bay in Castle Harbour, Bermuda, *Nemastoma gelatinosum* M. Howe, the second species of Nemastomatales reported in the flora (Schneider, 2003). Howe (1918) stated that his new species *N. gelatinosum* "may possibly include the plants somewhat doubtfully referred… to *Platoma cyclocolpa* [sic, see Athananasiadis, 2000], to which it bears much resemblance in structure, but, if so, the species is remarkably protean in habit. *N. gelatinosum* is a softer, more gelatinous… suffrutescent plant, with all parts predominantly subterete, while the so-called *Platoma cyclocolpa* is a plane membranous plant, with a marginal fringe of lobules or crenations." Thus, from the time of its description, the possible relationship of *N. gelatinosum* with *P. cyclocolpum* was considered by Howe (1918).

Over the past few years, we have been able to collect the small but distinctive, flattened and marginally proliferous plants of so-called *Platoma cyclocolpum* only during the winter months (Figs 3, 4), and large, irregularly branched *Nemastoma gelatinosum* in summer (Figs 5-7), allowing for the morphological and molecular comparisons provided below. At present, these two species represent the only members of the emended Nemastomatales (Saunders & Kraft, 2002) in the waters of Bermuda (Schneider, 2003).

MATERIAL AND METHODS

Standard Methods

Underwater collections were made by scuba, and specimens were air-dried fresh onto herbarium paper with fragments desiccated in silica gel and



Figs 1-7. Bermuda collections of *Platoma gelatinosum,* comb. nov. **1.** W.G. Farlow collection as *Nemastoma cervicornis* nom. nud., 1881. Scale bar = 1 cm. **2.** F.S. Collins collection as *Platoma cyclocolpum,* Castle Harbour, Apr. 1912. Scale bar = 1 cm. **3.** *CWS/CEL* 08-22-25, off Gurnet Rock from Castle Harbour, Feb. 2008, winter morph. Scale bar = 1 cm. **4.** *CWS/CEL* 09-30-21, off Gurnet Rock, Mar. 2009, winter morph. Scale bar = 1 cm. **5.** *CWS/CEL* 10-24-1 (DNA0357), Cathedral Rock, Aug. 2010, summer morph. Scale bar = 1 cm. **6.** *CWS/CEL* 10-24-1 (DNA0359), Cathedral Rock, Aug. 2010, summer morph. Scale bar = 3 cm. **7.** *CWS/CEL* 06-14-6, off Frick's Beach, Jul. 2006, summer morph. Scale bar = 5 cm.

others preserved in 4-5% Formalin-seawater for anatomical study. Site locations were taken using a Garmin™ GPS III Plus (Olathe, Kansas, USA). Field habit photographs were taken using a Nikon D50 digital camera (Tokyo, Japan), herbarium specimens were scanned on an HP Photosmart Premium scanner model C-309a (Hewlett-Packard Company, Palo Alto, California, USA), and photomicrographs were taken using Carl Zeiss Axioskop 40 microscope (Oberkochen, Germany) equipped with a model 4.2 Spot InSight QE digital camera (Diagnostic Instruments, Sterling Heights, Michigan, USA). The digital images were composed in Adobe Photoshop™ CS5 Extended v. 12.0.2 (Adobe Systems, San Jose, California, USA). Voucher specimens are deposited in MICH, MSM, NY, UNB, the Bermuda Natural History Museum and the first author's herbarium. When listed, herbarium abbreviations follow the online *Index Herbariorum* (http://sweetgum.nybg.org/ih/) and standard author initials are from Brummitt & Powell (1992).

