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**Two new species of Solieriaceae (Rhodophyta, Gigartinales) from the euphotic and mesophotic zones off Bermuda, *Meristotheca odontoloma* and *Tepoztequiella muriamans***

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Right Header: Schneider *et al.*: Two new Bermuda Solieriaceae

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## ABSTRACT

Using mitochondrial COI-5P and plastid *rbcL* sequences, as well as morphological characteristics, two new species of Solieriaceae are added to the flora of Bermuda. Specimens collected over the past two decades representing those distributed in the early exsiccata, *Phycotheca Boreali-Americana* as *Eucheuma gelidium* (= *Meristotheca gelidium*) are shown to be a unique species of *Meristotheca*, *M. odontoloma* *sp. nov.* A recent collection from a depth of 60 m off the islands is shown to be the same as a single specimen found in Bermuda in 1953 at 55 m and identified at the time as *Agardhiella ramosissima*. These deep-water collections are described as the second species in the new genus *Tepoztequiella*, *T. muriamans* *sp. nov.* Based on shared morphological characteristics, other collections of *M. gelidium* and *A. ramosissima* from the western Atlantic may require molecular analysis to determine if they represent either of the two new species. Our molecular investigations also confirmed that there are two species of *Meristotheca* from Lord Howe I., Australia, and *M. halymenioides* *comb. nov.*, based upon *Mychodea halymenioides*, is removed from synonymy with *M. papulosa*.

## KEYWORDS

COI-5P, *Meristotheca halymenioides* *comb. nov.*, *rbcL*, Western Atlantic

## INTRODUCTION

Few species of the Solieriaceae (Gigartinales) have been reported since the onset of macroalgal collecting in the oceanic islands of Bermuda during the last half of the 1800s. Local specimens of two were distributed in the early exsiccata, *Phycotheca Boreali-Americana* (*P.B.-A.*), one as no. 1886, *Eucheuma isiforme* (*C.Agardh*) *J.Agardh* (= *Eucheumatopsis isiformis* (*C.Agardh*) Núñez-Resendiz, Dreckmann & Senties), the other as no. 2184, *Eucheuma gelidium* (*J.Agardh*) *J.Agardh* (= *Meristotheca gelidium* (*J.Agardh*) *E.J.Faye & Masuda*) (*Collins et al.* 1912, 1917). The

remaining Solieriaceae historically reported in Bermuda are *Agardhiella floridana* (Kylin) P.W.Gabrielson ex S.M.Guimarães & E.C.Oliveira, *A. ramosissima* (Harvey) Kylin and *Wurdemannia miniata* (Sprengel) Feldmann & Hamel (Schneider 2003).

Since initiating the Bermuda Barcode Project (Cianciola *et al.* 2010), numerous new species of marine macroalgae have been discovered in these western Atlantic islands. Some of the new species were found to have been misidentifications of taxa well known in the Caribbean Sea (Schneider *et al.* 2018b), the origin of the Gulf Stream that since the Pleistocene has been largely responsible for redistributing southern tropical species of seaweeds to this northwestern Atlantic archipelago (Thomas 2004). Others historically reported from Bermuda have not been re-discovered in the past 35 years and therefore cannot be verified in today's flora (Schneider & Flook 2017). For example, we have not collected specimens of *Agardhiella floridana* from Bermuda, nor have archival specimens been located in NY, the main repository for specimens in the Collins & Hervey (1917, as *Meristotheca duchassaingii* J.Agardh) report or elsewhere. This report could possibly have been a misidentification of a foliose species of *Halymenia* or *Chrysymenia*.

Here we discuss two species in the Bermuda flora, each representing different genera of the Solieriaceae. Gene sequencing of recent collections has allowed us to place one historical record of a species into a modern phylogenetic context. The second species was collected on the 2016 Nekton XL Catlin cruise of the R/V *Baseline Explorer* from a depth of 60 m in the mesophotic zone off Bermuda and also determined genetically as a member of the Solieriaceae. This collection matched an historical deep-water specimen collected over a half century ago.

