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Systematics of the Gracilariales (Rhodophyta) including new subfamilies, tribes, subgenera, and two new genera, *Agarophyton gen. nov.* and *Crassa gen. nov.*

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Abstract

The Gracilariales is a red macroalgal order and the main global source of the economically important agar, a marine phycocolloid. Independent comparative morphological and molecular phylogenetic studies over the last 20 years have revealed the existence of seven major clades recognizable as distinct genera. Of these major clades only four free-living genera have been widely accepted taxonomically: *Curdiea, Melanthalia, Gracilariopsis*, and *Gracilaria*. Three other clades comprise the reinstatement of the genus *Hydropuntia* and the proposal of two new genera, *Agarophyton* and *Crassa*, described herein. Based on new *rbc*L DNA sequences, and along with a reassessment of published comparative morphological and molecular phylogenetic studies, we argue that the latter three genera represent distinct evolutionary lineages in the Gracilariaceae, and propose a new classification for the order Gracilariales. Our new proposal incorporates the most current understanding of the evolutionary history of the order, establishes a natural and stable classification system, and provides the basis for the recognization of intra-family ranks. Our classification scheme reconciles all molecular phylogenetic studies published to date.

Keywords: Agar, *Agarophyton*, *Crassa*, *Gracilaria*, Gracilariaceae, *Hydropuntia*, marine algae, phylogeny, *rbc*L, Rhodophyta, seaweed

Introduction

The marine red algal order Gracilariales Fredericq & Hommersand (1989a) is one of the ~42 current orders in the phylum Rhodophyta (Guiry & Guiry 2018). The Gracilariales have a wide geographic distribution, ranging from the tropical to polar regions. Some species in the order are the main source of phycocolloid agar in the world (Armisen 1995; Zemke-White & Ohno 1999). Phycocolloids are water-soluble, gel-forming polysaccharides produced by various macroalgae and used extensively in the microbiological, pharmaceutical, chemical, medical, molecular, and food industries (Oliveira *et al.* 2000). The vast majority of Gracilariales species are characterized by plants displaying robust, cylindrical to flat erect thalli, ranging between a few centimeters to 40 cm tall. When present, Gracilariales are often conspicuous members of the marine benthic communities, performing relevant ecological roles in coastal marine ecosystems (e.g., Smith *et al.* 2004; Thomsen *et al.* 2013).

The Gracilariales contain a single family, the Gracilariaceae Nägeli (1847), with up to five free-living genera: *Curdiea* Harvey (1855: 333), *Gracilaria* Greville (1830: 121), *Gracilariopsis* E.Y. Dawson (1949: 40), *Hydropuntia* Montagne (1842: 7), *Melanthalia* Montagne (1843: 296), and four parasitic genera (Gerung *et al.* 1999, 2002): *Congracilaria* Yamamoto (1986: 287), *Gracilariocolax* Weber-van Bosse (1928: 394–396), *Gracilariophila* Setchell et Wilson in Wilson (1910: 81), and *Holmsella* Sturch (1926: 604). Among the non-parasitic genera, the Australasian *Curdiea* and *Melanthalia* have not demonstrated taxonomic ambiguities at the generic level. In contrast, *Gracilaria*, *Gracilariopsis* and *Hydropuntia* have had a more debatable taxonomic history (detailed in Liao & Hommersand 2003;

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Gurgel & Fredericq 2004). Some taxonomists have advocated merging all three genera into a single, all-encompassing genus, e.g., *Gracilaria* sensu Gargiulo *et al*. (1992) or sensu Abbott (1995), while others recognize only *Gracilariopsis* as a distinct taxon from a *Gracilaria-Hydropuntia* complex.

In the past decade, many taxonomic studies have confirmed the generic distinctiveness of *Gracilariopsis* based on morphological (Fredericq & Hommersand 1989b, 1990b; Gurgel *et al*. 2003a; Hau & Lin 2006; Norris & Gurgel 2014) and molecular evidence (Bird *et al*. 1992, 1994; Goff & Coleman 1994; Bellorin *et al*. 2002; Gurgel *et al*. 2003a,b; Gurgel & Fredericq 2004; Iyer *et al*. 2005; Bouzon *et al*. 2000). However, the taxonomic status of *Hydropuntia* as a distinctive genus from *Gracilaria sensu stricto,* has remained questionable (e.g., Abbott *et al.* 1991, Bellorin *et al.* 2002, Lyra *et al*. 2015, Iha *et al*. 2018). Several studies have also suggested that a cluster of *Gracilaria* species centered around *G. chilensis* Bird, McLachlan et E. C. Oliveira (1986: 2928–2931) may represent yet another undescribed genus as noted and proposed by Ryan & Nelson (1991), Nelson & Ryan (1991), Liao & Hommersand (2003), and Gurgel & Fredericq (2004).

