



Taxonomic Transfer of the Red Algal Genus *Gloiosaccion* to *Chrysymenia* (Rhodymeniaceae, Rhodymeniales), Including the Description of a New Species, *Chrysymenia pseudoventricosa*, for the Gulf of Mexico

W. E. SCHMIDT^{1,*}, C. F. D. GURGEL² & S. FREDERICQ¹

¹Department of Biology, University of Louisiana at Lafayette, Lafayette, LA, 70504-3602, USA

²Departamento de Botânica, Centro de Ciências Biológicas, Universidade Federal de Santa Catarina, Florianópolis, SC 88040-970, Brazil

*Corresponding Author: Email: william.schmidt.algae@gmail.com; Tel: +1-337-482-1291, Fax: +1-337-482-5660

Abstract

Gloiosaccion Harvey, with type *G. brownii* (Rhodymeniaceae, Rhodymeniales), is a red algal genus characterized by the presence of large, hollow and saccate vesicle-shaped thalli arising from small solid axes. Whereas *Gloiosaccion* has traditionally been viewed as being closely related to *Botryocladia* (Agardh) Kylin, a multi-marker phylogenetic analysis based on chloroplast-encoded *rbcL* and UPA and nuclear LSU rDNA sequences instead places *Gloiosaccion brownii* and *G. pumila* in the *Chrysymenia* clade that includes the generitype *C. ventricosa* (Lamouroux) J. Agardh. *Gloiosaccion* is reduced to synonymy with *Chrysymenia* J. Agardh, a taxonomic move first advocated by De Toni in 1900. In addition to *C. brownii* (Harvey) De Toni, “*Gloiosaccion brownii* var. *firmum* Harvey and “*G. pumilum* J. Agardh are recognized as the distinct species *Chrysymenia coriacea* comb. et stat. nov. and *C. pumila* (J. Agardh) Weber-van Bosse, respectively. A new species, *C. pseudoventricosa* sp. nov. is proposed to accommodate specimens going under the name *C. ventricosa* (J.V. Lamouroux) J. Agardh from the Gulf of Mexico and Caribbean Sea.

Key words: algae, Australia, biodiversity, Caribbean, *Chrysymenia*, Gulf of Mexico, LSU rDNA, marine, morphology, *Gloiosaccion*, phylogeny, *rbcL*, rhodolith, Rhodophyta, seaweeds, sp. nov., UPA

Introduction

The Rhodymeniales remains one of the most distinctive and well-defined orders of red algae (Fritsch 1945; Sparling 1957; Irvine and Guiry 1980; Hawkes and Scagel 1986; Kraft and Woelkerling 1990; Hommersand and Fredericq 1990; Saunders *et al.* 2007; Saunders and McDonald 2010) currently encompassing over 300 species in 42 genera and six families (Guiry and Guiry 2015), i.e. the Rhodymeniaceae (Harvey 1849), Champiaceae (Kützing 1843), Lomentariaceae (J. Agardh 1876), Faucheaceae (Saunders *et al.* 1999), Hymenocladaceae and Fryeellaceae (Le Gall *et al.* 2008). The Rhodymeniaceae traditionally has been split morphologically into two groups, separated by solid and hollow genera. The hollow genera of the Rhodymeniaceae are *Botryocladia* (J. Agardh) Kylin (1931), *Gloiosaccion* Harvey (1859), *Irvinea* Guiry in Saunders *et al.* (1999), and *Chrysymenia* J. Agardh (1842), taxa that are most commonly distributed in warm-temperate to tropical environments (Abbott and Littler 1969, Brodie and Guiry 1988, Lozada-Troche *et al.* 2010).

With the finding that offshore deepwater rhodolith bed communities in the Gulf of Mexico (Fredericq *et al.* 2014, Felder *et al.* 2014, Richards *et al.* 2014) are surprisingly rich in representative members of Rhodymeniaceae (Gavio and Fredericq 2003, 2005; Fredericq *et al.* 2009; Schmidt 2009), increased taxon sampling in the region has enhanced our understanding of the biodiversity and systematic relationships among the order. Towards this goal, chloroplast-encoded *rbcL*, the Universal Plastid Amplicon (UPA), and nuclear large subunit ribosomal DNA (LSU) markers were selected due to their power in the resolution below, at and above (e.g., Fredericq *et al.* 2003, Sherwood *et al.* 2010, Lin *et al.* 2012) the species level within the red algae.

Genera of Rhodymeniaceae with hollow thalli are currently characterized by both subtle and unstable features that overlap among taxa. For example, the genus *Chrysymenia* with generitype *C. ventricosa* (Lamouroux) J. Agardh (1842) has been historically defined by the presence of “an almost” completely hollow thallus that lacks diaphragms and internal rhizoids, and where the only solid portion is limited to the stipe. *Cryptarachne* (Harvey) Kylin (1931),

however, a genus once considered a subgenus of *Chrysymenia* by Harvey (1859a), is characterized by the very same thallus organization, but with internal rhizoids. Most phycologists today, starting with the work of Okamura (1936), disagree about the taxonomic value of internal rhizoidal filaments to separate these two genera, recognize their presence in the type of *Chrysymenia*, and consequently consider these two taxa congeneric (Wynne 2005). Another species, *Chrysymenia divaricata* Durant (1850), described from New York State, is currently regarded as a taxonomic synonym of *Lomentaria divaricata* (Durant) Wynne, replacing *L. baileyana* (Harvey) Farlow on the basis of taxonomic priority (see Wynne 2013).

In Agardh's (1842) original concept of the genus, *Chrysymenia* contained a section called *Botryocladia* that was later elevated to generic rank by Kylin (1931). *Botryocladia* is the second largest genus in the Rhodymeniaceae in terms of number of species with 46 species currently accepted taxonomically (Guiry and Guiry 2015). *Botryocladia* is circumscribed by one to several hollow vesicles borne on simple and solid ramisymphodial axes, axes and vesicles that may or may not be branched, and with all vesicles lacking internal diaphragms and rhizoidal filaments (Gavio and Fredericq 2003, 2005). The presence of larger, solid axes substantially differentiates *Botryocladia* from *Chrysymenia* (Feldmann 1945, Kylin 1956, Norris 1989, Norris and Ballantine 1995, Wynne 2005). Other taxa placed in *Chrysymenia* were found to represent different genera (e.g. Wynne 2013). *Irvinea*, a genus segregated out of *Botryocladia*, shares the presence of vesicles borne on a solid axis with the latter (Saunders *et al.* 1999). Whereas the morphological characters said to differentiate *Irvinea* include the presence of strongly protruding cystocarps, rosettes of cortical cells, and gland cells borne on modified medullary cells, i.e. glandiferous cells, the main rationale for the erection of *Irvinea* came from gene sequence analysis (Saunders *et al.* 1999). Morphological characters that delineate *Irvinea* have also been observed in species that currently are still placed in *Botryocladia* (Schneider and Lane 2008, Afonso-Carillo *et al.* 2006).

Gloiosaccion Harvey (1859a), a genus limited to the temperate Australian coast, was first circumscribed based on the presence of large, hollow and saccate vesicle-shaped thalli arising from minute solid axes (stipes). It was originally mistaken for *Halosaccion* Kützing (1843), a genus with a similar external habit and currently a common member of the Palmariales from the North Pacific Ocean and temperate regions. Harvey (1859a) later re-examined a specimen and found its interior not to be filled with water or air, as is the case in *Halosaccion*, nor to be composed of dense layers of rounded cells, but instead filled with a gelatinous substance and with a more lax and softer structure. Harvey described the thallus as consisting of three separate strata, i.e., a medulla composed of large gelatinous-filled cells, an intermediate layer of round-angular pigmented cells, and a cortical layer of minute anticlinal cells; the cystocarp was immersed in the intermediate stratum.

Gloiosaccion has generally been accepted as a taxonomically valid genus by many, including J. Agardh (1892), Kylin (1931), and Womersley (1950); however, De Toni (1900) considered the type, *G. brownii*, a species of *Chrysymenia*, but without providing an explanation. On the other hand, in a paper describing *Botryocladia senegalensis*, Feldmann and Bodard (1965) considered that *G. brownii* should not be separated from *Botryocladia* as they viewed the *Gloiosaccion* habit to represent an overdevelopment of the bladder. Subsequently, Silva (1980) formally proposed the merger of *Gloiosaccion* into *Botryocladia*. Womersley (1950), however, resurrected the genus on the basis of the presence of anticlinal filaments cut off by mid-cortical cells, the slight protrusion of the cystocarp, and the development of the tetrasporangia positioned at the base of the anticlinal cortical filaments. Womersley's (1950) resurrection of *Gloiosaccion* was supported at the molecular level using small subunit ribosomal DNA sequences (Saunders *et al.* 1999) because *G. brownii* showed a sister relationship to *Chrysymenia ornata* (J. Agardh) Kylin (1931) and did not fall within the *Botryocladia* clade; however, only two species of *Chrysymenia* were used in the dataset (Saunders *et al.* 1999), i.e. *C. ornata* Kylin and *C. wrightii* Harvey, a clade that resolved as sister to *Botryocladia*.

Many of the hollow Rhodymeniaceae members that lack diaphragms are not necessarily regarded as natural groups (Saunders *et al.* 1999, Wilkes *et al.* 2005). Owing to increased taxon sampling, the present study provides a critical taxonomic re-evaluation of the generic and species concepts centered around *Gloiosaccion* and *Chrysymenia*.

Material and methods

Samples of Rhodymeniales investigated for this study are listed in Table 1. Vouchers were preserved upon collection in the field in 5% Formalin/seawater for morphological studies, in silica gel for molecular studies, and pressed on herbarium sheets for archival preservation. Vouchers are deposited in the Algal Herbarium of the University of Louisiana at Lafayette, USA (LAF), and the *Gloiosaccion* herbarium specimens are housed in the South Australian State Herbarium, Australia (AD).