## **MATERIAL AND METHODS**

### **Collection and morphological methods**

Collections from the mesophotic zone off the coast of Bermuda were made on the Nekton 2016 XL Catlin cruise of the R/V *Baseline Explorer* by a team of technical re-breather divers (Global Underwater Explorers, High Springs, Florida, USA) equipped with closed-circuit JJ-CCR CE Edition rebreathers (JJ-CCR ApS, Copenhagen, Denmark) modified to GUE configuration, and Triton 1000-2 class submersibles (Vero Beach, Florida, USA) with mechanical arms. Voucher specimens are deposited in the herbaria under each species and herbarium abbreviations follow the online *Index Herbariorum* (Thiers 2019). Collection site locations were recorded with a Garmin™ eTrex H GPS (Olathe, Kansas, USA) or, on the R/V *Baseline Explorer*, using a Beier Radio DP1 (dynamic positioning, Beier Integrated Systems, Mandeville, Louisiana, USA) to receive ship board GPS. Live specimens chosen for DNA analysis were photographed using a Canon Powershot s90 digital camera (Canon Inc., Tokyo, Japan), then fragments of individuals were dried in silica gel for DNA extraction, and preserved with 4–5% formaldehyde in sea water for anatomical study. Finally, the remainder of the specimens were pressed fresh on herbarium paper as permanent vouchers. Thin-sections were made with an American Optical freezing microtome model 880 (San Diego, California, USA) and mounted in 30% corn syrup with acidified 1% aniline blue in a ratio of 20:1. Dried specimens were scanned on an Epson ET-2650 scanner (Seiko Epson Corporation, Suwa, Nagano, Japan), and photomicrographs were taken using Zeiss Axioskop 40 microscope (Oberkochen, Germany) equipped with a Spot Idea 28.2–5MP digital camera (Diagnostic Instruments, Sterling Heights, Michigan, USA). In order to determine if newly sequenced collections of Solieriaceae had been previously collected in Bermuda, the Macroalgal Herbarium Portal (<http://macroalgae.org/portal/index.php>) was accessed and early collections observed. A deep-water specimen of *Agardhiella ramosissima* from the islands was located and morphologically similar to the 2016 mesophotic collection. It was received on loan from MICH [no. 641029].

## Molecular methods

Specimens used for molecular analysis in the current study are listed in Table S1. DNA extractions followed Saunders & McDevit (2012). PCR amplification and sequencing of COI-5P and *rbcL* were as outlined previously in Saunders & Moore (2013). Barcode gap analysis was used to assign the Bermuda specimens to genetic groups and completed in Geneious 10.2.4 (<https://www.geneious.com>; Kearse *et al.* 2012) using uncorrected divergence values. To place these species into a wider phylogenetic context, COI-5P and *rbcL* sequences were generated for a representative of each Bermuda species, as well as related taxa from the Solieriaceae as outgroup taxa (Table S1) following Saunders & Moore (2013). To expand our analyses, *rbcL* data (as well as COI-5P for *Meristotheca cylindrica* Núñez-Resendiz, Dreckmann & Senties and *Tepoztequiella rhizoidea* Núñez-Resendiz, Dreckmann & Senties) were downloaded from GenBank for additional Solieriaceae (GenBank accession numbers on Fig. 1). Two single-gene alignments were generated: COI-5P with 20 sequences of 664 bp (base pairs) and *rbcL* with 26 sequences and 1358 bp. The gene alignments were analysed separately in Geneious with maximum likelihood (GTR+I+G) using RAxML (Stamatakis 2014) with partitioning by codon and 500 bootstrap replicates. Since no conflicts were detected, a concatenated COI-5P and *rbcL* alignment was constructed (27 sequences, 2022 bp) with analyses as described for the single gene alignments, but with partitioning by gene and codon and with 1000 bootstrap replicates (Fig. 1). The tree was rooted on the branch between *Eucheuma/Betaphycus* and the remaining taxa (Núñez-Resendiz *et al.* 2017b).