The taxonomy of the genus *Hydropuntia* has a dynamic history. Montagne described the genus with a single species (generitype: *Hydropuntia urvillei* Montagne, 1842: 7) based on the presence of pronounced constrictions along the thallus and at the base of branches and branchlets. Agardh (1852: 581–583, under "XVC. *Corallopsis*" on p. 583, not p. "483" that was mistakenly numbered) merged *Hydropuntia* Montagne (1842) with *Corallopsis* Greville (1830: liii), and Kylin (1956) later placed *Corallopsis* in synonymy with *Gracilaria.* In 1963 Chang & Xia (1963: 120) created *Polycavernosa* (generitype: *Polycavernosa fastigiata* C.F. Chang et B-.M. Xia 1963: 120) to include *Gracilaria* species with confluent, branched spermatangial conceptacles deeply immersed within the thallus. *Hydropuntia urvillei* was later placed in *Polycavernosa* by Xia & Abbott (1987, as *P. urvillei* B.-M. Xia et I.A. Abbott). Noticing the creation of a superfluous name, Wynne (1989) recognized *H. urvillei* as the generitype of *Hydropuntia* and based on nomenclatural priority, he reinstated *Hydropuntia*, subsuming *Polycavernosa* as a synonym. Despite its reinstatement, *Hydropuntia* has been considered a synonym of *Gracilaria* by some phycologists (e.g., Abbott *et al.* 1991; Gargiulo *et al*. 1992, Abbott 1995, Plastino & Oliveira 1997, Bellorin *et al*. 2002, Lyra *et al*. 2015, Iha *et al*. 2018). Still others recognized it as a distinct genus, either as *Polycavernosa* (e.g., Chang & Xia 1963; Xia [Bangmei] and Abbott 1985; Fredericq & Norris 1985) or *Hydropuntia* (e.g., Xia & Abbott 1987; Fredericq & Hommersand 1990b; Kapraun 1993; Wynne 1989; Gurgel & Fredericq 2004; Conklin *et al*. 2014, Yang & Kim 2015; Núñez-Resendiz *et al*. 2015), or as a subgenus of *Gracilaria* (e.g., Tseng & Xia 1999).

The initial disagreement on the distinction of *Hydropuntia-Gracilaria* is the result of apparent incongruence between morphological and molecular data. Initial reports describing spermatangial characters that are diagnostic of both genera started the debate (Abbott *et al*. 1991). It is well known that a morphology-based taxonomy of *Gracilaria sensu lato* species is a challenging endeavor due to the subtlety of developmental and anatomical features to differentiate a large number of species, presence of morphological homoplasies in both vegetative or reproductive characters, and the existence of cryptic and pseudo-cryptic species complexes. Recent molecular surveys conducted on marine red macroalgae, such as DNA barcode projects, have confirmed the existence of a plethora of cryptic, pseudo-cryptic, overlooked or misidentified, often sympatric species that indicate a much higher diversity than was previously recognized (e.g., Payo *et al*. 2013), including cases in the Gracilariaceae (Gulbransen *et al*. 2012). Morphological analyses of species-complexes treated as a single species inevitably lead to unnatural classification schemes (e.g. Lyra *et al*. 2015). In light of these new revelations, old reports of morphological overlap between *Gracilaria* and *Hydropuntia* species most likely represent the presence of multiple similar-looking species within a single collection that were assumed to belong to a single morphological entity.

Independent molecular phylogenetic analyses derived from a variety of nuclear, chloroplast, and mitochondrial markers, including multi-marker approaches, have unequivocally shown that the two evolutionary lineages represented by the genus *Hydropuntia* are distinct from *Gracilaria sensu stricto* (18S rDNA: Bird *et al*. 1992; *rbc*L: Gurgel & Fredericq 2004; *cox*2-*cox*3 spacer: Nüñez-Resendiz *et al*. 2015; *cox*1: Conklin *et al*. 2014; multi-gene concatenated 5-markers: Lyra *et al*. 2015). Furthermore, these studies have shown that *Gracilaria chilensis, G. tenuistipitata* Chang et B.-M. Xia, and *G. vermiculophylla* (Ohmi) Papenfuss form a distinct and basal evolutionary lineage within the *Gracilaria sensu lato* complex, worth recognition as a distinct genus (see tree topologies in Bird *et al*. 1992, 1994; Goff *et al*. 1994; Bellorin *et al*. 2002; Byrne *et al*. 2002; Cohen *et al*. 2004; Gurgel & Fredericq 2004; Lyra *et al*. 2015), a conclusion that corroborates previous morphological studies (i.e., Bird *et al*. 1990; Ryan & Nelson 1991; Nelson & Ryan 1991). To date the taxonomic significance of this basal lineage and its formal recognition as a new genus has not been done.

Among all molecular markers used in intra-ordinal Gracilariales systematics, the chloroplast-encoded *rbc*L gene has consistently provided well-supported phylogenetic topologies and far more resolution at the generic and species levels (e.g., Gurgel & Fredericq 2004; Gurgel *et al*. 2003a,b; Gurgel *et al*. 2004a,b; Gurgel *et al*. 2008; Hommersand & Freshwater 2009; Lin 2008; Muangmai *et al*. 2014). Therefore, *rbc*L-based phylogenies have allowed a reassessment of a natural classification scheme in the Gracilariales.

In the last decade, many distinct species have been sequenced, and this large molecular systematic sampling enables a reevaluation of the systematics and phylogeny of the Gracilariales. In this study we propose a new natural classification of the Gracilariales on the basis of *rbc*L DNA sequence analyses, recognizing two new genera, *Agarophyton* gen. nov., and *Crassa* gen nov., and the reinstated *Hydropuntia* as a distinct genus.