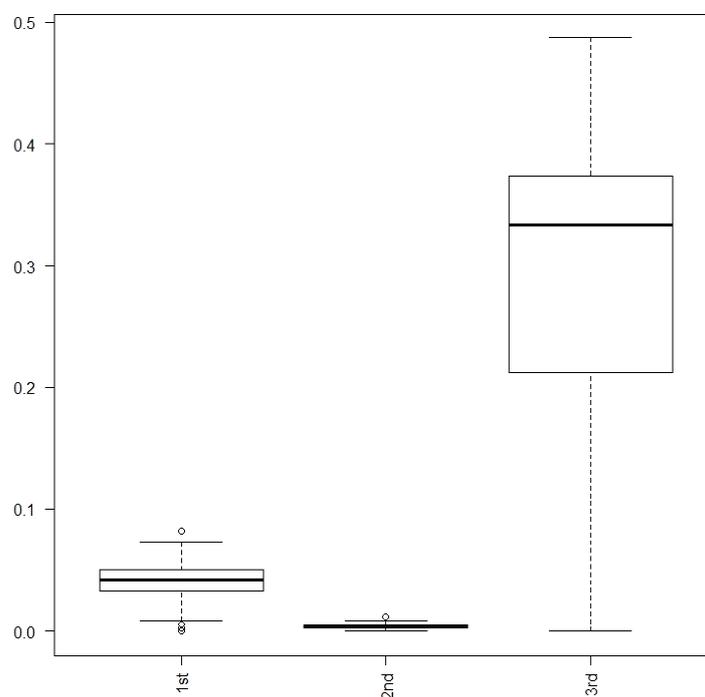
TABLE 1. Collection information of samples used in this study. *Denotes sequences newly generated for this study. AM = Allan Millar; BW = Brian Wysor; MG = Michael Guiry; CFDG = Fred Gurgel; MHH = Max H. Hommersand; SF = Suzanne Fredericq; SL = Sandra Lindstrom; WN = Wendy Nelson

Taxa	Collection information /collector / Voucher	GenBank accession No.		
		<i>rbcL</i>	LSU	UPA
<i>Botryocladia pyriformis</i> (Børgesen) Kylin	Offshore LA, USA; 28°05'900N, 91°02'410 W; 4.vi.05 57–59m, SF (WES39)	KT154691*	KT154739*	KT154718*
<i>Botryocladia pyriformis</i> (Børgesen) Kylin	Offshore LA, USA; 27°56'429N, 92°00'460 W; 9.vii.06 64–73m, SF (WES58)	KT154746*	KT154740*	KT154719*
<i>Botryocladia occidentalis</i> (Børgesen) Kylin	Campeche Banks, Mexico, 22°16' 020N, 90° 43'230W; 7.vi.05, 51–52m, SF (WES38)	KT154690*	KT154741*	KT154717*
<i>Champia parvula var prostrata</i> L.G. Williams	Offshore LA, USA; 28°02'510N, 92°26'880 W; 23.vi.05, 60–74m, SF (WES7)	KT154748*	KT154744*	KT154721*
<i>Chrysymenia agardhii</i> Harvey (Ballantine <i>et al.</i> 2010)	La Parguera, Puerto Rico	EU715133	-	-
<i>Chrysymenia brownii</i> (Harvey) De Toni	Port McDonnell, SA, Australia; 21.ix.95, MHH (WES108)	HQ400575*	KT154734*	KT154708*
<i>Chrysymenia coriacea</i> (Harvey) W. E. Schmidt, Gurgel & Fredericq, comb. et stat. nov.	Tarcoola Beach, WA, Australia; 21.ix.95, MHH (WES118)	HQ400574*	KT154733*	KT154709*
<i>Chrysymenia halymenioides</i> Harvey	Campeche Banks, Mexico, 22°16' 020N, 90° 43'230W; 7.vi.05, 51–52m, SF (WES17)	HQ400584*	KT154730*	KT154705*
<i>Chrysymenia halymenioides</i> Harvey	Campeche Banks, Mexico, 22°15' 150N, 90°43' 290W; 7.vi.05, 52–53m, SF (WES19)	HQ400585*	-	-
<i>Chrysymenia halymenioides</i> Harvey	Campeche Banks, Mexico, 22°11' 330N, 91°08' 710W; 17.vi.05, 49–53m, SF (WES10)	HQ400586*	KT154729*	KT154704*
<i>Chrysymenia halymenioides</i> Harvey	Louisiana, USA, 27°55' 070N, 92°23' 080W; 22.vi.05, 58–71m, SF (WES23)	HQ424470*	KT154731*	KT154706*
<i>Chrysymenia littleriana</i> J.N. Norris & Ballantine	Diamond Rock, Martinique, 14°26' 94N, 61°02'410W; 14.vi.95, SF (WES136)	HQ400583*	KT154728*	KT154703*
<i>Chrysymenia nodulosa</i> J.N. Norris & Ballantine	Isla de Culebra, Puerto Rico, 18°20' 263N, 65°20' 533W; 3.vi.95, SF (WES148)	HQ400577*	KT154722*	KT154698*
<i>Chrysymenia nodulosa</i> J.N. Norris & Ballantine	Isla de Culebra, Puerto Rico, 18°20' 263N, 65°20' 533W; 3.vi.95, SF (WES142)	HQ400578*	KT154724*	-
<i>Chrysymenia nodulosa</i> J.N. Norris & Ballantine	Isla de Culebra, Puerto Rico, 18°20' 263N, 65°20' 533W; 3.vi.95, SF (WES96)	HQ400579*	KT154723*	KT154699*
<i>Chrysymenia ornata</i> Kylin	Jervis Bay, Jervis Bay Territory, Australia; 24.x.95, AM (WES311)	HQ400587*	KT154735*	KT154711*
<i>Chrysymenia planifrons</i> (Melvill) J. Agardh	Long Bay Point, Panama, 9°24' 00N, 82°13' 30W; 17.x.98, BW (WES312)	HQ400580*	KT154725*	KT154700*
<i>Chrysymenia pseudoventricosa</i> W. E. Schmidt, Gurgel & Fredericq, sp. nov.	Campeche Banks, Mexico, 22°10' 420N, 91°09' 550W; 4.vi.05, 42–43m, SF (WES16)	HQ400581*	KT154726*	KT154701*
<i>Chrysymenia pseudoventricosa</i> W. E. Schmidt, Gurgel & Fredericq, sp. nov.	Campeche Banks, Mexico, 21°48' 048N, 91°54' 962W; 13.vi.05, 30–38m, SF (WES88)	HQ400582*	KT154727*	KT154702*
<i>Chrysymenia pumila</i> (J. Agardh) Weber-van Bosse	Edithburgh Pier, Yorke, Peninsula, SA, Australia, 35°05' 040N, 137°49'056 E; 17.i.10, 2–3m, CFDG, (AD-A90892, LAF1094)	HQ400576*	-	KT154710*
<i>Chrysymenia</i> sp.	Florida Middle Grounds, FL, USA, 28°34' 240N, 84°28' 770W; 4.vii.06, 46–47m, SF (WES143)	HQ400588*	KT154738*	KT154712*
<i>Chrysymenia</i> sp.	Florida Middle Grounds, FL, USA, 28°30' 500N, 84°28' 188W, 4.vii.06, 45–47m, SF (WES145)	HQ400589*	KT154737*	KT154713*
<i>Chrysymenia</i> sp.	Florida Middle Grounds, FL, USA, 28°41' 790N, 84°23' 300W; 4.vii.06, 43–44m, SF (WES146)	HQ400590*	KT154736*	KT154714*
<i>Chrysymenia ventricosa</i> (J. V. Lamouroux) J. Agardh	Cap Oullerstril, Côte des Albères, France, 17.vii.84, 24m, MG	KT154745*	KT154732*	KT154707*
<i>Rhodymenia californica</i> Kylin	Mosquito Pass WA, USA 2.vii.98, 30–40m, BW (WES101)	KT154747*	KT154743*	KT154716*
<i>Rhodymenia coralline</i> (Bory de Saint Vincent) Greville	La Herradura, Coquimbo, Chile 19.i.95, SF (WES119)	HQ400593*	KT154742*	KT154715*

TABLE 2. Primers newly designed for this study.

Primer Name	Targeted Gene	Primer Sequence
BCR_28S_F232	LSU	5' -CGC RAA CAT TGA TTG GGC- 3'
BCR_28S_R441	LSU	5' -TGT TTC TCC CGA CAA GC- 3'
Chrys_UPA_F149	Plastid 23S (UPA)	5' -CAA GGA ACA GTC TCA GG- 3'
Chrys_UPA_R213	Plastid 23S (UPA)	5' -CCT GAG AGA ACC TTT GCA CG- 3'
Chrys_rbcL_R290	<i>rbcL</i>	5' -AGA YGA ATT AGG YAC AGC- 3'
Chrys_rbcL_F976	<i>rbcL</i>	5' -ATG CCG GTA CAG TAG TAG G- 3'
RhodyF421	<i>rbcL</i>	5' -GAA GAT ATG CGT ATT CC- 3'
RhodyF744	<i>rbcL</i>	5' -CTG CTG CTA CAA TGG AA- 3'
RhodyR744	<i>rbcL</i>	5' -TTC CAT TGT AGC AGC AG- 3'
RhodyR935	<i>rbcL</i>	5' -ATT ACA CGG AAA TTC ATA CC- 3'
RhodyR1434	<i>rbcL</i>	5' -AGC TGT ATC TGT AGA AG- 3'

Box plot depicting the distribution of pairwise nucleotide differences (uncorrected) for the first, second, and third codon positions from the *rbcL* alignment.



Morphological Analysis. Light microscopy observations were made on samples preserved using different methods, in 5% Formalin/seawater, silica gel or as herbarium-pressed material. Silica gel-dried samples and herbarium pressed vouchers were rehydrated in distilled water for 20 min prior to observation. Samples were rinsed with seawater to remove excess mucilage. Vegetative and reproductive structures were sectioned manually using a stainless steel razor blade. Longitudinal, cross and oblique sections were stained with 1% aqueous aniline blue (Cho and Fredericq 2006). Slides were then mounted in a 50% Karo/water solution with phenol to retard microbial growth. Micrographs were taken with a Polaroid DMC le Digital camera attached to an Olympus BX60 microscope.

Molecular Data Acquisition. Total DNA was extracted from silica gel-dried specimens using a DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA) following the manufacturer's instructions. PCR and sequencing of chloroplast-encoded *rbcL* was conducted using the methods and primers described in Lin *et al.* (2012). Additional gene-specific primers for Rhodmeniaceae were newly designed for PCR amplification (Table 2). A portion of LSU rDNA and UPA were also amplified and sequenced using the primers and PCR protocol referenced in Sherwood *et al.* (2010). PCR products were gel-purified and sequenced in-house on both directions using the BigDye™ Terminator v. 3.1 (Life Technologies Grand Island NY, USA) on a ABI 3130xl Genetic Analyzer. All extracts are deposited in the Seaweeds Lab at the University of Louisiana at Lafayette.