Molecular Methods

Samples used in molecular analyses are recorded in Table 1. Total DNA was extracted from silica-dried specimens following Saunders & McDevit (2011). For purposes of collection assignment to genetic species, the COI-5P region of the mitochondrial genome (Saunders, 2005; 2008) was amplified with the primers GWSFn (Le Gall & Saunders, 2010) and GWSRx (Saunders & McDevit, 2011). To facilitate a comparison to data in GenBank for *P. chrysymenioides,* the partial plastid RUBISCO large subunit (*rbc*L) was amplified following Vis *et al.* (2007). For phylogenetic analyses, the large subunit ribosomal DNA (LSU) was amplified according to Harper & Saunders (2001). All PCR products were sequenced using a Big Dye Terminator Cycle Sequencing Ready Reactions DNA sequencing kit (Applied Biosystems, Foster City, CA). For LSU and *rbc*L, the products were sequenced with their specific PCR primers, as well as additional internal primers as outlined in Harper & Saunders (2001) and Le Gall & Saunders (2007). Final sequences (excluding the 5' and 3' primer regions) were assembled using Sequencher TM 4.10 (Gene Codes Corporation, Michigan) and based on bidirectional data.

Multiple alignments were prepared in MacClade version 4.06 (Maddison & Maddison, 2003). For species identification, a neighbor joining (NJ) analysis of the COI-5P alignment with uncorrected distances was completed using PAUP* (Swofford, 2003) in Geneious (Drummond *et al.*, 2009). For phylogenetic analyses of the LSU alignment, maximum likelihood (ML) analysis was completed with a GTR + I + G model of evolution using PHYML in Geneious (Drummond *et al.,* 2009). Robustness was assessed through analyses of 200 bootstrap repetitions under maximum likelihood as outlined.

RESULTS-DISCUSSION

Plants historically identified in Bermuda as *Platoma cyclocolpum* (Figs 1, 2) were collected exclusively during the winter/spring months (Collins & Hervey, 1917). We have been fortunate to collect this species off Bermuda's south shore in the past few years (Figs 3, 4), each time with few individuals, none being reproductive (*CWS/CEL* 08-22-25, 15 Feb. 2008, vic. Gurnet Rock, off mouth of

Table 1. List of specimens used in this study with collection details and BOLD accession numbers for COI-5 data and GenBank accession numbers for LSU and *rbc*L data. Sequences produced for this study are shown in **bold type**.

Taxa	*Voucher no.*	*Collection site*	*Collector(s)*	*Accession numbers*		
				COI-5'	*LSU*	*rbcL*
Adelophycus corneus (J.Agardh) Kraft	GWS000386	Queenscliff Jetty, Port Phillip Heads, Victoria, Australia	L.E. Phillips, G.T. Kraft	ND	DQ343704	ND
Nemastoma dichotoma J.Agardh	GWS001452	Islas Columbretes (Castellon de la Plana), western Mediterranean	C. Rodriguez-Prieto	ND	DQ343705	ND
Nemastoma gelatinosum M.Howe	CWS06-14-6	off Frick's Beach,	C.W. Schneider, C.E. Lane	ND	**JN653455**[1]	ND
Nemastoma gelatinosum	CWS10-5-9 (BDA0015, 0016 0018-0020)	off Frick's Beach, Tuckers's Town, Bermuda (12 m)	C.W. Schneider, C.E. Lane, D. McDevit T. Popolizio	**BERMR015-10** **BERMR016-10** **BERMR018-10** **BERMR019-10** **BERMR020-10**	ND ND ND ND ND	ND ND ND ND ND
Nemastoma gelatinosum	CWS10-14-23 (BDA0176)	Tobacco Bay, St George's, Bermuda (2 m)	C.W. Schneider, C.E. Lane, D. McDevit, T. Popolizio	**BERMR102-10**	ND	ND
Nemastoma gelatinosum	CWS10-24-1 (BDA0357-0359)	Cathedral Rock, off Castle Harbour, Bermuda (17 m)	C.W. Schneider, C.E. Lane, D. McDevit T. Popolizio	**BERMR207-10** **BERMR208-10** **BERMR209-10**	ND ND ND	ND ND ND
Nemastoma gelatinosum	CWS10-29-5 (BDA0438)	West of High Pt., Bermuda I., Bermuda (36 m)	C.W. Schneider, D. McDevit, T. Popolizio	**BERMR264-10**	ND	ND

Table 1. List of specimens used in this study with collection details and BOLD accession numbers for COI-5 data and GenBank accession numbers for LSU and *rbc*L data. Sequences produced for this study are shown in **bold type** *(continued)*.