Material and methods

Morphological Analyses and Vouchers. Morphological data were primarily assessed from specimens of Gracilariaceae directly studied by the authors. Voucher specimens were deposited at LAF, AD, and US Alg. Coll. (herbarium abbreviations follow those of Holmgren *et al*. 1990; Thiers 2016). Species identifications were based on comparative morphology, original descriptions, critical analysis of published literature, and on the type method (e.g., Silva 1952; McNeill *et al*. 2012). Names of authors of taxa follow those given by Brummitt & Powell (1992).

Molecular Data Acquisition. Newly generated sequences were produced from silica gel-dried specimens. DNA extractions were done using the DNeasy Plant DNA Minikit (Qiagen, Germany). Protocols for gene amplification, automated sequencing, and multiple sequence alignment are identical to those given in Gurgel & Fredericq (2004).

Sequence Alignment. Two Gracilariaceae alignments were constructed. The first larger alignment contained 68 *rbc*L sequences corresponding to 67 members of the Gracilariales and one sequence of *Rhodymenia pseudopalmata* (J.V. Lamouroux) P.C. Silva (1952: 265) as an outgroup. Different outgroup sequences were tested in preliminary analyses and the use of *R. pseudopalmata* produced the most topologically stable trees between distinct analytical methods (i.e., maximum likelihood and Bayesian) and with better supported internal nodes (data not shown). This alignment was used to assess relationships within Gracilariales. The second alignment corresponds to a smaller dataset comprised of only 36 selected members of the Gracilariales. This alignment was designed to clarify the phylogenetic relationships within the genus *Gracilaria sensu lato* and the generic relationships within this group. For this analysis, six to seven taxa of each genus were used, along with two species of *Gracilariopsis* as outgroups. Species identification, specimen collection information, and GenBank accession numbers are listed in Appendix 1. Newly generated *rbc*L sequences were compiled with Sequencher v 4.9 (Gene Codes Corp., Ann Arbor, MI, USA). DNA sequence alignments were built using ClustalW (Larkin *et al*. 2007) implemented in MEGA 5.2.2 (Tamura *et al*. 2011).

Phylogenetic Analysis. Presence of phylogenetic signal was assessed via the skewness test (or g_1 statistics, Hillis & Huelsenbeck 1992; Hillis *et al*. 1993) using 100,000 random trees. Datasets extensively skewed to the left were considered to contain significant amounts of hierarchical structure or phylogenetic signal. For both alignments, no codon partition strategies were implemented as previous partitioned analyses failed to improve results (i.e., improve phylogenetic support, data not shown). The best model of nucleotide substitution identified for both alignments was the GTR+I+G model by jModeltest 2.1.4 (Darriba *et al*. 2012). This model was selected by all weighted and unweighted versions of Akaike and Bayesian information criteria (including the Decision Theory method) using a BIONJ base tree for likelihood calculations, the 88 substitution models option without a maximum likelihood optimization approach. Bayesian phylogenetic analyses were conducted on both alignments using MrBayes v.3.04 (Ronquist *et al*. 2012), two independent runs of four chains of the Markov Chain Monte Carlo (one cold, three hot), sampling 1 tree every 1000 generations for 10 million generations, starting from random trees and using default prior parameters. Posterior probabilities were obtained via majority rule consensus tree as implemented by PAUP* (Swofford 2002) computed from the trees saved after the burn-in removal. Burn-in was visualized by plotting the log likelihood values of each tree against generation numbers and finding the exact point of search convergence on that coincided on both Markov Chain Monte Carlo independent runs. This visualization was done in either Geneious Pro v.5.5.9 (Drummond *et al*. 2012) or Tracer v.1.6. Tree topologies were examined and exported in FigTree v.1.4.2 (Rambout 2009).

Results

Phylogeny. The 68 taxa alignment contained 1,459 base pairs (bp) of which 929 bp were constant (64%) and 530 bp were parsimony-informative (36%). Tree lengths of 100,000 randomly generated trees had a skewed distribution

($g_1 = -0.6347$, $P < 0.01$), indicating the presence of non-random structure. The Bayesian trees for the long and short datasets were fully resolved (Figs. 1, 2). The long dataset tree is represented by one of the 18,002 trees saved after burn-in removal (Fig. 1). In the long tree, seven well-supported major lineages were recognized, each corresponding to a distinct genus. Thus, all non-parasitic genera herein recognized in the Gracilariales formed well-supported clades: the sister genera *Curdiea* (PP = 1.0) and *Melanthalia* (PP = 1.0); *Gracilariopsis* (PP = 0.94), *Hydropuntia* (PP = 1.0), *Crassa* gen. nov. (PP = 0.99), *Gracilaria* (PP = 1.0) and *Agarophyton* gen. nov. (PP = 0.98).

The short, 36-taxa alignment contained 1,467 base pairs (bp). Tree lengths of 100,000 randomly generated trees had a skewed distribution ($g_1 = -0.5776$, $P < 0.01$), indicating the presence of non-random structure. The short dataset tree is also represented by one of the 18,000 trees saved after a 20% burn-in removal (Fig. 2). In the short dataset results, three well-supported clades were recognized within *Gracilaria sensu lato*, each corresponding to a distinct genus: *Gracilaria, Hydropuntia*, *Crassa* gen. nov., and *Agarophyton* gen. nov. (Fig. 2).