## RESULTS

Between species variation was clear in COI-5P with ~6% divergence between the closest related genetic groups of Solieriaceae. Within species COI-5P variation was low for those species with more than a single collection (Table S1), typically 0–1 bp divergence (0.2%) for *Mychodea halymenioides* Zanardini (n = 28), recent Bermuda collections of *Meristotheca* (n = 6), and *Mer.* sp. 1Jeju (n = 10). The same was true for Lord Howe specimens of *Mer. procumbens* P.W.Gabrielson & Kraft (n = 33), which were 4 bp different from two identical sequences for specimens from the adjacent mainland Australia (Coffs Harbour, NSW; Table S1). This difference suggests population- rather than species-level division, but further study is warranted. Similarly, a deep-water specimen of *Tepoztequiella* from Bermuda was 6 bp divergent (0.9%) from a North Carolina specimen, which indicates a separate species. Published COI-5P data for *T. rhizoidea* were 2.4–3.0% divergent from the Bermuda collection consistent with allied, but distinct, species.

Therefore, based upon our phylogenetic analyses, we were able to distinguish two unique species in Bermuda, one each in clades for the genera *Meristotheca* and *Tepoztequiella* (Fig. 1). Furthermore, as we have included specimens collected in the Pacific and Indian Oceans in our analyses, we uncovered two species of *Meristotheca* on Lord Howe Island, Australia, consistent with earlier reports (Gabrielson & Kraft 1984; Millar & Kraft 1993). *Meristotheca procumbens* was described from Lord Howe I. and, despite genetic differences, our specimens show morphological similarities to that species (Table S1). The second Australian species was assigned to *M. papulosa* (Montagne) J.Agardh in the previous studies (Gabrielson & Kraft 1984; Millar & Kraft 1993). Gabrielson & Kraft (1984) studied an isotype of *Mychodea halymenioides*, also with its type locality at Lord Howe I., and included it as a synonym of *M. papulosa*. Based on our genetic data, it is clear that the range of bona fide *M. papulosa* does not extend to Lord Howe I. and that the genetic group assigned this name in that flora is a distinct species for which the name

*Mychodea halymenioides* Zanardini is available (Gabrielson & Kraft 1984). Consequently, a new combination is effected here:

***Meristotheca halymenioides* (Zanardini) G.W.Saunders & Kraft *comb. nov.***

Basionym: *Mychodea halymenioides* Zanardini 1874. *Phyceae australicae novae vel minus cognitae. Flora* 57, p. 501.

We also confirm the presence of this species at Norfolk Island, Australia (Table S1), where it likewise had been referred to *Meristotheca papulosa* (Millar 1999).

Along with their genetic differences, the two new Bermuda species have unique morphological and anatomical features that differentiate them from their congeners. As such, the following new species of *Meristotheca* and *Tepoztequiella* from the western Atlantic Ocean are presented here:

***Meristotheca odontoloma* C.W.Schneider, E.S.Peterson & G.W.Saunders *sp. nov.***

**Figs 2–7**

DESCRIPTION: Plants firm, fleshy, light to dark rosy-red, axes prostrate to 7 cm long, attached by basal cartilaginous discoid holdfasts and secondary holdfasts issued from branch margins; main axes markedly compressed to flattened, often arcuate (Figs 2–4), between 1–7 mm diam., percurrent when young, becoming obscured by branches with age, sharply tapering to acute apices, dentations at times developing into new axes, irregularly alternate to sub-oppositely branched to 2–3 orders with some adventitious branches (Figs 3, 4); branches 3–34 mm long and 724–1709 µm thick, ultimate spine-like branches flattened to terete, to 9 mm long, occasionally



dense, causing margins to appear spinose-proliferous, some dentations elongating into secondary holdfasts; medulla of loosely arranged filaments, 2–19  $\mu\text{m}$  diam., giving rise to the radially organised inner cortex of 3–5 layers of hyaline, radially elongate to rounded, thick-walled cells (Fig. 5), innermost cortical cells 138–214  $\mu\text{m}$  width, 175–240  $\mu\text{m}$  length; outermost inner cortical cells 78–116  $\mu\text{m}$  width, 102–154  $\mu\text{m}$  length; tapering to the outer 2-layered cortex of densely pigmented, elongate cells 2–7  $\mu\text{m}$  width, 5–13  $\mu\text{m}$  length; tetrasporangia in loosely scattered patches throughout the outer cortex (Fig. 6) except at tips and on older main axes; tetrasporangia irregularly obovoid or ovoid to ellipsoid, zonately divided, 15–26  $\mu\text{m}$  diam. and 19–35  $\mu\text{m}$  long (Fig. 7).