Taxa	*Voucher no.*	*Collection site*	*Collector(s)*	*Accession numbers*		
				COI-5'	*LSU*	*rbcL*
Platoma cyclocolpum (Mont.) F.Schmitz	GWS000133	Gran Canaria, Canary Islands, Spain	M.D. Guiry	**ABMMC3700-09**	DQ343706	ND
Platoma cyclocolpum	GWS011425	Langton I., Sir Joseph Banks Group, South Australia	K.R. Dixon	**ABMMC3894-09**	ND	ND
Platoma cyclocolpum	G0394	NE of White Island, Easter Group, Abrolhos I., Western Australia	G.T. Kraft G.W. Saunders	**ABMMC3699-09**	ND	ND
'*Platoma cyclocolpum*' (winter morph)	CWS08-22-25	off Gurnet Rock, vic. Castle Harbour, Bermuda (17 m)	C.W. Schneider, C.E. Lane	**ABMMC3695-09**	**JN653456**[1]	ND
'*Platoma cyclocolpum*' (winter morph)	CWS09-30-21	off Gurnet Rock, *loc. cit.*	C.W. Schneider, C.E. Lane	**ABMMC3696-09**	**JN653457**[1]	**JN653454**
Predaea aurora Kraft & G.W.Saunders	GWS000465	Vivone Bay, Kangaroo I., South Australia	G.T. Kraft, G.W. Saunders	ND	AF419126	ND
Predaea kraftiana A.Millar & Guiry	GWS00132	Coffs Harbour, New South Wales, Australia (culture)	M.D. Guiry	ND	EF033618	ND

Table 1. List of specimens used in this study with collection details and BOLD accession numbers for COI-5 data and GenBank accession numbers for LSU and *rbc*L data. Sequences produced for this study are shown in **bold type** *(continued)*.

Taxa	*Voucher no.*	*Collection site*	*Collector(s)*	*Accession numbers*		
				COI-5'	*LSU*	*rbcL*
Schizymenia dubyi (Chauvin ex Duby) J.Agardh	G0041	Port MacDonnell, South Australia	G.T. Kraft, G.W. Saunders	ND	AF419128	ND
Schiymenia pacifica (Kylin) Kylin	GWS000584	Pacina Beach, Bamfield, British Columbia, Canada	G.W. Saunders	ND	AF419129	ND
Titanophora weberae Børgesen	GWS001999	Neds Beach, Lord Howe I., New South Wales, Australia	G.W. Saunders	**ABMMC5060-09**	ND	ND
Titanophora weberae	GWS002018	North Head Gutters, Lord Howe I., New South Wales, Australia	G.T. Kraft	**ABMMC5068-09**	ND	ND
Titanophora weberae	GWS002092	Malabar Reef, Lord Howe I., New South Wales, Australia	G.W. Saunders	**ABMMC5108-09**	**JN653458**	ND