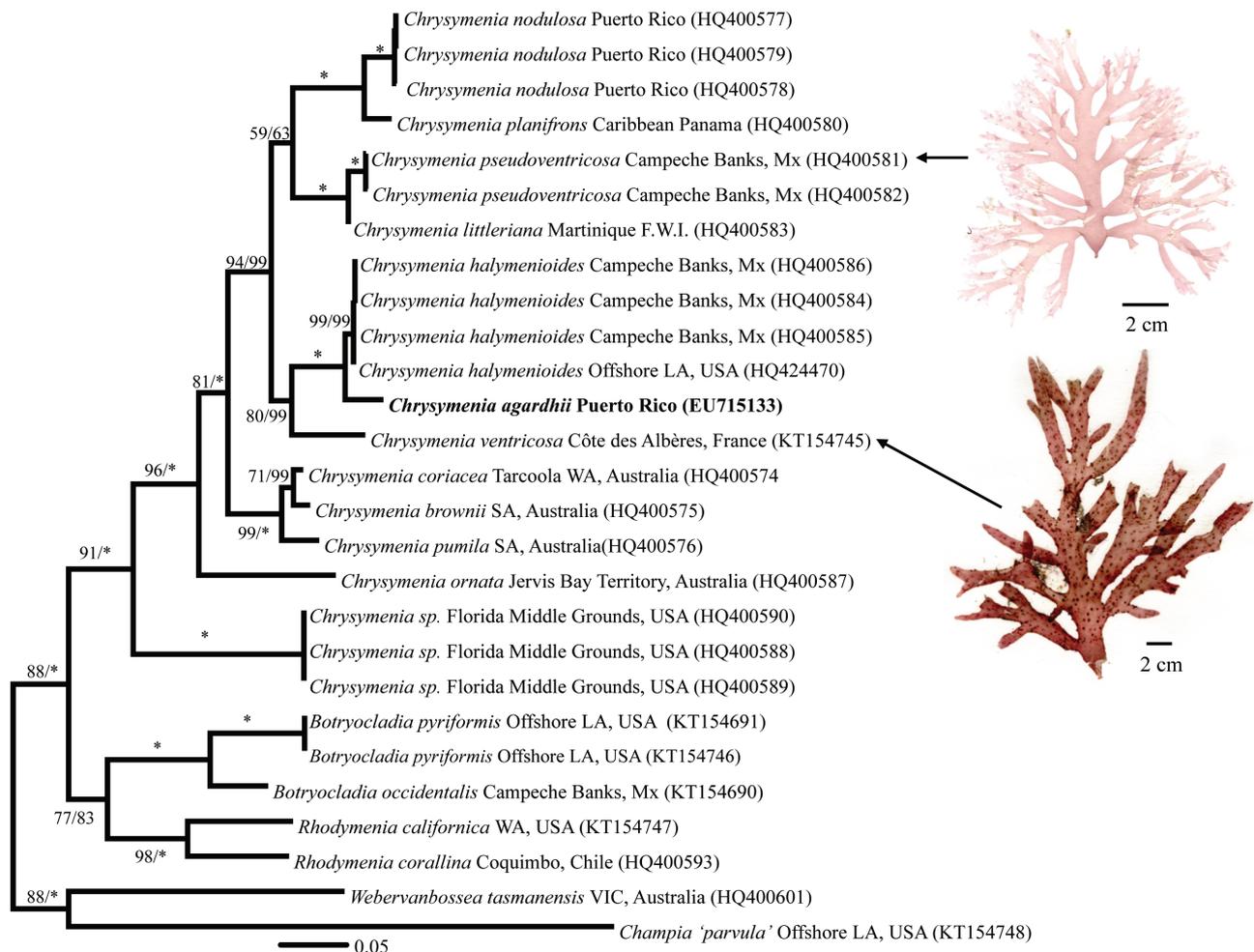


FIGURE 1. Phylogram showing the position of 23 newly generated sequences (not bold-faced) of Rhodymeniaceae that includes the generitype of *Chrysymenia*, i.e. *C. ventricosa*, and 2 outgroup taxa (*Webervanbossea*, Faucheaceae; *Champia*, Champiaceae) inferred from RaxML analysis of *rbcL* sequences. Numbers indicate bootstrap values at right, and BP values at left; *denotes full support. Scale bar indicates number of substitutions per site.

Multigene Alignment. Resulting sequences were assembled with Sequencher v. 5.2 (Gene Codes Corporation). An additional *rbcL* sequence of *Chrysymenia agardhii* (EU715133) was downloaded from the public NCBI database GenBank and added to the data set (Table 1). The newly generated *rbcL*, LSU and UPA sequences (KT#, HQ#) (Table 1) were then manually aligned in Mega v. 5.2.2 (Tamura *et al.* 2011).

Phylogenetic Analysis. Two phylogenetic analyses were conducted: 1) an *rbcL*-based analysis based on 26 sequences of *Chrysymenia*, *Gloiosaccion*, *Botryocladia* using *Webervanbossea tasmaniaensis* (Faucheaceae) and *Champia "parvula"* (Champiaceae) as the outgroup (Fig. 1), and 2) a concatenated *rbcL*, LSU and UPA-based analysis using the same DNAs and outgroups of the taxa analyzed in Fig. 1 but excluding one of the 4 *C. halymenioides* taxa (Fig. 2). The subsequent alignments were separately analyzed in Partitionfinder (Lanfear *et al.* 2012) to determine the best fitting model of evolution and data partition. The analyses each resulted in the selection of the General Time Reversible model plus gamma and a proportion of invariable sites with five partitions (UPA, LSU and the 3 codon positions of *rbcL*) on the basis of two information criteria, i.e. Akaike information criterion corrected (AICc) and Akaike information criterion (AIC). A box plot depicting the distribution of pairwise nucleotide differences (uncorrected) for the first, second, and third codon positions from the *rbcL* alignment was produced in R using the Ape Package (Paradis *et al.* 2004).

The alignments of both the *rbcL* and concatenated datasets were analyzed by Maximum likelihood (ML) as implemented by RAXML v. 2.4.4 (Stamatakis 2006) with the above models and partition scheme with 1000 restarts to find the tree with the lowest likelihood score and 1000 Bootstrap (BS) replications.

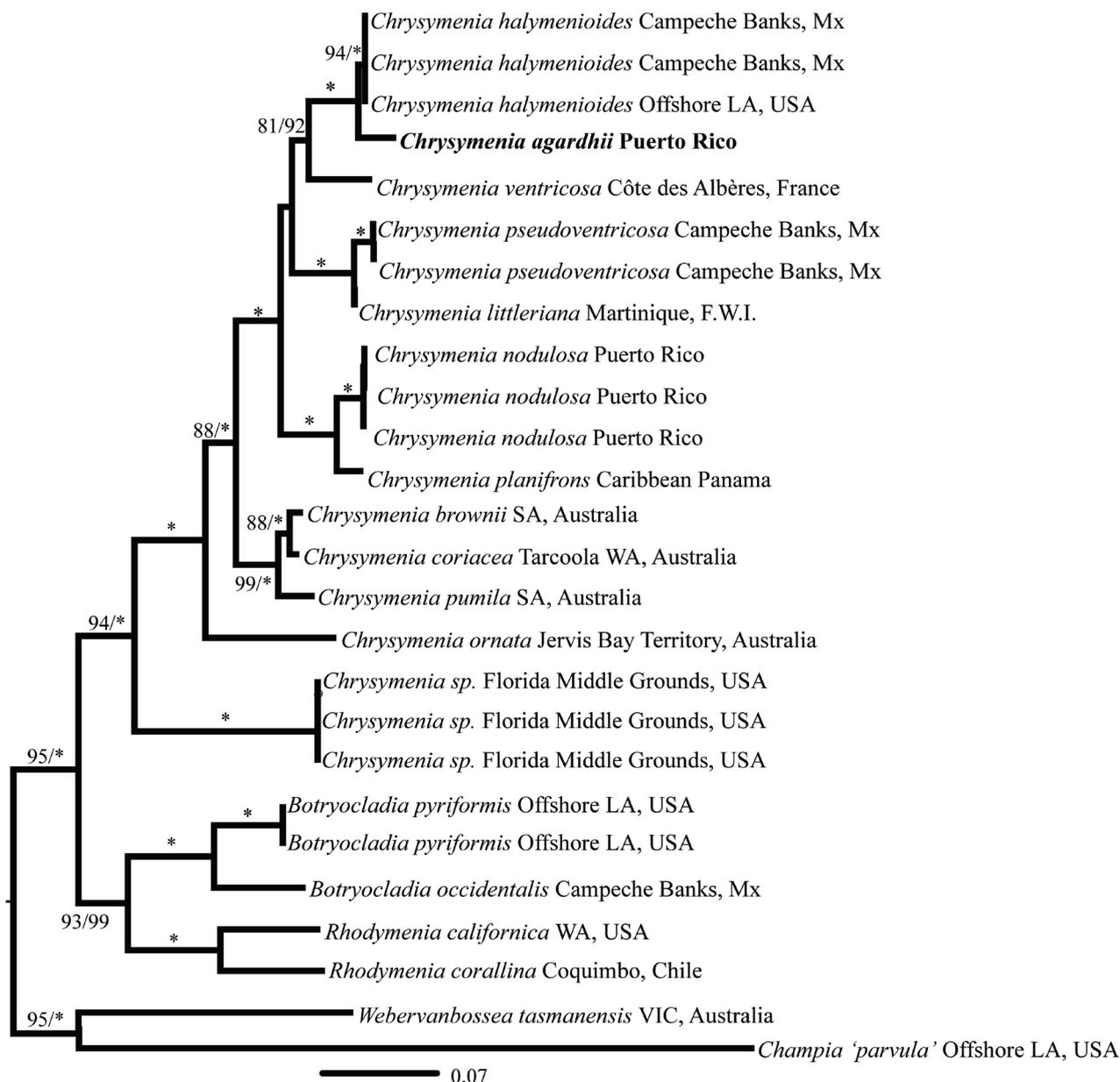


FIGURE 2. Phylogram showing the position of concatenated *rbcL*, UPA and LSU sequences (all newly generated sequences not bold-faced) of Rhodymeniaceae that includes the generitype of *Chrysymenia*, *C. ventricosa*, and 2 outgroup taxa (*Webervanbossea*, Faucheaceae; *Champia*, Champiaceae) inferred from RaxML analysis. Numbers indicate bootstrap values at right, and BP values at left; *denotes full support. Scale bar indicates number of substitutions per site

A Bayesian MCMC (Markov Chain Monte Carlo) was also applied to the aligned dataset using MrBayes v. 3.2.5 (Huelsenbeck & 2001, Ronquist & Huelsenbeck 2003, Ronquist *et al.* 2012). The Bayesian analysis consisted of two independent runs of 5 million generations with sampling every 1000 generations for a total of 10,002 trees. Convergence was visualized using Tracer v. 1.6 (Rambaut *et al.* 2014) and the first 10 percent of the trees of each run was discarded as burnin. The resulting Posterior Probabilities from Bayesian consensus trees were mapped on the ML tree. A distance matrix was also resolved from the branch lengths of the ML tree using the function *cophenetic.phylo* of the APE Package in R (Paradis *et al.* 2004).

