BLOOM OF THE GIANT ANADYOMENE GIGANTODICTYON SP. NOV. (ANADYOMENACEAE, CLADOPHORALES) FROM THE OUTER SLOPE (25–50 m) OF THE BELIZE BARRIER REEF¹

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A giant form of Anadyomene, most similar to Anadyomene pavonina (J. Agardh) Wille, a rare and diminutive alga endemic to Florida, appeared as up to 10 m long net-like strands covering 10%-80% of a 0.5 km region of the 25-50 m deep Belizean outer reef slope where none had been present up to 12 months earlier. This new species, described herein as Anadyomene gigantodictyon Littler et D. S. Littler, is characterized by a unistratose blade or cluster of blades formed by the polychotomous branching of uniseriate veins, with the interstices, or spaces between the veins, completely or partially filled with cells that are smaller than those of the veins, with cylindrical to ovate cells. The cells at mid-blade are 1.7-2.0 mm in length and 0.2-0.3 mm diameter; interstitial cells are parallel and not juxtaposed. All cells are joined in one plane and form species-specific, fan-shaped patterns with secondary interstitial cells loosely or tightly woven.

Key index words: algal bloom Anadyomene; Anadyomenaceae; Anadyomene gigantodictyon; Belize Barrier Reef; Cladophorales

Anadyomene J. V. Lamouroux 1812 (Anadyomenaceae, Cladophorales) is characterized by a unistratose blade or cluster of blades formed by the polychotomous branching of uniseriate veins, with the interstices, or spaces between the veins, completely or partially filled with cells that are smaller than those of the veins. All cells are joined in one plane and form species-specific, fan-shaped patterns with secondary interstitial cells loosely or tightly woven. Blades are attached to the substrata by rhizoids, which may intertwine to form a stipe. Rhizoids develop as downward extensions of the veins and are usually restricted to the basal or ventral prostrate portions of the blade (Littler and Littler 1991).

Anadyomene is distinguished from the closely related genus *Microdictyon* by its more or less continuous expanse with or without various sized circular perforations, whereas the latter has a more open consistent reticulate structure (trapezoid or rectangular mesh). The terminal filaments of the blade of *Microdictyon* (sister group based on immunological data, character compatibility analyses and nuclear encoded rRNA sequence data) are generally free, and the lateral filaments anastomose (mostly at their tips) below the ragged margin. In the genus *Anadyomene*, by contrast, the rapid and complete joining of all apical segments results in an entire margin and a blade that is usually continuous; although, in two previously described species, the blades have various sized perforations. *Struvea*, another closely related genus, differs from *Anadyomene* by its mesh-like blade, nonseptate stalk and central axis.

The genus Anadyomene has 13 currently accepted taxa worldwide with eight reported from the tropical and subtropical western Atlantic (http://www. algaebase.org). In the past, Cystodictyon J. E. Gray (1866) was split from Anadyomene and distinguished by its perforate blades; it comprised only the type species, Anadyomene leclancheri Decne. [homotypic synonym: Cystodictyon leclancheri (Decne.)] J. E. Gray, from the Pacific, until J. Agardh added Cystodictyon pavonina, from Florida, in 1894. Heydrich (1894) rejected the genus Cystodictyon. Wille (1910) considered Cystodictyon a section of Anadyomene and transferred C. pavonina to Anadyomene. Although A. leclancheri has consistently been placed in Anadyomene by authors since Heydrich (Gilbert 1946, 1961, Velasquez et al. 1975, Silva et al. 1987, 1996), most, except Wille, continued to segregate C. pavonina (Kützing 1849, Harvey 1858, Farlow 1876) until Littler and Littler (1991) monographed the tropical western Atlantic species and included all perforate forms within the genus Anadyomene. Wille also reduced Calomena (misspelled Calonema) to a section of Anadyomene, into which he merged Gray's third genus, Grayemma.

Recent molecular study has shown Anadyomene to be a polyphyletic group (Leliaert et al. 2007) including Microdictyon and two species of Cladophora [Cladophora liebetruthii Grunow and Cladophora catenata (L.) Kütz.]. Leliaert et al. (2007) also showed that the siphonocladalean tree is nonmonophyletic in all families and most genera

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(Cladophora, Siphonocladus, Anadyomene, Microdictyon, Valonia, Phyllodictyon, Boodlea, Struvea, Chamaedoris, and Cladophoropsis), with the notable exceptions of the genus Dictyosphaeria and some monotypic genera. Herein, we follow Leliaert et al. (2007) in considering that present phylogenetic hypotheses need more conformation with additional, unlinked genetic markers (including organelle genes and non-rDNA nuclear loci) before undertaking drastic taxonomic changes in the group; this is definitely the case for the Anadyomene/Microdictyon clade.