Gracilariales Fredericq et Hommersand, 1989a: 225

Gracilariaceae Nägeli, 1847: 240

Gracilariaceae subfam. Gracilarioideae Stizenberger, 1860: 41, *emend.*

TYPE: *Gracilaria compressa* (C. Agardh) Greville 1830: 125, basionym: *Sphaerococcus compressus* C. Agardh 1822: 308; which is now *Gracilaria bursa-pastoris* (S.G. Gmelin) P.C.Silva 1952: 265; basionym: *Fucus bursa-pastoris* S.G.Gmelin 1768: 121, pl. VIII [8]: fig. 3. This is the type species for the genus, subfamily, family, and order.

DIAGNOSIS: Free-living or parasitic. Tetrasporangia either in sori or not associated with any special development of cortical cells; spermatangial parent cells of outer cortical, subcortical and intercalary cell origin, distributed either as conceptacles of different depths and shapes (i.e., cavities within the thallus) or cortical and superficial, without the formation of nemathecia; gonimoblast individual cells often irregular in shape, gonimoblast mass not filling the entire cystocarp cavity; carposporangia formed in short files; transition between gonimoblasts and carposporangia gradual or pronounced at different stages of maturity, mature carposporangia large and conspicuously differentiated from mature gonimoblasts.

GENERA IN SUBFAM. GRACILARIOIDEAE: *Agarophyton* (herein), *Crassa* (herein), *Gracilaria* (including *Congracilaria* Yamamoto*, Gracilariophila* Setchell et H.L.Wilson - in part, and *Gracilariocolax* Weber-van Bosse), *Gracilariopsis* Dawson (including *Gracilariophila* in part) and *Hydropuntia* Montagne.

REMARKS: On the basis of phylogenetic results only, *Congracilaria* and *Gracilariophila* should be subsumed into one of three of the genera in the subfam. Gracilarioideae (Ng *et al*. 2014, 2015, 2016). The generitype *Congracilaria babae* H. Yamamoto (1986: 287) was treated as belonging in the genus *Gracilaria* by Ng *et al*. (2014, as *Gracilaria babae* (H. Yamamoto) Ng, P.-K. P.-E.Lim et S.-M.Phang). Ng *et al*. (2014) also suggested *Gracilariocolax* Weber-van Bosse (1928) to be congeneric with *Gracilaria*. Due to their highly modified morphology, we refrain from making a taxonomic opinion on the alloparasite *Holmsella* Sturch (Fredericq & Hommersand 1990c).

Gracilarioideae tribe Gracilarieae Willkomm, 1854: 147, *emend.*

DIAGNOSIS: Spermatangia always forming cavities of differing shapes and depths into the thallus; spermatangial parent cells interacting with either medullary cells or cortical cells; cystocarps with tubular gonimoblast cells connecting gonimoblast mass to the pericarp.

GENERA IN TRIBE GRACILARIAEAE: *Agarophyton, Crassa, Gracilaria*, *Hydropuntia.*

Gracilaria Greville 1830:iiv, 121

GENERITYPE: *Gracilaria bursa-pastoris* (S.G. Gmelin) P.C. Silva (1952: 265)

BASIONYM: *Fucus bursa-pastoris* S.G. Gmelin 1768: 121. Note: the conserved generitype is *Gracilaria compressa* (C. Agardh) Greville (1830: 121); basionym: *Sphaerococcus compressus* C. Agardh (1822: 308), but see Steentoft *et al.* (1991: 633), Silva (1994: 263), and Silva *et al*. (1996: 917).

PERTINENT SYNONYMS: *Congracilaria* Yamamoto, *Gracilariophila* Setchell et H.L.Wilson (in part), *Gracilariocolax* Weber-van Bosse.

TYPE LOCALITY: Cádiz, Iberian Peninsula, southwestern Spain.