For the *rbcL* dataset, the resulting distance matrix was used to find species boundaries in a stand-alone version of Automatic to Barcode Gap Discovery (ABGD) (Puillandre *et al.* 2011). General Mixed Yule Coalescence (GMYC) model as implemented by the *Splits* Package in R (Fujisawa and Barraclough 2013) with a single threshold model was also used to determine species boundaries. The requisite ultrametric tree for the GMYC analysis was generated

in Beast v. 1.8.1 (Drummond *et al.* 2012) using a relaxed log-normal clock with a constant population coalescent as a prior and the best fitting model and partition as described above. MCMC Chains were run for 10 million generations with sampling every 1000th generation resulting in 10,000 trees. The quality of the run was assessed in Tracer v. 1.6 (Rambaut and Drummond 2007) to ensure that ESS values were >200 with the default burnin (1,000 trees). Tree annotator v. 1.8.1 (Drummond *et al.* 2012) was used to summarize the resulting 9001 trees after burnin, targeting the maximum clade credibility tree with preserved node heights.

Results

On the basis of the *rbcL* phylogenetic analysis (Fig. 1), the generitype *C. ventricosa* from the western Mediterranean France is unambiguously distinct from the species reported under that name for the Gulf of Mexico. The latter forms the basis for a new species, *C. pseudoventricosa* sp. nov. Both taxa are nested in separate clades within *Chrysymenia*. *C. ventricosa* belongs in a well supported (BS=80, BP=99) clade that includes *C. halymenioides* Harvey from the NW and SW Gulf of Mexico, and *C. agardhii* Harvey from Puerto Rico. This clade, in turn, is sister to low supported clade (BS=59, BP=63) comprising two fully supported (*) subclades: one subclade representing *C. pseudoventricosa* sp. nov. from the SW Gulf of Mexico and *C. littleriana* J.N. Norris & Ballantine from Martinique, FWI, and the other subclade representing *C. nodulosa* J.N. Norris & Ballantine from Puerto Rico and *C. planifrons* (Melville) J. Agardh from Caribbean Panama. These *Chrysymenia* clades are sister (BS=81, BP=*) to a strongly supported clade (BS=99, BP=*) that includes Australian taxa currently placed in *Gloiosaccion* (*G. brownii* Harvey [including *G. brownii* var. *firmum* and *G. brownii* var. *coriaceum*] and *G. pumilum* J. Agardh). Results of the ABGD and GMYC analyses support the separation of three species encompassing the genus “*Gloiosaccion*”. Since the genus *Gloiosaccion* forms a monophyletic group residing inside *Chrysymenia* it is here merged with *Chrysymenia*.

Sister to the above mentioned clades is *C. ornata* Kylin from Australia with strong support (BS=96, BP=*). In turn, an undescribed species from the vicinity of the Florida Middle Grounds in the SE Gulf of Mexico clusters with strong support (BS=91, BP=*) to the other *Chrysymenia* taxa. The resulting *rbcL*-based phylogeny recovered twelve distinct species in the genus *Chrysymenia*. Purposefully omitted from the dataset in the present paper is *Chrysymenia enteromorpha* Harvey (1853), a common species throughout the Gulf of Mexico and the Caribbean; the correct taxonomic position of this species forms the subject of a separate paper that will be discussed along with the *Chrysymenia* sp. from the vicinity of the Florida Middle Grounds, and with which it has been confused; this *Chrysymenia* sp. will form the basis of a new species. The entire *Chrysymenia* clade is strongly supported (BS=91, BP=*), distinct from the genera *Botryocladia* and *Rhodymenia* in the Rhodymeniaceae. The species topology in the concatenated *rbcL*, LSU and UPA analysis (Fig. 2) is congruent with that of the *rbcL* tree shown in Fig. 1 except for the sister clade relationship of *C. ventricosa* and the fact that the support values for most nodes increased.

All samples of *Chrysymenia* newly sequenced in this study were also analyzed morphologically (Schmidt 2009). With the exception of *C. ornata* from Australia (Kylin 1931), all materials examined contain internal rhizoidal filaments. Illustrated here are the habits of the type specimen of *Chrysymenia ventricosa* (J.V. Lamouroux) J. Agardh and *Gloiosaccion brownii* Harvey, and available characters that distinguish Mediterranean *Chrysymenia ventricosa* from *C. pseudoventricosa* from the Gulf of Mexico.

While this publication focused on the monophyletic members of *Chrysymenia*, forthcoming publications will address the non-monophyly of taxa currently placed in *Chrysymenia* (Schmidt *et al.*, in prep).

***Chrysymenia ventricosa* (J.V. Lamouroux) J. Agardh 1842, p. 106**

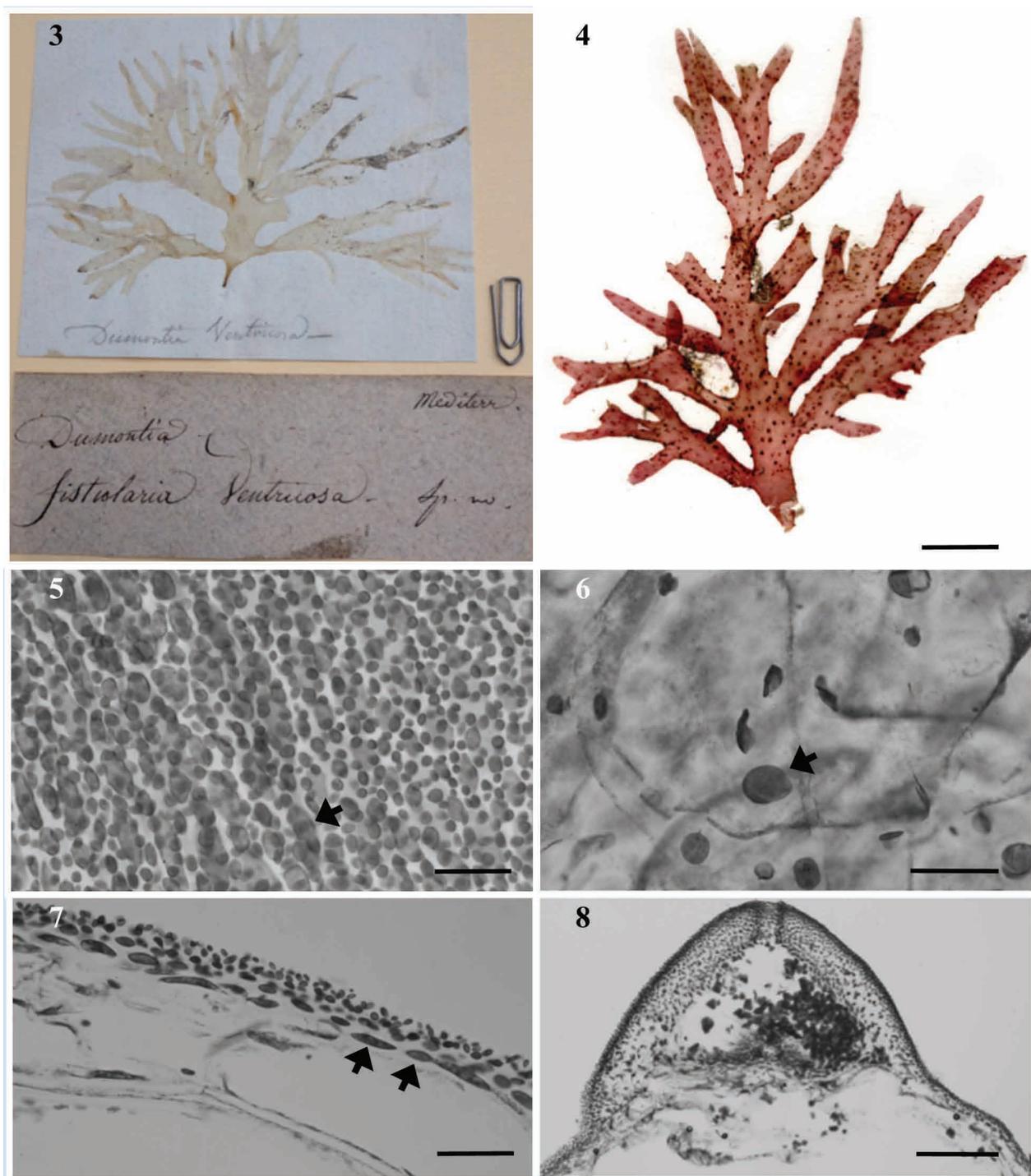
Figures 3–8

TYPE LOCALITY: “In Mari Gaditano. Ad oras maris Mediterranei Galliae” (from sea around the Straits of Gibraltar, on shores of Spanish Mediterranean Sea)

TYPE MATERIAL: Mediterranean, no indication about collector, (C 19/f 33), grey label (Fig. 3) is by the hand of Lamouroux; extra label written by J.F. Chauvin, his successor at Caen (Dr. Chantal Ballard, pers. comm.) mentions *Fistularia ventricosa*, a cornetfish (*Fistularia* Linnaeus 1758). The independence of botanical and zoological nomenclature of *F. fistularia* is moot since the algal name was not formally described.

BASIONYM: *Dumontia ventricosa* J.V. Lamouroux 1813, p. 45, pl. 4, fig. 6

SYNONYMS: *Halymenia ventricosa* (J.V. Lamouroux) C. Agardh 1822, p. 212



FIGURES 3–8. *Chrysymenia ventricosa* (J.V. Lamouroux) J. Agardh. 3) Habit of type specimen from the Mediterranean, in Lamouroux Herbarium, Caen. 4) Habit of carposporophytic specimen from Cap Oullestreil, Côte des Albères, Mediterranean France. Scale bar 2 cm. 5) Surface view showing elongate subcortical cells (arrow) below surface cells. Scale bar 30 µm. 6) Cross section showing multiple, solitary gland cells (arrow) at periphery of a medullary cell. Scale bar 60 µm. 7) Longitudinal section showing layer of narrow, periclinal subcortical cells (arrows) subtending a cortex of 2–3 layers of small roundish cells; and large, hyaline medullary cells. Scale bar 50 µm. 8) Cross section through mature carposporophyte. Scale bar 200 µm.

Chrysymenia digitata Zanardini 1863, p. 287

Chrysymenia ventricosa var. *digitata* (Zanardini) Hauck 1883, p. 159

MATERIAL EXAMINED: carposporophytic specimen, Cap Oullestreil, Côte des Albères, Pyrénées, Mediterranean France, 17.vii.84, coll. M.D. Guiry, Fig. 4. See Table 1.

GEOGRAPHIC DISTRIBUTION: Mediterranean. The occurrence of *C. ventricosa* outside this area is doubtful (Florida, Greater and Lesser Antilles, Southern Caribbean, Bermuda, Canary Islands, Venezuela, French Polynesia; see records in Taylor 1960, Littler and Littler 2000, Payri *et al.* 2000).