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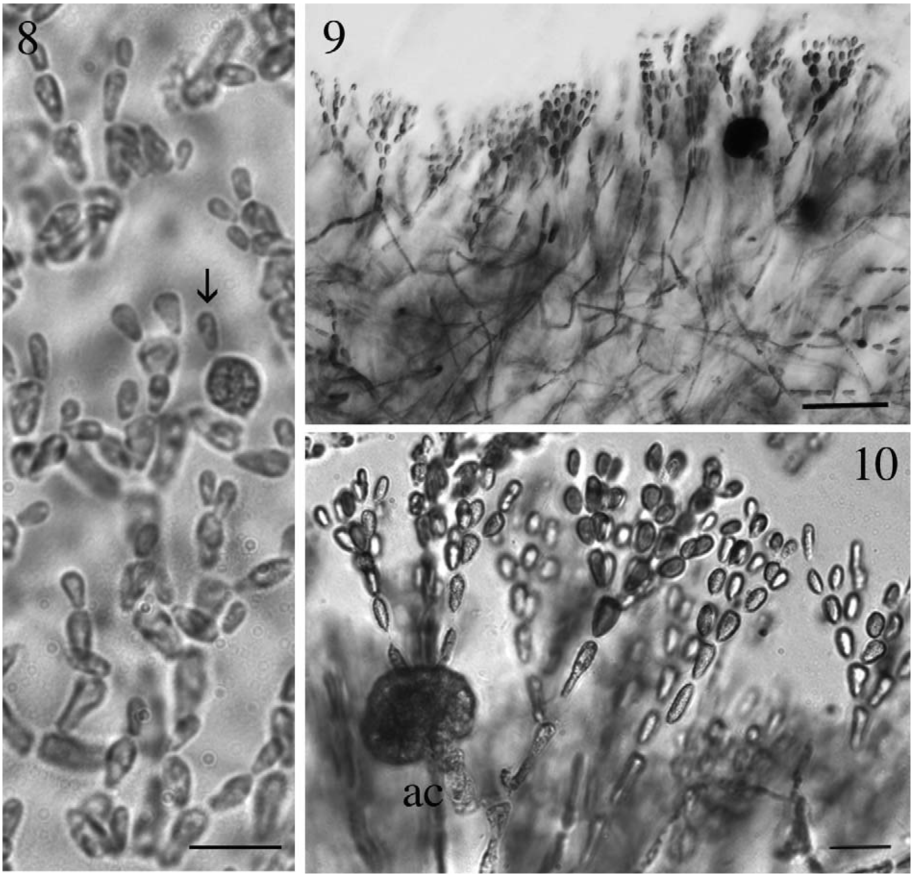
[1] These collections of *Platoma gelatinosum* have virtually identical LSU sequences – CWS06-14-6 was included in our phylogenetic analyses.

Castle Harbour, 32°20.162'N, 64°39.731'W, depth 17.4 m; *CWS/CEL* 09-30-21, 19 Mar. 2009, *loc. cit.*, 16-17 m). *Nemastoma gelatinosum* is an abundant member of the south shore deepwater flora of Bermuda in summer/early autumn with reproductive plants as large as 15 cm high and 15 cm wide common late in the growing season. We have regularly collected specimens from June through August from 5-44 m in depth (selected specimens, Table 1). These summer plants are highly variable, from small individuals with compressed branches issued mostly in a single plane (Fig. 5), to larger, highly branched plants with subterete to compressed branches (or lobes) issuing pseudodichotomously in all directions (Figs 6, 7). Some individuals bear branches proliferously from their main axes, starting as small lobes in early summer and later developing into elongated branches.

Taxonomic results

When Athanasiadis (1988) proposed a generic circumscription for *Nemastoma* using the generitype, *N. dichotomum* J. Agardh, he provided considerably more detailed anatomy/morphology than was found in the generic protologue (Agardh, 1842). A few of his highlighted characters (terminal gland cell position, intercalary auxiliary cell distal on specialized cortical filaments, lack of secondary pit connections &c.) disallowed retention of some species at the time residing within *Nemastoma*, although formal transfers were not affected. For example, Athanasiadis (1988) noted that *N. confusum* Kraft *et* D.M. John should be excluded from the genus by virtue of its intercalary gland cells (demonstrated by Kraft & John, 1976), an assessment accepted by subsequent workers (Masuda & Guiry, 1994; Kajimura, 1997), but until recently, not acted upon. Gabriel *et al.* (2011) moved *N. confusum* to *Platoma*.