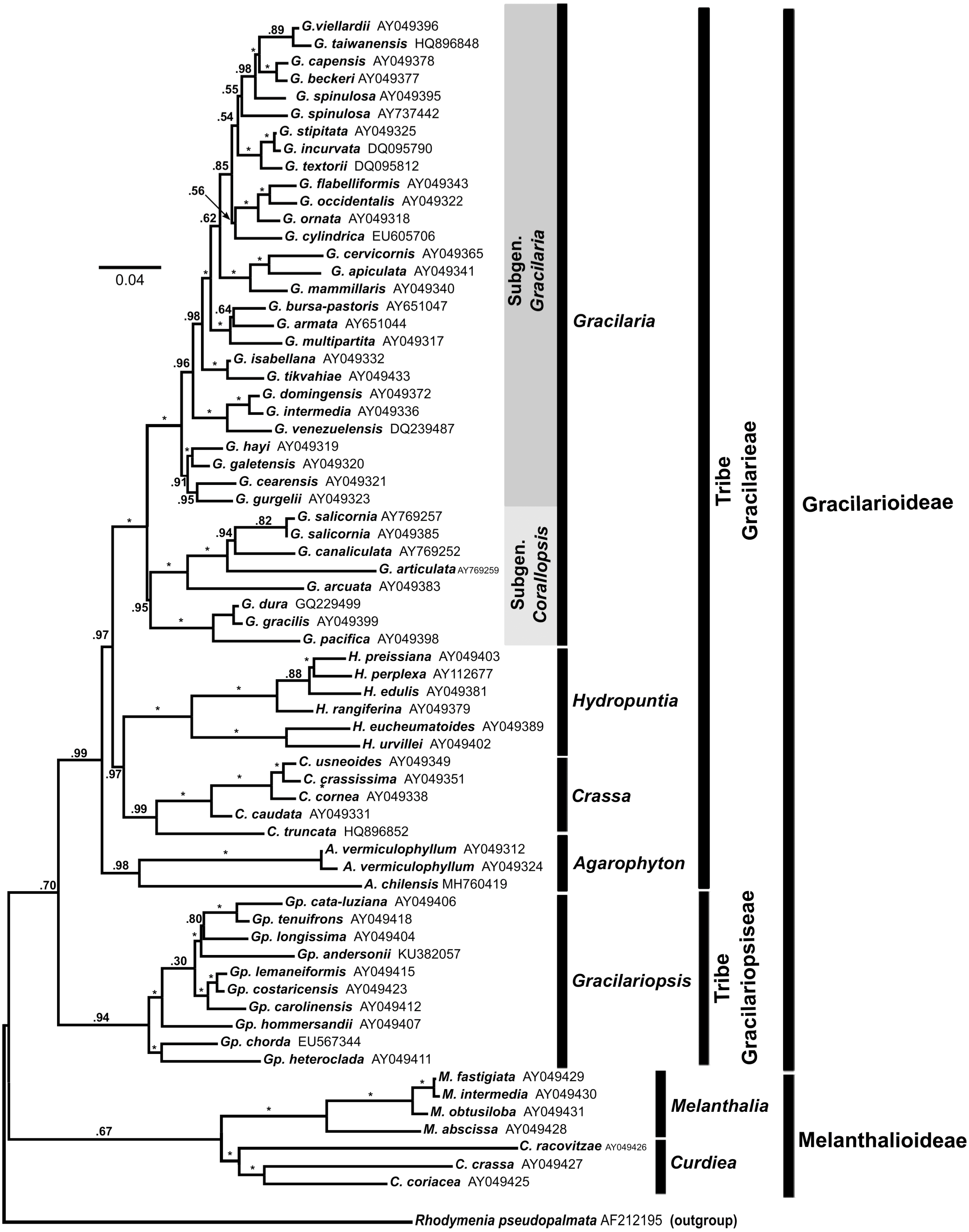

FIGURE 1. One of 18,002 ML trees of the marine red algal order Gracilariales derived from a Bayesian phylogenetic analysis (after burn-in removal). Molecular data used: *rbc*L DNA sequence alignment composed of 68 taxa and 1,459 bp. New taxonomic proposal for the order is presented. Numbers above branches correspond to Bayesian posterior probabilities (PP); * = 1.0 PP.