HABIT, VEGETATIVE AND REPRODUCTIVE STRUCTURE: The type specimen of *C. ventricosa* (Fig. 3) was not available for study, and only a dried herbarium specimen that lacked the basal part of a stipe and holdfast (Fig. 4) was analyzed. The thallus, about 17 cm tall, erect, terete to moderately compressed (Figs. 3–4), consists of a leading axis bearing alternate to opposite lateral side branches appearing sparsely but broadly pinnulate, giving the thallus a digitate appearance (Figs 3, 4). None of the side branches are constricted at their base (Figs. 3, 4). The thallus surface is completely corticated (Fig. 5), composed of two-to-three cortical cell layers of small roundish cells (Fig. 7) subtended by a layer of elongate, narrow subcortical cells and two medullary layers of large hyaline cells (Fig. 7). The elongate, periclinal subcortical cells are readily visible from a surface view (Fig. 5). Pyriform gland cells (Fig. 6) are pinched off singly and thallus inward from the peripheral cytoplasm of any unmodified subcortical or medullary cell (Fig. 6), with several gland cells of different sizes typically cut off from a single vegetative cell (Fig. 6). Ostiolate, hemispherical carposporophytes are scattered over the thallus surface (Fig. 4) and protrude from the surface. Mature carposporophytes reach about 0.8 cm in diameter, and lack an enveloping network of filaments around the globular mass of carposporangia (Fig. 8). Male and tetrasporangial thalli were not seen.

REPRESENTATIVE SEQUENCES: KT154745 (*rbcL*), KT154732 (LSU), KT154707 (UPA).

***Chrysymenia pseudoventricosa* W. E. Schmidt, Gurgel and Fredericq, sp. nov.**

Figures 9–16.

HOLOTYPE: sample LAF-NSF-II-78-2 (WES 16), Campeche Banks, Southeastern Gulf of Mexico, Mexico, 22°10'420"N, 91° 09'550"W), 42–43 m depth sample NSF-II-106-3, vegetative plant, attached to rhodolith. Figs. 9–14, *leg.* Suzanne Fredericq, deposited in LAF.

ETYMOLOGY: the specific epithet refers to the similarity in habit with *C. ventricosa*.

SYNONYM: *Chrysymenia ventricosa* in part

MATERIAL EXAMINED: Campeche Banks, SE Gulf of Mexico, Mexico, LAF-NSF-II-63-1 (WES 88), 21°48'048" N, 91°54'962" W), 30–38 m depth; LAF-NSF-II-106-3, 22°10'420" N, 91° 09'550" W, 18.vi.2005, dredged from a depth of 37–43 m, attached to rhodolith; sample NSF-II-106-3, vegetative plant. See Table 1.

GEOGRAPHIC DISTRIBUTION: Gulf of Mexico, Florida, Caribbean, Bermuda, Canary Islands [see records in Taylor (1960), Littler and Littler (2000) as *C. "ventricosa"*]

HABIT AND VEGETATIVE STRUCTURE: Thalli up to 10.5 cm tall and 13 cm in width, terete to moderately compressed, with a thickness of approximately 4.5 mm, from a small attachment stipe of 2 mm in height, and a small discoid holdfast (Fig. 9). The blade is hollow and filled with mucilage. Gland cells are pyriform, solitary (Fig. 10), or borne on unmodified medullary cells (Fig. 11). The thallus is completely corticated (Fig. 12), composed of three-to-four pigmented cortical cell layers (Fig. 13), a larger layer of roundish subcortical cells, and one-to-two medullary layers of hyaline cells (Fig. 14). The middle portion of the stipe is of complete solid construction, with pigmented cortical cells transitioning into large hyaline medullary cells filling the solid mass with rhizoidal filaments (Fig. 15). Internal filaments develop either from transformed medullary cells, or invading medullary cells (Fig. 16). Female, male and tetrasporangial thalli were not seen.

REPRESENTATIVE SEQUENCES: HQ400581 (*rbcL*), KT154726 (LSU), KT154701 (UPA).

***Chrysymenia brownii* (Harvey) De Toni 1900, p. 545, Figs. 17–23**

BASIONYM: *Gloiosaccion brownii* Harvey 1859a, pl. 83 (including var. *α membranaceum*)

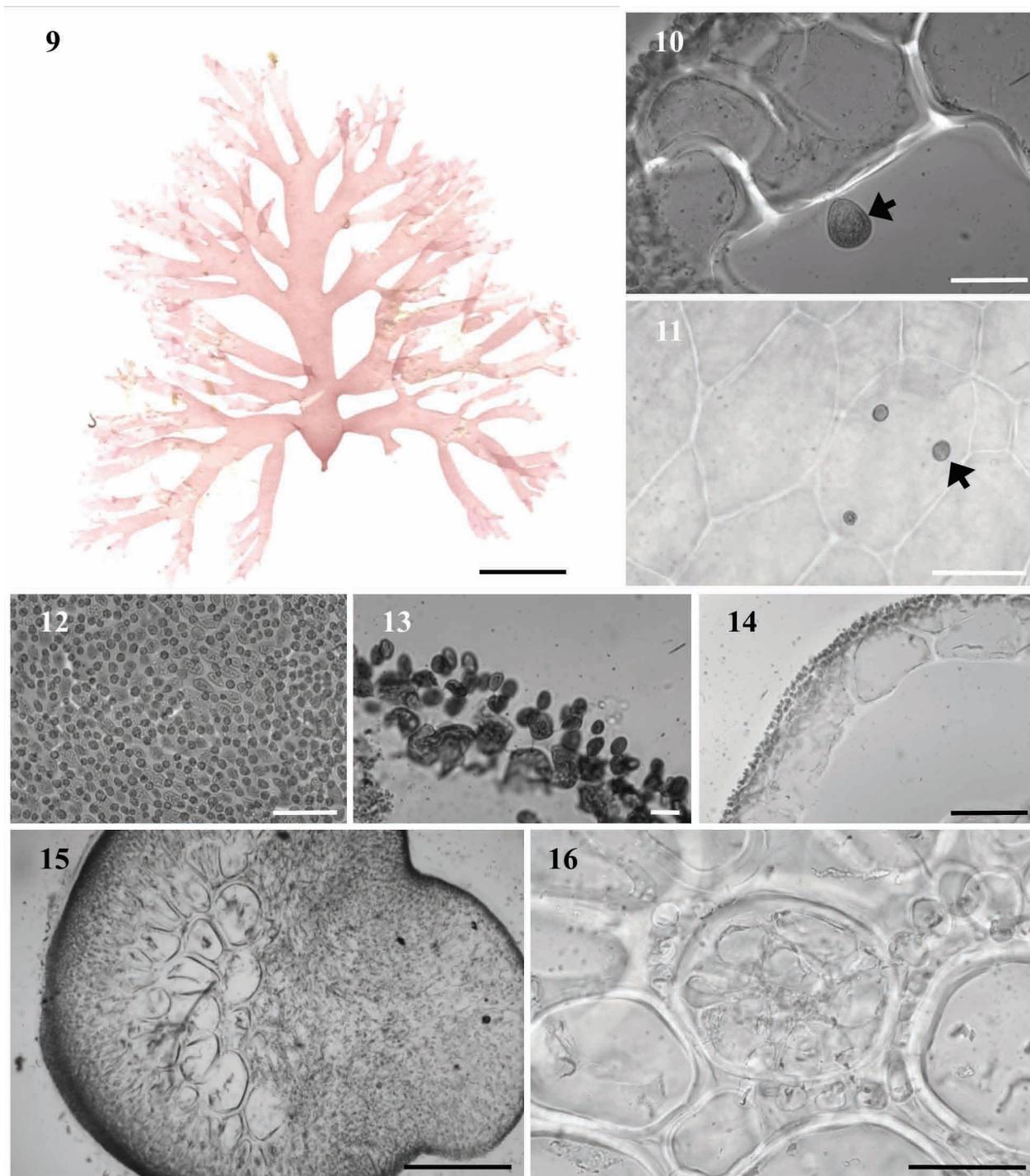
SYNONYMS: *Halosaccion hydrophora sensu* Harvey 1855, p. 556 (non Postels & Ruprecht 1840: 19, pl. 35C)

Gloiosaccion hydrophora J. Agardh 1892, p. 85

Botryocladia brownii (Harvey) G. Feldmann and Bodard 1965, pp. 9–10

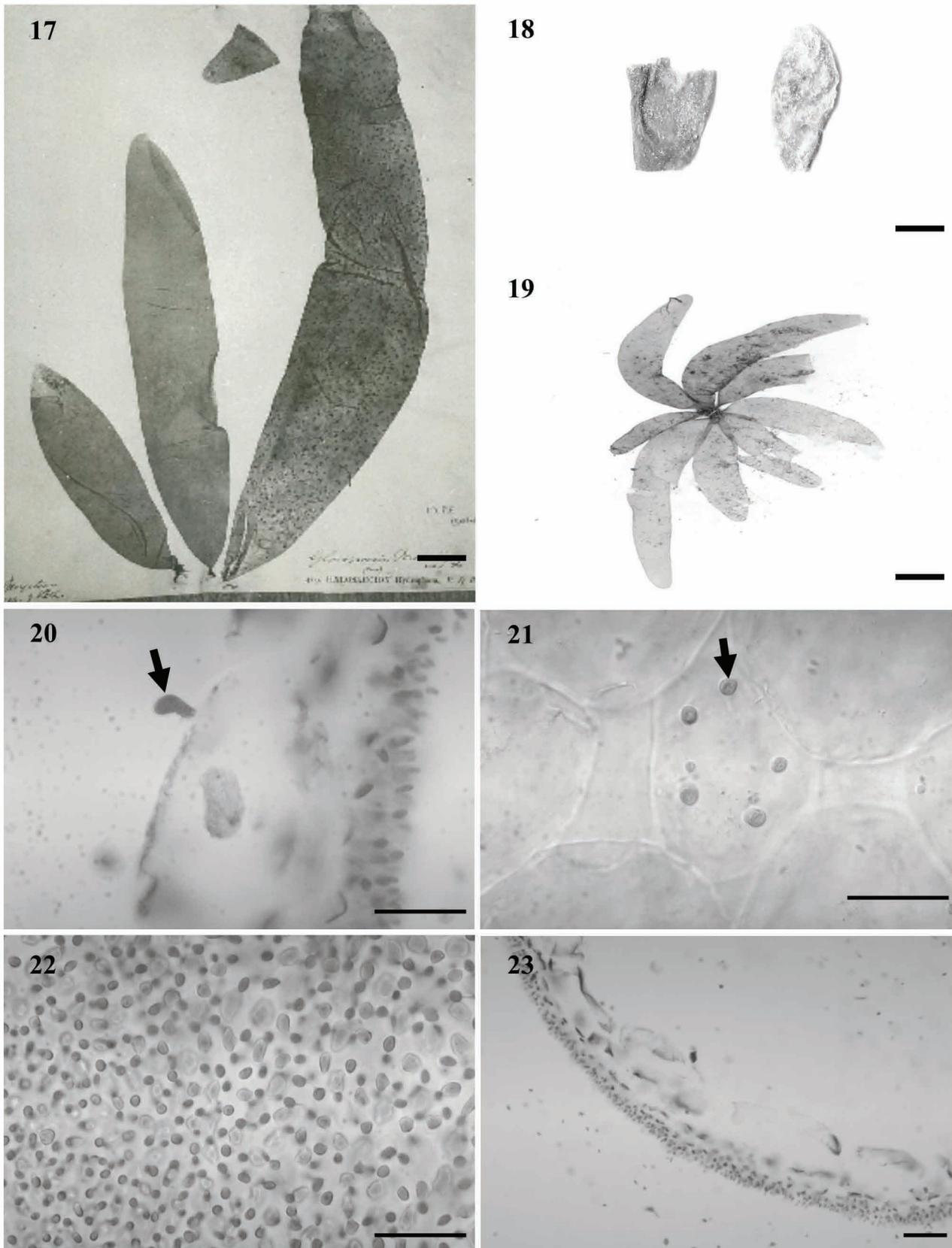
TYPE: Georgetown, Tasmania, Australia (Harvey, Alg. Aust. Exsiccata no. 419); lectotype designated by Womersley in 1952) in Herb. Harvey, TCD.