DIAGNOSIS: Differing from *Meristotheca gelidium* by its prostrate, flattened axes, fewer orders of branching, outer cortical cell diameters, and length of ultimate spine-like branches and size of tetrasporangia (Table 1). It is also differentiated by its *rbcL* and COI-5P gene sequences.

ETYMOLOGY: *odonto-* (Gr. comp.) for toothed, and *loma* (Gr. f.) for fringe or border, literally “having toothed margins”.

TYPE COLLECTION: *C.W. Schneider (CWS)/Christopher E. Lane (CEL)* 10-5-14 [BDA0026], 19 Aug. 2010, off Frick’s Beach, Tucker’s Town, Bermuda I., 32°19.93333’ N, 64°40.34500’ W, depth 10 m = Holotype, MICH (Fig. 2); Isotypes, UNB [BDA0027], Herb. CWS.

SELECTED COLLECTIONS: **Bermuda** – *A.B. Hervey, P.B.-A.* no. 2184 (Collins *et al.* 1917, as *Eucheuma gelidium*), 10 Feb. 2014, St. David’s I.; *CWS/CEL* 06-8-16, 20 Jun. 2006, west of Eastern Blue Cut channel marker, off Somerset Is., 32°23.36833’ N, 064°53.38333’ W, depth 12

m; *CWS/CEL* 06-14-12, 06-14-13, 21 Jun. 2006, south of Frick's Beach, Tucker's Town, Bermuda I., 32°19.94500' N, 64°40.35000' W, depth 10 m; *T.R. Popolizio (TRP)* 12-36-3 [BDA 0883], 18 Feb. 2012, Cathedral Rock, south of Castle Harbour, 32°20.51833' N, 64°39.40333' W, depth 15–17 m; *TRP* 12-40-6 [BDA 0927], ⊕, 13 Mar. 2012, Gurnet Rock, mouth of Castle Harbour, 32°20.37833' N, 64°39.74667' W, depth 13 m; *TRP* 12-83-7 [BDA1262, 1263], 24 Jun. 2012, Natural Arches, south of Bermuda I., 32°19.8000' N, 64°41.11333' W, depth 7 m; *TRP* 12-124-3 [BDA1510], 26 Sept. 2012, Horseshoe Bay, south shore Bermuda I., 32°14.94000' N, 64°49.01000' W, depth 6 m; *TRP* 12-152-3, 17 Nov. 2012, wreck of the Cristobal Colon, north shore Bermuda I., Bermuda, 32°29.10333' N, 64°43.20333' W, depth 18 m (Figs 3, 4); *TRP* 12-158-7 [BDA1713], 27 Nov. 2012, Southwest Breaker, west end of Bermuda I., 32°13.88167' N, 64°51.95333' W, depth 10 m.

MISAPPLIED NAME FOR BERMUDA: *Eucheuma gelidium*, *P.B.-A.* no. 2184 *sensu* Collins *et al.* (1917).

DISTRIBUTION: At present, endemic to Bermuda, western Atlantic Ocean.

***Tepoztequiella muriamans* C.W.Schneider, E.S.Peterson & G.W.Saunders *sp. nov.***

### **Figs 8–14**

DESCRIPTION: Plants firm, fleshy, compressed, light rosy-red, 10.5–12.8 cm tall, attached by cartilaginous, discoid holdfasts; main axes markedly compressed, 1–6 mm diam., percurrent, alternately to oppositely pinnately branched to 3-4 orders (Figs 8–10), with or without adventitious branches, branch length 3–54 mm, branch thickness 1.44–1.62 mm, smaller ultimate