MATERIALS AND METHODS

Specimens were collected by scuba diving. Dried herbarium specimens, wet preserved material, and living plants were examined macroscopically and portions were prepared on microscope slides for anatomical study. Thallus segments were mounted using a 20% glucose syrup (Karo Syrup; Corn Products Inc., Westchester, IL, USA) solution in distilled water containing a trace of phenol. All anatomical composite images were made with Canon EOS 5D digital camera (http://www.usa.canon.com) on a Zeiss Universal Microscope (Carl Zeiss MicroImaging GmbH, Oberkochen, Germany); internal measurements were made with a calibrated ocular micrometer, also photographed under the same magnifications to overlay and assure accuracy. The holotype and isotypes are deposited in the U.S. Herbarium, and abbreviations follow Holmgren et al. (1990).

Herbivory was assayed according to the methods of Littler and Littler (2007) using the major colonizer, community dominant and highly palatable cosmopolitan alga Acanthophora spicifera (M. Vahl) Børgesen (Lewis and Wainwright 1985). This ubiquitously abundant red alga is a preferred food item by both parrotfishes and surgeonfishes (Lewis and Wainwright 1985, Littler et al. 2006), as well as by sea urchins (Littler et al. 1983). Both A. spicifera and A. gigantodictyon were cut into 7.0 cm lengths and attached to dead coral-rubble fragments by thin rubber bands. Replicates (N = 15) were placed haphazardly on the reef flat for 6 h at midday, collected, and again measured. Percent eaten was determined for the remeasured algal segments and the results (% lost) were analyzed using oneway analysis of variance (ANOVA) followed by the Bonferroni (Dunn) t-test (SAS 2003, v. 9.1; SAS Inst. Inc., Cary, NC, USA). A >50% loss per 6 h (<6 h half-life) indicates a healthy level of herbivory (Littler and Littler 2007). Visual estimates of cover were determined from video transect.

SPECIES TREATMENT

Anadyomene gigantodictyon sp. nov. (Anadyomenaceae, Cladophorales), Figures 1 and 2.

Diagnosis: Thallus tenuis, reticulatatus, implicatus, in diametro ad 3 m in lentho ad 10 m, atroviridis. Laminae altus perforatus; foramin in diametro ad 5 cm. Margines et perforatus peripheralis marginatus per cellulis elongates venatis constati, saepa cum interdum parvulus cellulae affixus latrorsus. Vena uniseriate; cellulae cylindrical ad ovate, procul medium-laminae lengitudo 1.7–2.0 mm, latitudo 0.2–0.3 mm. Areae interstitialis ramis minoribus regulariter ordinaltis impletae, non juxtapose.

Thallus thin, net-like, tangled, to 3 m diam. and 10 m in length, dark green. Blades highly perforate; perforations to 5 cm diam. Margins and perforation peripheries bordered by elongated vein cells, often with intermittent small cells attached laterally. Veins uniseriate; cells cylindrical to ovate, at mid-blade length 1.7–2.0 mm, width 0.2–0.3 mm. Interstitial cells parallel, not juxtaposed.

Holotype: D&ML 70721 US, Gills Reef, Belize, Central America (16°44.602′ N, 88°4.351′ W); 25–50 m deep; 22 August 2009; collected by D. S. Littler, M. M. Littler, C. C. Brooks, B. L. Brooks.

Etymology: Named for the extremely large and net-like thallus.

Distribution: At present, *A. gigantodictyon* is limited to Belize, Central America, occurring on the outer fore-reef slope over a limited depth range from 25 m to 50 m deep (see above).

Representative specimens examined: Belize, Central America: South Reef (16°41.385' N, 88°04.213' W), 51–60 m deep (D. S. Littler, M. M. Littler, B. L. Brooks. 15.v.2001. D&ML 60665 US); Gills Reef (16°44.602' N, 88 04.351' W), 25–50 m deep (D. S. Littler, M. M. Littler, C. C. Brooks, B. L. Brooks. 27.viii.2009. D&ML 7070846 US).

Habit: Thallus thin, net-like, trailing, to 3 m in diameter and 10 m in length, dark grass-green. Blades highly perforate; perforations variable to

Fig. 1. Anadyomene gigantodictyon sp. nov. D&ML 70721 US. (a) Mature vein linked by basal haptera. (b) Interstitial spaces incompletely filled with small pinnately and pectinately arranged cells, generally not juxtaposed. (c) Outer margins and perforation peripheries bordered by elongated vein cells; small cells on margins of rapidly growing areas.





FIG. 2. Anadyomene gigantodictyon sp. nov. D&ML 70721 US. (a) Habit of the living holotype of A. gigantodictyon showing unique characters of the perforate thallus. (b) Diver demonstrating thickness of the expansive overgrowing mat at 40 m deep on the Belize Barrier Reef outer slope. (c) A. gigantodictyon overgrowing gorgonian coral.

5 cm diam., well defined, delineated by vein cells, often with intermittent small cells attached laterally. Margins entire when mature, also delineated with vein cells often with intermittent small cells attached laterally and distal to parent cell. Initially attached by minute rhizoids at irregular points on margins, later overtopping or tangling among underlying organisms.