SPECIMENS EXAMINED: Port McDonnell, South Australia, coll. M. H. and F. Hommersand, 11.xi.95 (WES108). See Table 1.



FIGURES 9–16. *Chrysymenia pseudoventricosa* W.E. Schmidt, Gurgel and Fredericq sp. nov. from the Campeche Banks, SW Gulf of Mexico. 9–14) Holotype, LAF-NSF-II-78-2 (WES16). 9) Habit of non-reproductive plant. Scale bar 2 cm. 10) Cross section at mid thallus region, showing spherical gland cell (arrow). Scale bar 40 μ m. 11) Surface view of medullary cells, with gland cells (arrow). Scale bar 100 μ m. 12) Surface view of thallus showing complete cortication. Scale bar 40 μ m. 13) Cross section of cortical layer at mid thallus region. Scale bar 4.5 μ m. 14) Cross section through mid thallus region showing pigmented cortical cells and hyaline medullary cells. Scale bar 100 μ m. 15–16) Vegetative specimen LAF-NSF-II-106-3. 15) Cross section through middle part of holdfast showing cortical cells, and medullary cells with dense aggregation of narrow internal filaments. Scale bar 0.5 mm. 16) Internal filaments inside a transformed or invaded medullary cell. Scale bar 100 μ m.

GEOGRAPHIC DISTRIBUTION: Geraldton, West Australia to Jervis Bay, N.S.W. and around Tasmania, Australia; Kermadec Isls (*vide* Nelson and Adams 1984, Womersley 1996), New Zealand (Adams 1994).



FIGURES 17–23. *Chrysiomenia brownii* (Harvey) DeToni. 17, 18), 20–23) WES108 and 19) *Chrysiomenia pumila* (J. Agardh) Weber-van Bosse. Scale bar 2 cm. 1094. 17) Type specimen of *G. brownii* var. *membranaceum*. Scale bar 2 cm. 18) Univesiculate thalli. Scale bar 1 cm. 19) Multivesiculate thallus. Scale bar 1 cm. 20, 21) Pyriform gland cell (arrow) cut off thallus inward from medullary cell in cross sectional view. Scale bar 100 μ m. 20) Surface view. Scale bar 40 μ m. 21) Surface view. Scale bar 100 μ m. 22) Thallus surface with complete cortication. Scale bar 40 μ m. 23) Cross section through mid thallus region showing pigmented cortical cells and hyaline medullary cells. Scale bar 100 μ m.

The type specimen of *Gloiosaccion brownii* Harvey (Fig. 17) at TCD was not available for examination. Univesiculate talli (Fig. 18) from south Australia were preserved in silica gel and rehydrated for vegetative characters. Pyriform gland cells are cut off thallus inward from medullary cells in cross sectional (Fig. 20) and surface (Fig. 21) views. The surface shows complete cortication (Fig. 22). The thallus interior is composed of three to six pigmented cortical cell layers and one to three medullary layers of hyaline cells (Fig. 23).

REPRESENTATIVE SEQUENCES: HQ400575 (*rbcL*), KT154734 (LSU), KT154708 (UPA).

***Chrysymenia coriacea* (Harvey) W. E. Schmidt, Gurgel & Fredericq, comb. et stat. nov.**

BASIONYM: *Gloiosaccion brownii* Harvey var. *coriaceum* Harvey 1859a, pl. 83

SYNONYM: *Gloiosaccion brownii* Harvey var. *coriacea* Harvey 1859b, p. 322

Gloiosaccion brownii Harvey var. β *firmum* Harvey 1859a, pl. 83

Halosaccion firmum sensu Harvey 1855, p. 556 (non Postels & Ruprecht 1840: 19, pl. 35B)

TYPE: Georgetown, Tasmania, Australia (Harvey, Alg. Aust. Exsiccata no. 420)

NOTE: Since *Chrysymenia firma* J. Agardh 1842 is the basionym for *Lomentaria firma* (J. Ag.) Falkenberg 1879, the 'firma' varietal epithet is rejected as it applies to the taxon *Gloiosaccion brownii* var. *firmum* (see ICBN, Saint Louis Code, Ch. 5, article 53). Womersley (1996) noted that Harvey (1859a, pl. 83) described two varieties, α *membranaceum* and β *firmum*, that probably correspond to young and older plants and were not worth recognizing, and that he (Harvey 1859b, p. 322) apparently changed *firmum* to *coriaceum*, referring to exsiccatum no. 420. The variety 'coriaceum' (*Gloiosaccion brownii* Harvey var. *coriaceum*), viewed as a superfluous or illegitimate name of variety 'firmum' (Silva *et al.* 1996) is here viewed as a legitimate substitute name for *G. brownii* var. *firmum* and is elevated to species level with a new combination and new status. The taxonomic status of *G. brownii* Harvey var. *furcatum* Harvey 1863: xlv (syntype localities western Australia and Georgetown, Tasmania) has not been clarified in this study.

TYPE LOCALITY: *Fide* Freemantle, Western Australia, Australia

DISTRIBUTION: Western and southern Australia (Womersley 1996, Huisman 2000), New Zealand (Adams 1994), Kermadec Isls (*fide* Huisman & Walker 1990, Nelson and Adams 2012), French Polynesia (*fide* N'Yeurt & Payri 2010).

SPECIMENS EXAMINED: MH.FH.21.xi.95 (WES118), Tarcoola Beach, Western Australia, Australia.

REPRESENTATIVE SEQUENCES: HQ400574 (*rbcL*), KT154733 (LSU), KT154709 (UPA).

***Chrysymenia pumila* (J. Agardh) Weber-van Bosse 1928: p. 469**

FIGURE 19.

BASIONYM: *Gloiosaccion pumilum* J. Agardh 1892, p. 85.

TYPE: Port Phillip Heads, [New Holland] Victoria, South Australia, coll. J. Br. Wilson (Womersley 1996: 54). Holotype in Herb. Agardh, LD 26407.

DISTRIBUTION: Southern Australia (Womersley 1996: 54), Indonesia (*fide* Weber-van Bosse 1928, Atmadja & Prud'homme van Reine 2012).

MATERIAL EXAMINED: Edithburgh Pier, Yorke Peninsula, South Australia, coll. C.F.D. Gurgel, 17.i.2010, 35°05'04" S, 137°49'56" E (AD-A90892).

HABIT: The specimen examined was air-dried on a herbarium sheet, and shows a distinct multi-vesiculate thallus (Fig. 19).

NOTE: Womersley (1996) views *G. pumilum* J. Agardh to be a slender and young plant of *G. brownii*.

REPRESENTATIVE SEQUENCES: HQ400576 (*rbcL*), KT154710 (UPA).

Discussion

The molecular evidence herein presented does not support the previous synonymy of *Gloiosaccion* with *Botryocladia* as accepted by Feldmann and Bodard (1965) and Silva (1980), nor the recognition of *Gloiosaccion* as a distinct genus as currently acknowledged (Womersley 1950, Saunders *et al.* 1999). *Gloiosaccion brownii* was originally described

by Harvey (1859a) as a univesiculate species consisting of two varieties namely var. *membranaceum*—the current type, and var. *firmum*. *Gloiosaccion brownii* var. *membranaceum* was described as delicately membraneous and rose-red, whereas *G. brownii* var. *firmum* was recognized for being coriaceous-membraneous and varying from livid purple to deep blood-red. The molecular evidence does not support the currently held opinion that “*Gloiosaccion*” is monospecific. Instead, our data indicate that the varieties are molecularly sufficiently distinct at the species level (on the basis of ABGD and GMYC analyses), as is the multi-vesiculate *Chrysomenia pumila* (J. Agardh) Weber-van Bosse. One specimen from each “variety” was observed in this study with the only observed difference for the univesiculate taxa the thickness of the outer membrane, 180–210 µm in *Chrysomenia brownii* vs. 260–309 µm in *C. coriacea*.

Saunders *et al.* (1999) using small subunit ribosomal DNA sequences supported Womersley’s resurrection of *Gloiosaccion* at the molecular level in that *G. brownii* showed a sister relationship to *Chrysomenia ornata* (J. Agardh) Kylin (1931) and that it did not fall within the *Botryocladia* clade. Saunders *et al.* (1999), however, used only two species of *Chrysomenia* in their dataset, i.e. *C. ornata* and *C. wrightii*, a clade that resolved as sister to *Botryocladia*. The present study includes a larger sampling of *Chrysomenia* species and multi-marker analysis and reveals that *Gloiosaccion* is not sister to *Chrysomenia* but indeed falls within the *Chrysomenia* clade.

Chrysomenia brownii, *C. coriacea* and *C. pumila* are similar to the other species of *Chrysomenia* analyzed in their vegetative structure and in possessing a very short stipe; however, unlike the situation in the other known *Chrysomenia* species, the stipe of *C. pumila* generates additional bladders. In addition, the stipes of *C. brownii* and *C. coriacea* specimens remain unbranched and those in *C. pumila* are branched. In this study, specimens with branched stipes have not been observed, but a top portion of a stipe of a single bladder specimen resembles that of other *Chrysomenia* species. In the thalli observed, large medullary cells cut off internal rhizoids that fill the central portion of the stipe, a characteristic suggested by Norris (1995) that may be useful in separating *Chrysomenia* from *Botryocladia* since many of the *Botryocladia* specimens studied so far have a solid pseudoparenchymatous medulla. In all thalli observed, large medullary cells cut off internal rhizoids that fill the central cavity, a characteristic that was suggested by Norris (1989) to be useful in separating *Chrysomenia* from *Botryocladia* since many of the *Botryocladia* specimens studied so far lack internal rhizoids.