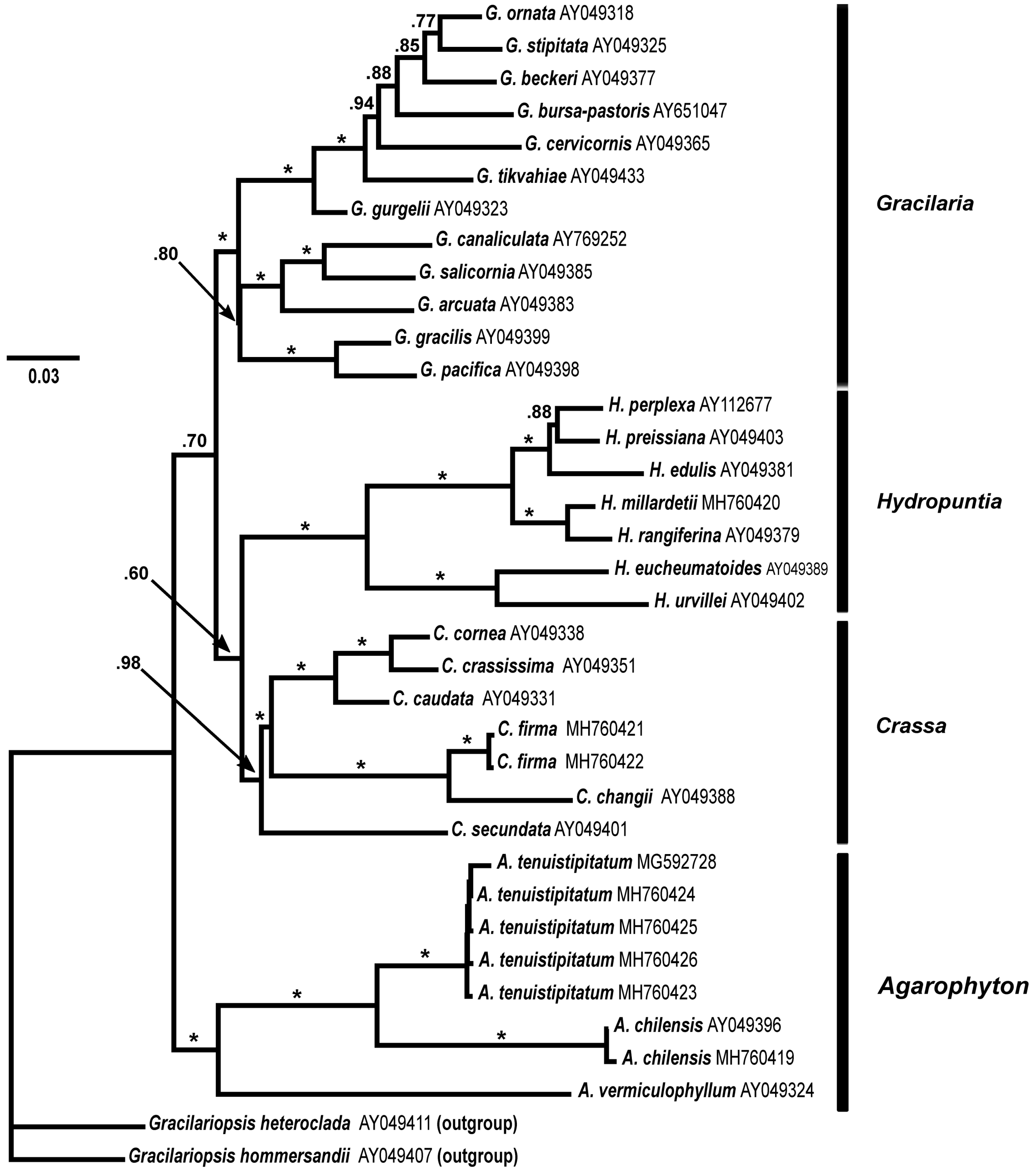

FIGURE 2. One of 18,000 ML trees of the marine red algal order Gracilariales derived from a Bayesian phylogenetic analysis (after burn-in removal). *Rbc*L sequence alignment composed of 36 taxa and 1,467 bp focusing on the relationhsips inside the large genus-complex *Gracilaria sensu lato*. New taxonomic proposal for the genera within *Gracilaria sensu lato* is presented. Numbers above branches correspond to Bayesian posterior probabilities (PP); * = 1.0 PP.

DIAGNOSIS: Tetrasporangia superficial, in both unmodified cortex or in sori. Spermatangial conceptacles of the shallow cortical type only (i.e., *textorii*-type or the *verrucosa*-type *sensu* Yamamoto 1975, 1978, 1984). Gonimoblast filaments consisting of vacuolated cells in center towards the base, becoming elongated and highly branched towards the outside and bearing carposporangia in branched chains, the carposporangia cut off by oblique division with the carpospores terminal, maturing basipetally; tubular nutritive cells numerous, variable in diameter, connecting to outer pericarp, initially fusing with single pericarp cell that may fuse progressively with neighboring pericarp cells, extending the length of the tubular nutritive cells to form a tube-shaped pericarp fusion cell that sometimes leaves behind remnant pit connections; carpogonial fusion cell with numerous enlarged nuclei, extending moderately through fusion with adjoining inner pericarp cell, becoming embedded longitudinally in the inner pericarp; cystocarp cavity formed schizogenously as the gonimoblasts grow by the dissolution of pit connections between inner and outer gonimoblast filaments; inner pericarp composed of straight cell rows, five to seven cells long, in which each cell contains an enlarged nucleus; fusion cell persisting or disintegrating at the mature stages of cystocarp development.

Gracilaria* subgen. *Gracilaria

DIAGNOSTIC FEATURES: Shallow cup-shaped cortical spermatangial conceptacles (i.e., *textorii*-type only, *sensu* Yamamoto 1975, 1978, 1984) and a cystocarp placenta composed of either disorganized clusters of gonimoblast cells of different cell sizes or gonimoblasts forming organized parallel cellular columns flabellate in shape in cross section. The latter character considered an autapomorphy in this subgenus (i.e., observed in *Gracilaria flabelliformis* (Gurgel *et al*. 2004b) and *Gracilaria* cf. *vieillardii* (Withell *et al*. 1994). Post-fertilization fusion cell persistent and often conspicuous (e.g., in *G. tikvahiae*).

PERTINENT SPECIES IN *GRACILARIA* SUBGEN. *GRACILARIA*: ***Gracilaria apiculata*** P. Crouan et H. Crouan; ***G. apiculata* subsp. *candelabriformis*** Gurgel, Fredericq et J.N. Norris; ***G. beckeri*** (J. Agardh) Papenfuss; ***G. bursa-pastoris*** (S.G.Gmelin) P.C.Silva; ***G. brasiliensis*** Gurgel et Yoneshigue-Valentin; ***G. capensis*** F.Schmitz ex Mazza; ***G. cervicornis*** (Turner) J.Agardh; ***G. coronopifolia*** J.Agardh, ***G. cuneata*** Areschoug, ***G. curtissiae*** J.Agardh; ***G. flabelliformis*** (P.Crouan et H.Crouan) Fredericq et Gurgel; ***G. flabelliformis* subsp. *aionae*** Gurgel, Fredericq et J.N.Norris; ***G. flabelliformis* subsp. *simplex*** Gurgel, Fredericq et J.N.Norris; ***G. galetensis*** Gurgel, Fredericq et J.N.Norris; ***G. hayi*** Gurgel, Fredericq et J.N.Norris; ***G. intermedia*** J. Agardh; ***G. intermedia* subsp. *ganesana*** Gurgel, Fredericq et J.N.Norris; ***G. gurgelii*** Freshwater (in Hardesty & Freshwater 2018) (referred to as *G. mammillaris* (Montagne) Howe in Gurgel & Fredericq 2004) ; ***G. multipartita*** (Clement) Harvey; ***G. occidentalis*** (Børgesen) M.Bodard, ***G. oliveirarum*** Gurgel, Fredericq et J.N.Norris; ***G. ornata*** Areschoug; ***G. cearensis*** (A.B.Joly et Pinheiro) A.B.Joly et Pinheiro; ***G. spinulosa*** (Okamura) C.F.Chang et B.-M.Xia; ***G. stipitata*** Withell, A.Millar et Kraft; ***G. tikvahiae*** J.McLachlan; ***G. textorii*** (Suringar) De Toni; ***G. venezuelensis*** W.R.Taylor; ***G. vieillardii*** P.C.Silva.; and ***G. yoneshigueana*** Gurgel, Fredericq et J.N.Norris.