Anatomy: Veins uniseriate; cells cylindrical to ovate, at mid-blade length (1.7-2.0 mm) to width (0.2-0.3 mm) ratio ~8:1, polychotomous branches 3-4(-6) at loci, radiating from random locations with no regular pattern. Connections between vein cells blunt; mature veins linked by basal haptera (Fig. 1a). Interstitial spaces incompletely filled with small pinnately and pectinately arranged cells, dumbbell- or H-shaped partly overlapping or straddling adjacent end cells; not linked by small haptera. Interstitial spaces incompletely filled with cells (Fig. 1b), generally not juxtaposed; circular perforations conspicuous, dominant. Outer margins (Fig. 1c) and perforation peripheries bordered by elongated vein cells. Cortication typically absent with only one exception observed.

RESULTS AND DISCUSSION

This is only the second perforate Atlantic Anadyomene with a vein/interstitial cell pattern that does not expand continuously from stipe to margin (Fig. 2a). The margin of A. pavonina closely resembles that of A. gigantodictyon in that elongated vein cells form the periphery in both. However, A. pavonina lacks the small marginal cells that expand laterally to extend the blades of A. gigantodictyon. A. pavonina possesses a flat, sessile blade with numerous large perforations and small interstitial cells in lateral contact with one another (juxtaposed), whereas A. gigantodictyon has similar small interstitial cells without lateral contact, having open spaces between cells. The entire thallus of A. gigantodictyon is much larger and much more open (with many more perforations) than A. pavonina or any other reported Anadyomene. During August 2009, large drape-like formations (>5 m long) of the green alga A. gigantodictyon sp. nov. (Fig. 2b) extended over a large region of the deep Belizean outer reef slope where none had been present. This area of the reef was intensely and annually studied for the previous 5 years without finding any fragment of the new species. The giant form of Anadyomene (Fig. 2b) is most similar to A. pavonina, a rare and diminutive alga (<20 cm high; Littler and Littler 1992) endemic to Florida. Members of the genus Anadyomene previously were known solely as solitary clumps (Littler and Littler 1991), including the large (to 45 cm tall, 26 cm wide) erect Anadyomene menziesii (J. E. Gray) J. Agardh. Of these, only Anadyomene stellata had been shown to be defended (chemically) against herbivory (Targett and Mitsui 1979). Interestingly, this new species also shows similar high resistance. During herbivory assays (N = 15) conducted alongside the palatable A. spicifera, just 4% (±0.3 SD) of A. gigantodictyon was consumed versus 77% (±24 SD) consumed for A. spicifera.

The newly described A. gigantodictyon is most abundant in the 25–50 m depth zone (from 10% to 80% cover, mean of 30%) over a horizontal range of ~0.5 km. It entangles and overgrows all other large and small biota (hard corals, gorgonians, sponges, and seaweeds) as a 5–35 cm thick suspended open network (Fig. 2c). The extensive mesh-like Belizean populations are similar (in habit) to the abundant herbivore-resistant *Microdictyon marinum* (Bory) P. C. Silva blooms predominant throughout the Bahamas (Littler and Littler 2000).

Upon returning to the site of this bloom in August 2010 and 2011, we observed that *A. gigantodictyon*

has persisted in reduced abundance over the same depth range and habitats as before. Fortunately, it has not spread or proved to be conspicuously harmful to the predominant underlying organisms, hypothetically, owing to its open-mesh morphology and thin (single-layered) transparent anatomy (Figs. 1, a–c; 2, a and c).

Key to the tropical western Atlantic species of Anadyomene.

1.	Blade perforate2
1.	Blade eperforate4
2.	Interstitial cells not juxtaposedAnadyomene gigantodictyon
2.	Interstitial cells juxtaposed
3.	Polychotomous branching only, interstitial cells random and
	oval in section, with a distinct stipeAnadyomene linkiana
3.	Polychotomous branching accompanied by pinnate lateral
	branching, interstitial cells generally parallel and H-shaped
	in section, without a distinct stipeAnadyomene pavonina
4.	Veins composed of several parallel uniseriate chains of
	cellsAnadyomene menziesii
4.	Veins composed of single uniseriate chains of cells5
5.	Interstitial cells random and oval in section
5.	Interstitial cells generally parallel and H-shaped in
	section7
6.	Interstitial cells 105–150 µm long, outer margin formed by
	elongated vein cellsAnadyomene howei
6.	Interstitial cells 37-60 µm long, outer margin formed by
	small ellipsoidal cellsAnadyomene saldanhae
7.	Rhizoids covering lower surfaces of mature blade, veins
_	usually dichotomously dividedAnadyomene rhizoidifera
7.	Rhizoids mainly in the basal regions of blades, veins mostly
	polychotomous, occasionally dichotomously divided8
8.	Growing edge smooth or lobed, composed of small
~	rounded or oval cellsAnadyomene stellata
8.	Growing edge irregularly lacerate, composed of elongated
	vein cellsAnadyomene lacerata

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