Thalli of *Chrysomenia* species are composed of multiple cell layers, with the medulla consisting of large hyaline medullary cells that can give rise to gland cells and to internal rhizoids. The medulla in *Chrysomenia* is either composed of a single layer of cells or of multiple cell layers that resemble those in “*Gloiosaccion*”; in the latter, however, cells of the middle portion of the cortex cut off a set of anticlinal filaments. Although an anticlinal arrangement of cells in *Chrysomenia* is not unknown, the cells are always associated with male sexual structures as documented in the anticlinal formation of spermatangia in *C. nodulosa* (Norris and Ballantine 1995). Furthermore, the degree of carposporophyte protrusion has been questioned as a reliable character to discriminate among genera of Rhodymeniales (Huisman 1996, Afonso-Carillo *et al.* 2006). Though similar in overall habit, *C. ventricosa* can be separated from *C. pseudoventricosa* in that the subcortical layer subtending the cortex is comprised of narrow, periclinal cells bearing 2–3 layers of cortical cells in the former, and roundish periclinal cells bearing 3–4 layers of cortical cells in the latter.

Conclusion. Seven currently recognized species listed for *Chrysomenia* (Wynne 2005, Guiry and Guiry 2015), i.e. *C. agardhii*, *C. halymenioides*, *C. littleriana*, *C. nodulosa*, *C. ornata*, *C. planifrons*, and *C. ventricosa* were sampled and analyzed in this study, the largest molecular study performed to date for this genus. The genus *Gloiosaccion* is reduced to synonymy with *Chrysomenia*, and two varieties of *G. brownii* are recognized at the species rank, i.e. *C. brownii* (Harvey) De Toni and *C. coriaceum* (Harvey) comb. et stat. nov. *Chrysomenia pumila* (J. Agardh) Weber-van Bosse, is more broadly recognized as a distinct species. The deep-water collections of *Chrysomenia* “*ventricosa*” reported for the Gulf of Mexico do not exemplify a range extension of the Mediterranean but instead represent a new species, *C. pseudoventricosa* sp. nov. The unnamed species from the Florida Middle Grounds awaits description and will be discussed vis-à-vis *Chrysomenia enteromorpha* Harvey in a forthcoming paper. In total, twelve distinct species of *Chrysomenia* are recognized in this study.

Acknowledgments

We thank Dr. Chantal Billard, University of Caen, for providing the image of the type specimen of *Dumontia ventricosa* Lamouroux housed at Caen. We are grateful to Dr. Fabio Rindi for the herbarium specimen of *C. ventricosa* from the Côtes d’Albères, and to Dr. Natalia Arakaki for providing figures 5–8. This study was supported in part by NSF grants DEB-0315995 and DEB-1456674 (ARTS) to SF, and University of Adelaide Faculty of Science Strategic Research

Initiative Funding, Field Naturalists Society of South Australia & Lirabenda Endowment Fund, Australian Biological Resource Study (ABRS) grant 09-062, South Australia Department Water Environment and Natural Resources, and AW NRM grant CCAW084690-3 to CFDG. The collectors listed in Table 1 are greatly acknowledged.

REFERENCES

- Abbott, I.A. & Littler, M.M. (1969) Some Rhodymeniales from Hawaii. *Phycologia* 8: 165–169.
<http://dx.doi.org/10.2216/i0031-8884-8-3-165.1>
- Adams, N.M. (1994) *Seaweeds of New Zealand: an illustrated guide*. Canterbury University Press, 370 pp.
- Afonso-Carrillo, J., Rodríguez-Prieto, J.C., Boisset, F., Sobrino, C., Tittley, I. & Neto, A.I. (2006) *Botryocladia chiajeana* and *Botryocladia macaronesica* sp. nov. (Rhodymeniaceae, Rhodophyta) from the Mediterranean and the Eastern Atlantic, and a discussion on the closely related genus *Irvinea*. *Phycologia* 45: 277–292.
<http://dx.doi.org/10.2216/04-97.1>
- Agardh, C.A. (1822) *Species algarum*. Volumen primum pars posterior. pp. [v–vi], 169–398. Lundae [Lund], ex officina Berlingiana.
- Agardh, J.G. (1842) *Algae Maris Mediterranei et Adriatici*, Paris, 264 pp.
- Agardh, J.G. (1876) *Epicrisis Systematis Floridearum*. Species genera et ordines algarum, vol 3. Part 1, Weigel, Leipzig, 724 pp.
- Agardh, J.G. (1892) *Analecta Algologica*. *Acta Universitatis Lundensis* 28:1–182.
- Atmadja, W.S. & Prud'homme van Reine, W.F. (2012) *Checklist of the seaweed species biodiversity of Indonesia with their distribution and classification: Rhodophyceae*. Coral Reef Information and Training Centre, Jakarta. Coral Reef Rehabilitation and Management Programme. Indonesian Institute of Sciences, pp. 1–72.
- Brodie, J. & Guiry, M.D. (1988) Life history of *Boryocladia adreana* sp. nov. (Rhodymeniales, Rhodophyta) from Portugal. *Phycologia* 27: 109–130.
<http://dx.doi.org/10.2216/i0031-8884-27-1-109.1>
- Cho, T. O. & Fredericq, S. (2006) Two creeping *Ceramium* species (Ceramiaceae, Rhodophyta) from the Florida Keys: *C. reptans* sp. nov. and recircumscription of *C. codii* (Richards) Mazoyer. *Phycologia* 45: 495–504.
<http://dx.doi.org/10.2216/05-44.1>
- De Toni, G.B. (1900) *Sylloge Algarum omnium hucusque Cognitarum, Vol 4. Florideae sect 2*. Patattii [Padova], pp. 387–776.
- Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*.
<http://dx.doi.org/10.1093/molbev/mss075>
- Durant, C.F. (1850) *Algae and corallines of the Bay & Harbor of New York, illustrated with natural types*. George P. Putnam Printed by Narine & Co., New York, pp. 1–43.
- Falkenberg, P. (1879) Die Meeres-Algen des Golfes von Neapel. *Mitteilungen der Zoologischen Station zu Neapel* 1: 218–277.
- Felder, D., Thoma, B., Schmidt, W., Sauvage, T., Self-Krayesky, S., Chistoserdov, A., Bracken-Grissom, H. & Fredericq, S. (2014) Seaweeds and decapod crustaceans on Gulf deep banks after the Macondo Oil Spill. *Bioscience* 64: 808–19.
<http://dx.doi.org/10.1093/biosci/biu119>
- Feldmann, G. (1945) Révision du genre *Botryocladia* Kylin (Rhodophycées Rhodymeniácees). *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 35: 49–61.
- Feldmann, G. & Bodard, M. (1965) Une nouvelle espèce de *Botryocladia* des côtes du Sénégal. *Bulletin de l'Institut Océanographique de Monaco* 65: 1–14.
- Fredericq, S., Anderson, R.J. & Lopez-Bautista, J. (2003) Systematic circumscription of some Phylloporaceae (Gigartinales, Rhodophyta) from the Cape region, South Africa, based on molecular evidence. *Proceedings XVIIth International Seaweed Symposium 2003*: 263–274.
- Fredericq, S., Cho, T.O., Earle, S.A., Gurgel, C.F.D., Krayesky, M., Mateo Cid, L.E., Mendoza Gonzáles, A.C., Norris, J.N. & Suárez, A.M. (2009) Seaweeds of the Gulf of Mexico. In: Felder, D.L. & Camp, D.K. (Eds.) *Gulf of Mexico: Its Origins, Waters, and Biota*. I. Biodiversity. Texas A&M Univ. Press, pp. 187–259.
- Fredericq, S., Arakaki, N., Camacho, O., Gabriel, D., Krayesky, D., Self-Krayesky, S., Rees, G., Richards, J., Sauvage, T., Venera-Ponton, D. & Schmidt, W.E. (2014) A dynamic approach to the study of rhodoliths: a case study for the northwestern Gulf of Mexico. *Cryptogamie Algologie* 35: 77–98.
<http://dx.doi.org/10.7872/crya.v35.iss1.2014.77>
- Fritsch, F.E. (1945) *The Structure and Reproduction of The Algae*. Volume II. University Press, Cambridge, 939 pp.
- Fujisawa, T. & Barraclough, T.C. (2013) Delimiting species using single-locus data and the Generalized Mixed Yule Coalescent Approach:

- A revised method and evaluation on simulated data sets. *Systematic Biology* 62: 707–724.
<http://dx.doi.org/10.1093/sysbio/syt033>
- Gavio, B. & Fredericq, S. (2003) *Botryocladia caraibica* sp. nov. (Rhodymeniales, Rhodophyta), a new species from the Caribbean. *Cryptogamie Algologie* 24: 93–106.
- Gavio, B. & Fredericq, S. (2005) New species and new records of offshore members of the Rhodymeniales (Rhodophyta) in the Northern Gulf of Mexico. *Gulf of Mexico Science* 1: 58–83.
- Guiry, M.D. & Guiry, G.M. (2015) Algaebase. Worldwide electronic publication, National University of Ireland, Galway. Available from: <http://www.algaebase.org> (accessed 1 May 2015)
- Harvey, W.H. (1849) *A manual of the British marine algae*. John Van Voorst, London, pp. i–lii, 1–252, 27 pls.
- Harvey, W.H. (1853) *Nereis boreali-americana*; or, contributions towards a history of the marine algae of the atlantic and pacific coasts of North America. Part II. Rhodospermeae. *Smithsonian Contributions to Knowledge* 5 (5): [i–ii], [1]–258, pls. XIII–XXXVI.
- Harvey, W.H. (1855) Some account of the marine botany of the colony of western Australia. *Transactions of the Royal Irish Academy* 22: 525–566.
- Harvey, W.H. (1859a) *Phycologia Australica*. Vol. 2. Lovell Reeve & Co., London, pp. i–viii, pls. LXI–CXX.
- Harvey, W.H. (1859b) Algae. In: Hooker, J.D. (Ed.) *The Botany of the Antarctic Voyage of H.M. discovery ships Erebus and Terror*. Part III. Vol. II. Flora Tasmaniae, pp. 282–343, pls. CLXXXV–CXCVI.
- Harvey, W.H. (1863) *Phycologia australica*. Vol. 5. Lovell Reeve, London, pp. [i]–x, v–lxxiii, pls. CCXLI–CCC.
- Hauck, F. (1883) *Die Meeresalgen Deutschlands und Oesterreichs* 2: 113–320.
- Hawkes, M.W. & Scagel, R.F. (1986) The marine algae of British Columbia and Northern Washington: Division Rhodophyta (Red Algae), Class Rhodophyceae, Order Rhodymeniales. *Canadian Journal of Botany* 64: 1549–1580.
<http://dx.doi.org/10.1139/b86-158>
- Hommersand, M.H. & Fredericq, S. (1990) Sexual Reproduction and Cystocarp Development. In: Cole, K.M. & Sheath, R.G. (Eds.) *Biology of the Red Algae*. Cambridge University Press, pp. 305–345.
- Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–5.
<http://dx.doi.org/10.1093/bioinformatics/17.8.754>
- Huisman, J.M. (1996) The red algal genus *Coelarthrum* Børgesen (Rhodymeniaceae, Rhodymeniales) in Australian seas, including the description of *Chamaebotrys* gen. nov. *Phycologia* 35: 95–112.
<http://dx.doi.org/10.2216/i0031-8884-35-2-95.1>
- Huisman J.M. (2000) *Marine plants of Australia*. University of Western Australia Press, Nedlands, 300 pp.
- Huisman, J.M. & Walker, D.I. (1990) A catalogue of the marine plants from Rottne Island, Western Australia, with notes on their distribution and biogeography. *Kingia* 1: 365–481.
- Irvine, D.E.G. & Guiry, M.D. (1980) Taxonomy of the Rhodymeniales, In: Desikachary, T.V. & Raja Rao, V.N. (Eds.) *Taxonomy of Algae. Papers Presented at the International Symposium on Taxonomy of Algae, Centre of Advanced Study in Botany, University of Madras*. Univ. Madras, Madras, India, pp. 287–303.
- Kraft, G.T. & Woelkerling, W.J. (1990) Rhodophyta. In: Clayton, M.N. & King, R.J. (Eds.) *Biology of Marine Plants*. Longman Cheshire, Melbourne, pp. 41–85.
- Kützing, F.T. (1843) *Phycologia generalis*. Leipzig, 458 pp.
- Kylin, H. (1931) Die Florideenordnung Rhodymeniales. *Lunds Universitets Arsskrift, N. F. Avdeling 2* 27 (11): 1–48.
- Kylin, H. (1956) *Die Gattungen der Rhodophyceen*. C.W.K. Gleerups Fölag, Lund, Sweden, 673 pp.
- Lamouroux, J.V.F. (1813) Essai sur les genres de la famille des thassiophytes non articulées. *Annales Muséum National D'Histoire Naturelle, par les professeurs de cet établissement* 20: 21–47, 115–139, 267–293.
- Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29: 1695–1701.
<http://dx.doi.org/10.1093/molbev/mss020>
- Le Gall, L., Dalen, J.L. & Saunders, G.W. (2008) Phylogenetic analyses of the red algal order Rhodymeniales support recognition of the Hymenocladaceae fam. nov., Fryellaceae fam. nov., and *Neogastroclonium* gen. nov. *Journal of Phycology* 44: 1556–1571.
<http://dx.doi.org/10.1111/j.1529-8817.2008.00599.x>
- Lin, S.M., Fredericq, S. & Hommersand, M.H. (2012) Developmental, phylogenetic and systematic studies of *Apoglossum* and *Paraglossum*, Apoglosseae, trib. nov. (Delesseriaceae, Rhodophyta). *European Journal of Phycology* 47: 366–383.
<http://dx.doi.org/10.1080/09670262.2012.719164>
- Linnaeus, C. (1758) *Systema Naturae*. Vol. I. Holmiæ, pp. [1–4], 1–824.
- Littler, D.S. & Littler, M.M. (2000) *Caribbean Reef Plants*. OffShore Graphics, Inc., Washington, D. C., 542 pp.
- Lozada-Troche, C., Ballantine, D.L. & Ruiz, H. (2010) *Cresia opalescens* gen. et sp. nov. (Rhodymeniaceae, Rhodophyta) from Puerto Rico, Caribbean Sea. *Cryptogamie Algologie* 31: 293–303.

- Nelson, W.A. & Adams N.M. (1984) Marine Algae of the Kermadec Islands. *Natural Museum of New Zealand Miscellaneous Series* 10: 1–29.
- Norris, J.N. & Ballantine, D.L. (1995) Two new species of the red alga *Chrysymenia* Agardh (Rhodymeniales: Rhodomeniaceae) from the tropical western Atlantic. *Proceedings of the Biological Society of Washington* 108: 153–165.
- Norris, R.E. (1989) Natalian *Botryocladia* (Rhodymeniales, Rhodophyceae) including description of a new long axis-forming species. *Botanica Marina* 32: 131–148.
<http://dx.doi.org/10.1515/botm.1989.32.2.131>
- N'Yeurt, A.D.R. & Payri, C.E. (2009) Four new species of Rhodophyceae from Fiji, Polynesia and Vanuatu, South Pacific. *Phycological Research* 57: 12–24.
<http://dx.doi.org/10.1111/j.1440-1835.2008.00517.x>
- Okamura, K. (1936) *Nippon Kaiso Shi* (Descriptions of Japanese algae). Uchida Rokakuho Publishing House, Tokyo, 990 pp.
- Paradis E., Claude, J. & Strimmer, K. (2004) APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics* 20: 289–290.
<http://dx.doi.org/10.1093/bioinformatics/btg412>
- Payri, C., N'Yeurt, A.D.R. & Orempuller, J. (2000) *Algae of French Polynesia. Algues de la Polynésie française*. Au Vent des Iles Editions, Tahiti, 320 pp.
- Postels, A. & Ruprecht, F. (1840) Illustrationes algarum in itinere circum orbem jussu imperatoris Nicolai I. Typis Eduardi Pratz., Petropoli [St. Petersburg], pp. [i–vi] + [i]+ iv + 28. [1–2, index], [Latin:] [–iv], [1]–22, [1–2, index], 40 pls.
- Puillandre, N., Lambert, A., Brouillet, S. & Achaz, G. (2011) ABGD, Automatic Barcode Discovery for primary species delimitation. *Molecular Ecology*. Available from: <http://www.wabi.snv.jussieu.fr/public/abgd/>
- Rambaut, A. & Drummond, A. (2014) Tracer v. 1.6. Available from: <http://tree.bio.ed.ac.uk/software/tracer>.
- Richards, J.L., Gabrielson, P.W. & Fredericq, S. (2014) New insights into the genus *Lithophyllum* (Lithophylloideae, Corallinaceae, Corallinales) from deepwater rhodolith beds offshore the NW Gulf of Mexico. *Phytotaxa* 190 (1): 162–75.
<http://dx.doi.org/10.11646/phytotaxa.190.1.11>
- Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
<http://dx.doi.org/10.1093/bioinformatics/btg180>
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.
<http://dx.doi.org/10.1093/sysbio/sys029>
- Saunders, G.W.I., Strachan, M. & Kraft, G.T. (1999) The families of the order Rhodymeniales (Rhodophyta): a molecular-systematic investigation with a description of Faucheaceae fam. nov. *Phycologia* 38: 23–40.
<http://dx.doi.org/10.2216/i0031-8884-38-1-23.1>
- Saunders, G.W., Wilkes, R.J. & Guiry, M.D. (2007) A nuclear small-subunit ribosomal DNA perspective on the taxonomic affinities of *Maripelta* (Rhodymeniales, Rhodophyta). *Cryptogamie Algologie* 28: 191–194.
- Saunders, G.W. & McDonald, B. (2010) DNA barcoding reveals multiple overlooked Australian species of the red algal order Rhodymeniales (Florideophyceae), with resurrection of *Halopeltis* J. Agardh and description of *Pseudohalopeltis* gen. nov. *Botany* 88: 639–667.
<http://dx.doi.org/10.1139/B10-038>
- Schmidt, W.E. (2009) *Systematics of the Red Algal Order Rhodymeniales with an Emphasis on Taxa from the Gulf of Mexico*. Unpubl. Ph.D. Dissertation, University of Louisiana at Lafayette.
- Schneider, C.W. & Lane, C.E. (2008) Notes on the Marine algae of the Bermudas. 9. The genus *Botryocladia* (Rhodophyta, Rhodymeniaceae), including *B. bermudana*, *B. exquisita* and *B. flookii* spp. nov. *Phycologia* 47: 614–629.
<http://dx.doi.org/10.2216/08-44.1>
- Sherwood, A., Kurihara, A., Conklin, K., Sauvage, T. & Presting, G. (2010) The Hawaiian Rhodophyta Biodiversity Survey (2006–2010): a summary of principal findings. *BMC plant Biology* 10: 258.
<http://dx.doi.org/10.1186/1471-2229-10-258>
- Silva, P.C. (1980) Remarks on red Algal Nomenclature VI. *Taxon* 29: 121–145.
<http://dx.doi.org/10.2307/1219605>
- Silva, P.C., Basson, P.W. & Moe, R.L. (1996) Catalogue of the benthic marine Algae of the Indian Ocean. *University of California Publications in Botany* 79: 1–1259.
- Sparling, S.R. (1957) The structure and the reproduction of some members of the Rhodymeniaceae. *University of California Publications in Botany* 29: 319–396.
- Stamatakis, A. (2006) RAxML-VI-HPC: Maximum Likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.

<http://dx.doi.org/10.1093/bioinformatics/btl446>

- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* 28: 2731–2739.
<http://dx.doi.org/10.1093/molbev/msr121>
- Taylor, W.R. (1960) *Marine Algae of the Eastern Tropical and Subtropical Coast of the Americas*. University of Michigan Press, Ann Arbor, 870 pp.
- Weber-van Bosse, A. (1928) *Liste des algues du Siboga, IV. Rhodophyceae. Troisième partie. Gigartinales et Rhodymeniales et tableau de la distribution des Chlorophycées, Phaeophycées et Rhodophycées de l'Archipel Malaisien*. Siboga-Expeditie Monographie 59d. E.J. Brill., Leiden, pp. 393–533, figs 143–213, pls XI–XVI.
- Wilkes, R.J., McIvor, L. & Guiry, M.D. (2005) The taxonomic position of *Maripelta rotata* (Rhodymeniaceae, Rhodophyta). *Cryptogamie Algologie* 26: 67–75.
- Womersley, H.B.S. (1950) The Marine Algae of Kangaroo Island. III. List of species 1. *Transactions of the Royal Society of South Australia* 73: 137–197.
- Womersley, H.B.S. (1996) *The Marine Benthic Flora of Southern Australia. Rhodophyta. Part IIIB. Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales*, Australian Biological Resources Study, Canberra, 392 pp.
- Wynne, M.J. (2005) *Chrysymenia tigillis* sp. nov. (Rhodymeniales, Rhodophyta) from the Sultanate of Oman, with a census of currently recognized species in the genus *Chrysymenia*. *Phycological Research* 53: 215–223.
<http://dx.doi.org/10.1111/j.1440-1835.2005.tb00374.x>
- Wynne, M.J. (2013) An older name for *Lomentaria baileyana* (Harvey) Farlow (Rhodymeniales, Rhodophyta). *Brittonia* 65: 113–117.
<http://dx.doi.org/10.1007/s12228-012-9267-8>
- Zanardini, G. (1863) Iconographia Phycologica Adriatica ossia scelta di ficee nuove o più rare del mare Adriatico, IV. *Memorie del reale Istituto Veneto di Scienze, Lettere ed Arti* 11: 269–306.