At the time Howe (1918) described *Nemastoma gelatinosum*, he mentioned neither gland cells nor reproductive features. None of these features were reported for *Platoma cyclocolpum* in Bermuda by either Collins & Hervey (1917) or Howe (1918), or for the western Atlantic by Taylor (1960). Like these earlier workers in Bermuda, we have collected only vegetative specimens of *P. cyclocolpum*, a fact that is addressed later in this paper. Our collections of *N. gelatinosum,* however, are mostly fertile, being dioecious with cystocarps embedded within the cortex of female gametophytes, and obovoid spermatangia borne on the outermost cortical cells of male gametophytes. Other anatomical observations show that *N. gelatinosum* has intercalary gland cells at the distal ends of cortical fascicles (Fig. 8), a loose medulla in a gelatinous matrix developing the assimilatory corticating fascicles (Fig. 9), supporting and auxiliary cells transformed from cortical cells directly above the basal cells of cortical fascicles (Fig.10), and post-fertilization gonimoblast filaments initiated directly from the auxiliary cell (Fig. 10). Following clarification of the generic limits of *Nemastoma* (Athanasiadis, 1988), these specific features suggested that *N. gelatinosum* is likewise a candidate for generic reassignment within the Nemastomatales. Furthermore, our specimens of *Platoma cyclocolpum* provided no vegetative anatomical characters to differentiate them from *N. gelatinosum*, only remaining distinct in their gross habits of plants collected in different growing seasons. Given Howe's (1918) comments of their potential relatedness quoted above and our own anatomical observations, these two Bermuda species seem to be perfect candidates for molecular comparison.



Figs 8-10. *Platoma gelatinosum,* comb. nov. **8.** Cortical cells showing intercalary gland cell under terminal vegetative cell (arrow). Scale bar = 25 µm (*CWS/CEL* 06-14-6). **9.** Cortical fascicles arising from medullary filaments with developing cystocarp. Scale bar = 100 µm (*CWS/CEL* 10-5-9). **10.** Developing cystocarp on auxiliary cell (ac), the basal cell of its specialized branch. Scale bar = 25 µm (*CWS/CEL* 10-5-9).

The Bermuda specimens of *Nemastoma gelatinosum* also conform anatomically in all details to *Platoma chrysymenioides* Gavio, Hickerson & Fredericq, from offshore of Louisiana, U.S.A. in the Gulf of Mexico. Gavio *et al.* (2005) demonstrated for *P. chrysymenioides* similar cell size dimensions, intercalary gland cells in distal portions of cortical branches, and supporting and auxiliary cells transformed from cortical cells directly above the basal cells of cortical fascicles that we observe in *N. gelatinosum*. Pre- and post-fertilization stages in Bermuda plants are the same as those described and illustrated for *P. chrysymenioides* (Gavio *et al*., 2005, figs 12-24), including gonimoblast filaments initiated directly from the auxiliary cell, characteristics correct for *Platoma* that do not conform with *Nemastoma* (Athanasiadis, 1988). Using *rbc*L sequence alignment, Gavio *et al.* (2005) demonstrated that their offshore Gulf of Mexico specimens were closely grouped in *Platoma* with *P. cyclocolpum* from the type locality in the Canary Islands.