Based on other published studies: ***G. hummii*** Hommersand et Freshwater (2009), ***G. stipitata*** Withell, Millar et Kraft (1994), ***G. brasiliensis*** Gurgel et Yoneshigue-Valentin in Gurgel *et al*. (2008), ***G. domingensis*** (Kützing) Sonder ex Dickie (Lyra *et al*. 2015); ***G. baiana*** Lyra, Gurgel, M.C.Oliveira et Nunes in Lyra *et al*. (2015); ***G. suzannae*** Soares, Gurgel et Fujii (2018); ***G. abbottiana*** (Gurgel, unpubl. data); ***G. coppejansii*** Muangmai, Lewmanomont, Prathep, Terada et Zuccarello (2017); ***G. lantaensis*** Muangmai, Zuccarello, Noiraksa et Lewmanomont (2014); ***G. denticulata*** Schmitz ex Mazza (Iyer *et al*. 2005); ***G. taiwanensis*** Lin, Liu et Payri (2012); ***G. huangii*** S.M. Lin, et De Clerck (2006); ***G. cuneifolia*** (Okamura) I.K.Lee et Kurogi (Ardito *et al*. 2017); ***G. parvispora*** Abbott (Ardito *et al*. 2017); ***G. falconii*** Ardito, Núñez-Resendiz, Dreckmann et Sentíes (2017); ***G. silviae*** Lyra, Gurgel, M.C.Oliveira et J.M.C. Nunes in Lyra *et al.* (2015).

***Gracilaria gardneri* (Setchell) Gurgel, J.N. Norris et Fredericq, *comb. nov*.**

BASIONYM: *Gracilariophila gardneri* Setchell 1923: 393.

TYPE LOCALITY: on *Gracilaria cunninghamii* Farlow ex J. Agardh; Santa Monica, Los Angeles County, California, USA.

Gracilaria* subgen. *Corallopsis* Gurgel, J.N. Norris et Fredericq, *stat. et comb. nov.

TYPE: *Corallopsis* Greville 1830: liii.

TYPE SPECIES: *Corallopsis salicornia* (C. Agardh) Greville 1830: liii; basionym: *Sphaerococcus salicornia* C. Agardh, 1820: pl. VI, which is now *Gracilaria salicornia* (C. Agardh) E.Y. Dawson 1954: 4.

TYPE LOCALITY: "*ad litora Unalaschka,*" [Alaska] (Agardh 1820, 1822); probably mistakenly cited, Dawson (1954: 4) noted locale more likely is from Manila Bay, Philippine Islands, and Abbott (1994) stated due to a mix-up of labels.

DIAGNOSIS: Spermatangia confined to deep cortical conceptacles or pits (i.e., the *verrucosa*-type *sensu* Yamamoto 1975, 1978) embedded only in the cortex and not interacting with medullary cells. Gonimoblasts composed of loosely arranged ovoid vacuolated cells bearing clusters of carposporangia at the periphery in short branched chains; nutritive tubular cells extending to top, sides, and base of outer pericarp, multinucleate, inflated towards base, sometimes with more than one tubular cell fusion with pericarp cell; pericarp fusion cells tubular or branched; pericarp cells arranged regularly in young cystocarps, the inner layers darkly staining and stretched laterally at maturity; carpogonial fusion cell multinucleate, cubic to ovoid in young carposporophytes, compressed in older cystocarps, embedded within inner pericarp. Tetrasporangia superficial, not in sori.

REMARKS: The name *Corallopsis* Greville (1830) appears in the same publication as *Gracilaria* and both are validly published names, with the latter conserved (Steentoft *et al*. 1991).

PERTINENT SPECIES IN *GRACILARIA* SUBGEN. *CORALLOPSIS*: ***Gracilaria articulata*** C.F.Chang et B.M.Xia; ***G. dura*** (C.Agardh) J.Agardh; ***G. gracilis*** (Stackhouse) Steentoft, Irvine et Farnham; ***G. canaliculata*** Sonder; ***G. pacifica*** I.A. Abbott; ***G. salicornia*** (C. Agardh) E.Y. Dawson.
Based on other published studies: *G. rhodymenioides* A. Millar (see Muangmai *et al*. (2017).

Agarophyton Gurgel, J.N.Norris et Fredericq, *gen. nov.*

TYPE: ***Agarophyton chilensis* (C.J.Bird, McLachlan et E.C.Oliveira) Gurgel, J.N.Norris et Fredericq, *comb. nov.***
BASIONYM: *Gracilaria chilensis* C.J.Bird, McLachlan et E.C.Oliveira 1986: 2929, figs. 2–13).
HOLOTYPE: NRCC-9131(a), ♀, Bird *et al*. (1986, fig. 2).
TYPE LOCALITY: Penco, Bahía de Concepción, Provincia de Concepción, Región del Biobío, Chile.
HETEROTYPIC SYNONYM: *Gracilaria sordida* W.A. Nelson (1987: 90, figs. 6–9).