branches less compressed to terete, tapering to bases and to acute to apiculate apices; medulla of loosely arranged filaments, 3–12  $\mu\text{m}$  diam., giving rise to the radially organised inner cortex of 3–4 layers of hyaline, regularly polygonal, thick-walled cells, 49–72  $\mu\text{m}$  diam., 83–135  $\mu\text{m}$  length (Fig. 11); tapering to the outer 1–2 layered cortex of densely pigmented, elongate cells 4–11  $\mu\text{m}$  diam., 12–25  $\mu\text{m}$  length; tetrasporangia scattered, embedded in the outer cortex throughout except at branch apices and on older main axes (Fig. 12), irregularly obovoid to ellipsoid in shape, zonately divided, 24–53  $\mu\text{m}$  diam., 41–73  $\mu\text{m}$  long (Fig. 13); cystocarps embedded in apices of ultimate branches (Fig. 14), carposporophytes 363–454  $\mu\text{m}$  diam., surrounded by a fine network of anastomosing filaments; carposporangia obovate, 22–30  $\mu\text{m}$  diam., 35–64  $\mu\text{m}$  long; spermatangia unknown.

DIAGNOSIS: Differing from *Tepoztequiella rhizoidea* by its smaller size yet much wider and compressed axes, a lack of rhizoids issued from medullary filaments, and much larger tetrasporangia (Table 1). It is also differentiated by its *rbcL* and COI-5P gene sequences.

ETYMOLOGY: *muriamans* (L. f., part.), literally “wall-loving”, for the deep-water habitat where it was growing on a ledge.

TYPE COLLECTION: *C.W. Schneider/T.R. Popolizio* 16-11-9 [BDA1980], ⊕, 28 July 2016, ledge north northeast of St. George’s I., Bermuda, 32°28.79600’ N, 64°35.68833’ W, depth 60 m = Holotype, MICH (Fig. 8); Isotype, ⊕, Herb. CWS [BDA1981] (Fig. 9).

PARATYPE COLLECTION: **Bermuda** – *A.J. Bernatowicz* 53-601 [as *Agardhiella ramosissima*], coll. *W.H. Sutcliffe, Jr./H. Lowenstam*, ♀, 18 Aug. 1953, dredged on offshore Challenger Bank, depth 55 m [MICH 641029] (Fig. 10).

DISTRIBUTION: At present, endemic to Bermuda, western Atlantic Ocean.

## DISCUSSION

*Meristotheca odontoloma* was previously reported as *M. gelidium* in Bermuda (Collins & Hervey 1917, as *Eucheuma gelidium*; Schneider 2003, as *Meristiella gelidium* (J.Agardh) D.P.Cheney & P.W.Gabrielson), a species with a long and complex taxonomic history in the western Atlantic starting in the 19<sup>th</sup> century. This species was initially described as *Sphaerococcus gelidium* J.Agardh for specimens in the West Indies (Agardh 1841), but was later moved to the genus *Eucheuma* (Agardh 1847). Owing to its similarity to *M. gelidium*, *M. odontoloma* was first included in the Bermuda flora in *P.B.-A.* (Collins *et al.* 1917, no. 2184 as *E. gelidium*). *Eucheuma gelidium* was subsequently moved by Gabrielson & Cheney (1987) to the new genus *Meristiella* based upon morphological and anatomical characteristics. In the same paper, Gabrielson & Cheney (1987) also moved *Eucheuma acanthocladum* (Harvey) J.Agardh to synonymy with what at the time was *Meristiella gelidium*, pointing out that Bermuda collections identified as *M. gelidium* were “questionable” for that species and could represent a distinct taxon. Guimarães & Oliveira (1996) moved *Meristiella echinocarpa* (Areschoug) D.P.Cheney & P.W.Gabrielson and *M. schrammii* (P.Crouan & H.Crouan) D.P.Cheney & P.W.Gabrielson into synonymy with *M. gelidium* to accommodate what they felt was intraspecific morphological variation. Faye *et al.* (2004) subsumed the genus *Meristiella* under *Meristotheca* citing conclusive molecular *rbcL* analyses, creating the new combination *Meristotheca gelidium*.