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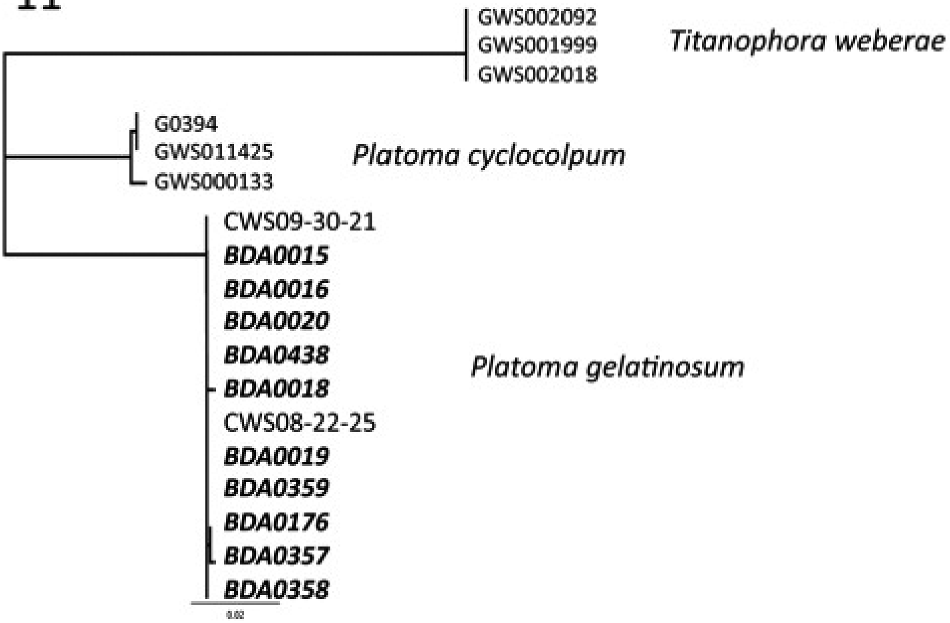

Fig. 11. Unrooted neighbor joining analysis based upon an alignment with uncorrected distances (PAUP in Geneious) for COI-5P. For the *Platoma gelatinosum* grouping, bolded/italicized codes represent specimens field identified as *Nemastoma gelatinosum* (= summer morphology) and the unhighlighted CWS numbers represent field identifications as *Platoma cyclocolpum* (= winter morphology). Refer to Table 1 for collection data.

Molecular results

We put the Bermuda species-level resolution into context using COI-5P sequences of both our 'winter' *Platoma cyclocolpum* and 'summer' *Nemastoma gelatinosum* from just offshore of the type locality in Tucker's Town Bay, Bermuda I. (Table 1). The result, supported by LSU data, indicated that the two seasonal morphologies in Bermuda represented different developmental stages of the same species (Fig. 11). It now became obvious that the winter specimens lacked reproduction because they were merely juvenile forms of the larger summer plants. By sequencing *P. cyclocolpum* from its type locality for this barcode comparison (GWS000133, Canary Islands), we further demonstrated that what had been labeled *P. cyclocolpum* from Bermuda as far back as the 1800s was indeed a different taxon from that of the same name in the eastern Atlantic (Fig. 11). Next, we sequenced LSU data from other species of the Nemastomatales to put our species into a broader phylogenetic context (Table 1; Fig. 12). Winter and summer stages of what we now recognize as a single entity clustered in the clade containing species of *Platoma*, a result not unexpected from our morphological observations.

Finally, we compared *rbc*L sequences of the Bermuda winter morphology (Table 1) with sequences of a paratype of *Platoma chrysymenioides* (GenBank AY294362; although this specimen was designated as an isotype by Gavio *et al.* (2005), it is, along with the other listed "isotype" merely a paratype specimen).

12

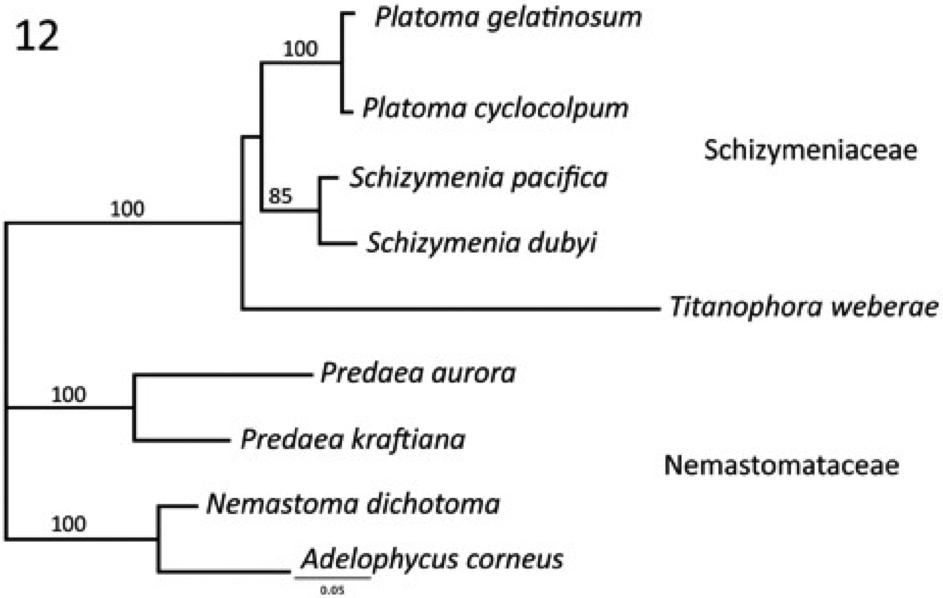

Fig. 12. Maximum likelihood tree generated from LSU sequence data with robustness results for 200 bootstrap replicates indicated along the branches.

The Bermuda specimens were a 100% *rbc*L sequence match with this recently described species from the Gulf of Mexico, a species with a habit, anatomy, and reproduction that, as stated earlier, perfectly matches the summer morphology of *Nemastoma gelatinosum*.

These molecular and morphological results necessitate the following name change:

Platoma gelatinosum (M. Howe) C.W. Schneid., McDevit, G.W. Saunders *et* C.E. Lane **comb. nov.** **(Figs 1-10)**

Basionym: *Nemastoma gelatinosum* M. Howe 1918, *Flora of Bermuda,* p. 536.

Heterotypic synonym: *Platoma chrysymenioides* Gavio, Hickerson *et* Fredericq 2005, p. 45, figs 3-24.

Misapplied name for Bermuda: *Platoma cyclocolpum* (Mont.) F. Schmitz *sensu* Collins *et* Hervey, 1917; *sensu* Howe, 1918; *sensu* Taylor, 1960 *pro parte*.

Distribution: As *Nemastoma gelatinosum,* this species was known only from Bermuda (type locality) and Florida (Littler & Littler, 2000) in the western Atlantic. As *Platoma cyclocolpum*, it was reported in the western Atlantic from the east and Gulf coasts of Florida and Caribbean islands (Taylor, 1960; Littler & Littler, 2000; Dawes & Mathieson, 2008). Recently, using *rbc*L sequence analysis, Gabriel *et al.* (2010) concluded that specimens from throughout the Gulf of Mexico including the same paratype *rbc*L sequence we utilized, specimens that would have been identified by workers as *P. cyclocolpum* in the past, are genetically the same as *P. chrysymenioides*, now a junior synonym of *P. gelatinosum*. These western Atlantic specimens were demonstrated to cluster in a distinct clade from *P. cyclocolpum* from the Canary Islands and the Azores, and our study corroborates their findings. Reports of *P. cyclocolpum* from the Caribbean proper

(Taylor, 1960; Littler & Littler, 2000) need verification as to their correct taxonomic placement. However, we must assume due to the great morphological plasticity of *P. gelatinosum,* including winter expressions that have the same appearance as *P. cyclocolpum*, that this latter species can be removed from the flora of the tropical and subtropical western Atlantic (Wynne, 2011) until proven otherwise by sequence analysis. *Platoma gelatinosum* has been reported in the eastern Atlantic from Madeira (Levring, 1974, as *N. gelatinosum*; Neto *et al*., 2001, as *N. gelatinosum*), and from Madagascar and Rodrigues I. in the Indian Ocean (Gabriel *et al*., 2010, as *P. chrysymenioides*), suggesting that this species might be more widespread in the tropics than is presently known. Gabriel *et al.* (2010, as *P. chrysymenioides*) developed *rbc*L sequences from their Indian Ocean specimens that aligned closely with *P. gelatinosum* from the Gulf of Mexico.

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