*Meristotheca odontoloma* has some similarities to *M. gelidium*, yet the two species differ in several ways (Table 1). The new species is basically prostrate with secondary attachments from branch margins and reaches a maximum thallus length of 7 cm, while the thallus height of the erect *M. gelidium* ranges from 10–40 cm. *Meristotheca odontoloma* exhibits only 2–3 orders of branching (Figs 2–4) whereas *M. gelidium* exhibits 4–5. Both species exhibit the presence of ultimate spine-like branches on their axes. Those on *M. gelidium* typically range from 4–36 mm in length compared with a maximum of 9 mm, although generally much shorter, in *M. odontoloma* (Figs 3, 4). In the new species, the spinose dentations can elongate becoming secondary holdfasts. The outer cortical cells in *M. odontoloma* reach 2–7 µm in diam. (Figs 5, 6), smaller than the 9–15 µm diam. in outer cortical cells of *M. gelidium*. Additionally, the tetrasporangia of *M. gelidium* are 34–51 µm long, whereas those of *M. odontoloma* are half that size at 19–35 µm in length (Fig. 7). Some young specimens of the Bermuda species have narrow, regularly dentate axes reminiscent of upper branch areas of mature *M. gelidium*, while other individuals develop early on as broad, nearly oval-shaped and dentate germlings somewhat similar to specimens of *M. tobagensis* W.R.Taylor. At maturity, the latter species is erect and morphologically distinct (Taylor 1962, pl. 2) from the smaller, prostrate *M. odontoloma*.

As shown by Saunders *et al.* (2006, fig. 26v), one of the six specimens from Tortuga I., Venezuela, on the isotype sheet of *Faucheia peltata* W.R.Taylor (MICH 1306350) did not represent what is presently *Asteromenia peltata* (W.R.Taylor) Huisman & A.Millar. However, the Venezuelan specimen is similar in habit to *Meristotheca odontoloma*. Lacking genetic information, however, we are reluctant to extend the range of the new species from Bermuda to the southern Caribbean Sea. Likewise, specimens identified as *Eucheuma echinocarpum* Areschoug in *P.B.-A.* (no. 745, Collins *et al.* 1900) from the drift off Indian River Inlet, Florida, have similarities to *M. odontoloma*, but are a diverse collection of specimens by Mrs. G.A. Hall

(search in the Macroalgal Herbarium Portal, <http://macroalgae.org/portal/index.php>). *Eucheuma echinocarpum* has a type locality in Brazil and is at present considered a synonym of *M. gelidium*. Nevertheless, the size and habit of an isoelectotype of *E. echinocarpum* illustrated by Gabrielson & Cheney (1987, fig. 6) bear little resemblance to *P.B.-A.* no. 745 or the new species described here. Ultimately, if these *P.B.-A.* isolates are to be considered as *M. odontoloma*, genetic confirmation of Florida specimens will be necessary.

Two other species of *Meristotheca* from the western Atlantic placed in synonymy with *M. gelidium*, including *Chrysymenia ? acanthocladia* Harvey and *Mychodea schrammii* P.Crouan & H.Crouan (Gabrielson & Cheney 1987), are not comparable to *M. odontoloma*. Type materials of both were illustrated by Gabrielson & Cheney (1987), and they are large, erect and narrow-bladed specimens that will remain as *M. gelidium* until DNA from their type localities might show they should be retained as distinct species.

*Tepoztequiella muriamans* has an overall habit remarkably reminiscent of the only other member of the genus, *T. rhizoidea*, but differs substantially in its anatomical structure and dimensions. The generitype was given its name for the attenuate rhizoids it produces from medullary filaments (Núñez-Resendiz *et al.* 2017b), but this does not appear to be a generic characteristic as they were not found in Bermuda specimens. Although the generitype produces secondary medullary filaments perpendicular to the main filaments of the medulla (Núñez-Resendiz *et al.* 2017b), *T. muriamans* produces clusters or fascicles of medullary filaments perpendicular to the originating medullary filament, either arising as a parallel cluster or arcing out like a candelabra (Fig. 11). The new deep-water species is shorter in height yet with much broader axes/branches than *T. rhizoidea*, making the two species easy to differentiate (Table 1). Likewise, the new species' tetrasporangia are 24–53 µm diam. and 41–73 µm long, huge in comparison to those of *T. rhizoidea* (5.0–11.5 x 16–25 µm).

*Tepoztequiella muriamans* has some morphological similarities to *Meristotheca cylindrica* with their narrow blade widths and branching patterns, although the latter has cylindrical axes that are more densely branched than the compressed axes of the new taxon from Bermuda (Núñez-Resendiz *et al.* 2017a; Ballantine *et al.* 2019). Axes of *M. cylindrica* are reported as tall as 32 cm but the new species reaches only 12.8 cm in height as known (Figs 8, 9; Table 1). The tetrasporangia of *M. cylindrica* are 18–25  $\mu\text{m}$  in diam., much smaller than those of *T. muriamans*, 24–53  $\mu\text{m}$  (Fig. 13, Table 1). Cystocarps of *M. cylindrica* are found laterally on branches or in marginal proliferations (Núñez-Resendiz *et al.* 2017a), while those of *T. muriamans* have only been located only on the terminal ends of short lateral branches that are swollen at the apices like a small round head pin (Figs 10, 14; Table 1). Ballantine *et al.* (2019) recently reported that the cystocarps on Puerto Rican specimens of *M. cylindrica* were borne singly or in clusters at branch apices or the margins of the branches. The carposporangia found in *M. cylindrica* range from 30–40  $\mu\text{m}$  in length, while those of *T. muriamans* are longer, 35–64  $\mu\text{m}$  (Table 1).

*Tepoztequiella muriamans* represents a new deep-water species collected off the coast of Bermuda from 60 m by technical re-breather divers. Searching archival records of deep-water species collected in these distant islands on the online Macroalgal Herbarium Portal, another collection of this species occurred in 1953 at a similar depth (55 m) for algal specimens gathered by U.S. Navy lockout divers off the coast of Bermuda (Schneider *et al.* 2019a). This 1953 collection was identified as *Agardhiella ramosissima* (Taylor 1960), a species with a type locality in Key West, Florida, and a distribution covering the warm-temperate to tropical regions of the western Atlantic to the Caribbean (Guiry & Guiry 2019). This archival collection represented the only report of *A. ramosissima* recorded in Bermuda (Schneider 2003). The morphology and anatomy of the 1953 specimen matched *T. muriamans* in vegetative characteristics, and fortunately was a gametophyte bearing cystocarps, enhancing the description of this new, rarely

collected, mesophotic species. Our new species is genetically distant from a North Carolina, USA specimen (GenBank AF099680) of the morphologically similar *A. ramosissima* for which *rbcl* was sequenced, the latter closely allied with *A. subulata* (C.Agardh) Kraft & M.J.Wynne. Molecular analyses of other deep-water specimens identified as *A. ramosissima* from the western Atlantic may be necessary to confirm their taxonomic placement.

After the recent reassignment of two genera to the Placentophoraceae by Dumilag et al. (2019), the Solieriaceae presently includes 16 genera, half being monotypic (Guiry & Guiry 2019), with three only recently having been described (Norris 2014; Núñez-Resendiz *et al.* 2017b, 2019b). Prior to our report here, one of these monotypic genera was *Tepoztequiella* from the western Gulf of Mexico and Caribbean, a genus sister to *Meristotheca* that was first discovered using molecular-assisted alpha taxonomy (MAAT; Núñez-Resendiz *et al.* 2017b). The genus *Meristotheca* was described in the 19th century by Agardh (1872) to accommodate the generitype, *M. papulosa* from Yemen on the Red Sea. Including *M. odontoloma* reported here, *Meristotheca* includes 14 species (Guiry & Guiry 2019), all of which have distributions in the world's warm temperate to tropical oceans. Interestingly, eight of the current species were described using molecular techniques within the past 15 years (Guiry & Guiry 2019; Núñez-Resendiz *et al.* 2019a), suggesting that the morpho-anatomy of *Meristotheca* is particularly challenging, making MAAT especially important for distinguishing species in the genus (Cianciola *et al.* 2010; Saunders 2008).

Prior to the regular use of genetic sequencing as part of taxonomic studies in Bermuda, the majority of species in the flora were also found in the Caribbean Sea, presumably having been distributed to the western Atlantic islands over geological time by the warm flowing Gulf Stream (Schneider 2003). Endemic species represented a minor component of the macroalgal flora of the islands at just over 1% (Schneider 2003), but since then 36 new species have been added to the



flora, 16 representing species previously thought to be species also known in the Caribbean (Schneider *et al.* 2018b). *Meristotheca odontoloma* and *Tepoztequiella muriamans* add to the list of species from Bermuda presently considered endemic to the islands, now accounting for 10.4% species of 280 red algae in the flora (unpublished data). This dramatic increase in the recognition of endemism over the past decade and a half reflects the ability of MAAT to differentiate regional and genetic differences among presumed widely distributed species, an ability that was difficult at best with alpha-taxonomy alone (Schneider *et al.* 2018a). As has been the case for many new species over this period, *M. odontoloma* is a species that was previously thought to be *M. gelidium* that also is found in the Caribbean but is now revealed to be a unique species endemic to Bermuda until possibly discovered elsewhere. The description of *T. muriamans* also adds to the uniqueness of the flora that has recently been discovered in mesophotic waters off the Bermuda platform (Schneider *et al.* 2019a, b).

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## Figure Legends

**Fig 1.** Concatenated COI-5P and *rbcL* RAxML tree, partitioned by gene and codon, GTR+I+G with 1000 bootstrap replications (only bootstrap values > 50 shown). Sequences taken from GenBank are indicated by including their accession numbers in parentheses (a single entry indicates *rbcL* sequences only, where there are two entries the accessions numbers refer to COI-5P and *rbcL*, respectively).

**Figs 2–7.** *Meristotheca odontoloma* sp. nov.

**Fig. 2.** Holotype specimen [*CWS/CEL* 10-5-14 (BDA0026)]. Scale bar = 1 cm.

**Figs 3, 4.** Habit of specimens [*TRP* 12-152-3]. Scale bars = 1 cm.

**Fig. 5.** Transverse-section of ultimate branch [*TRP* 12-152-3]. Scale bar = 200  $\mu\text{m}$ .

**Fig. 6.** Scattered tetrasporangia in surface view of cortex [*TRP* 12-152-3]. Scale bar = 100  $\mu\text{m}$ .

**Fig. 7.** Mature zonate tetrasporangium in cortex [*TRP/CWS* 12-40-6]. Scale bar = 25  $\mu\text{m}$ .

**Figs 8–14.** *Tepoztequiella muriamans* sp. nov.

**Fig. 8.** Holotype specimen [*CWS/TRP* 16-11-9 (BDA1980)]. Scale bar = 2 cm.

**Fig. 9.** Isotype specimen [*CWS/TRP* 16-11-9 (BDA1981)]. Scale bar = 2 cm.

**Fig. 10.** Challenger Bank collection with terminal cystocarps (arrows) on ultimate branches [*AJB* 53-601 = MICH 641029]. Scale bar = 2 cm.

**Fig. 11.** Partial transverse-section near branch tip showing filament clustering in central medulla [*CWS/TRP* 16-11-9]. Scale bar = 200  $\mu\text{m}$ .

**Fig. 12.** Tetrasporangia in various stages of development, surface view of cortex [*CWS/TRP* 16-11-9]. Scale bar = 150  $\mu\text{m}$ .

**Fig. 13.** Mature zonate tetrasporangium in transverse-section of outer cortex [*CWS/TRP* 16-11-9]. Scale bar = 50  $\mu\text{m}$ .

**Fig. 14.** Ultimate branch apex with embedded terminal cystocarp [*AJB* 53-601 = MICH 641029]. Scale bar = 250  $\mu\text{m}$ .



2020

# Two new species of Solieriaceae (Rhodophyta, Gigartinales) from the euphotic and mesophotic zones off Bermuda, *Meristotheca odontoloma* and *Tepoztequiella muriamans*

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