DIAGNOSIS: Algae with slender, cylindrical thalli; base crustose; main axis branching variable, subdichotomous to irregular, sometimes secund; secondary branches when present abundant, of variable lengths, also irregularly distributed along the main axes; cortical cells radially elongated, abrupt transition between cortex and medulla. Tetrasporangia cruciately divided. Spermatangial conceptacles of multiple kinds; forming shallow pits developed from cortical cells and flanked by elongated club-shaped cortical cells next to shallow, *chilensis*-type of conceptacles *sensu* Yamamoto (1984); to spermatangial resembling *verrucosa*-like conceptacles but without the cortical cell development as seen in *Gracilaria* subgen. *Corallopsis* keeping a clear separation between medullary cells and spermatangial-parent cells; to more morphologically complex cases of fused medullary conceptacles resembling the *henriquesiana*-type *sensu* Yamamoto (1984). Gonimoblast mass ampulliform or obpyriform, not completely filling the cystocarp cavity; inner gonimoblasts subglobose to oval, smaller outer gonimoblasts gradually giving rise to distinct radial chains of carposporangia at different stages of maturity, outer mature carposporangia obpyriform. Tubular nutritive cells either present or absent, when present tubular cells restricted to gonimoblast cells in vicinity of carpogonial fusion cells linking directly to inner pericarp cells or cortical cells. New tubular cells added at margin of gonimoblast mass as the cystocarp enlarges and carposporophyte develops a v-shaped concave base. New tubular cells particularly prominent along junction between carposporophyte base and pericarp. Multinucleate gametophytic cells enlarging, becoming deeply stained and interconnected by prominent pit connections in the vicinity of fused tubular cells. Pericarp cells contacted by gonimobast tubular cells not fusing with neighboring cells. Cells of sterile gonimoblasts large and pseudoparenchymatous.

EPITHET: The generic name, *Agarophyton* is formed from Malayan and Greek words. *Agar-* is derived from the Malay “agar-agar” (a gelatinous substance from seaweed; see: McHugh 2003) which we have joined with an “*-o-* “ to the Greek *-phyton*, thus the name means “agar-plant.” The type species, *A. chilensis,* and other species of this genus are currently the main sources of agar in the world (Zemke-White & Ohno 1999).

REMARKS: In addition to the generitype, two other species are recognized to belong in *Agarophyton.* A fourth and still undescribed species in this genus has been recognized by Cohen *et al.* (2004) from specimens collected in New Zealand and southern Australia.

PERTINENT SPECIES IN *AGAROPHYTON*:

Agarophyton chilensis (C.J. Bird, McLachlan et E.C.Oliveira) Gurgel, J.N.Norris et Fredericq, *comb. nov.*

BASIONYM: *Gracilaria chilensis* C.J.Bird, McLachlan et E.C.Oliveira 1986: 2928, figs. 2–13.
HOLOTYPE: NRCC-9131 (♀).
TYPE LOCALITY: Penco, SE corner of Bahía Concepción, Concepción Province, Bío Bío Region, Chile.

Agarophyton tenuistipitatum (C.F. Chang et B.-M. Xia) Gurgel, J.N.Norris et Fredericq *comb. nov.*

BASIONYM: *Gracilaria tenuistipitata* C.F.Chang et B.-M.Xia 1976: 102, 161, figs. 6(1–5), 7(1–3), pl. I: fig. 3 (typus).
HOLOTYPE: AST 66-543a (♀); AST 66-534b (♂).
TYPE LOCALITY: Bohe, Bohe Gang (harbor), Dianbai Xian, Guangdong Province, China.

Agarophyton vermiculophyllum (Ohmi) Gurgel, J.N.Norris et Fredericq *comb. nov.*

BASIONYM*:* *Gracilariopsis vermiculophylla* Ohmi 1956: 271, figs. 1–4, pls. 1–2. HOLOTYPE: HAK, *Ohmi-200.*
SYNONYM: *Gracilaria vermiculophylla* (Ohmi) Papenfuss (1967: 101).
TYPE LOCALITY: Gomejima, Akkeshi-ko (shallow estruary adjoins Akkeshi Bay), Hokkaido Is., Japan.

REMARKS: *Gracilaria vermiculophylla* is a highly invasive species. Within the last 20 years, *G. vermiculophylla* has been introduced in the Eastern Pacific and Eastern and Western North Atlantic on numerous occasions by the shipping and import of Japanese oysters to North America and Europe (Bellorin *et al.* 2004; Rueness 2005; Thomsen *et al*. 2006; Freshwater *et al*. 2006; Saunders 2009; Kim *et al*. 2010; Piñón-Gimate *et al*. 2012), or possibly as a component of seaweed/seagrass mixture used as commercial soil conditioner (Abreu *et al*. 2011). The success of *G. vermiculophylla* as an invasive species and known habitat modifier have raised ecological and environmental concerns (Wallentinus & Nyberg 2007; Williams & Smith 2007).

Hydropuntia Montagne (1842: 7)

GENERITYPE: *Hydropuntia urvillei* Montagne (1842: 7)
PERTINENT SYNONYMS: *Corallopsis urvillei* (Montagne) J.Agardh (1876: 410)
Polycavernosa urvillei (Montagne) B.M.Xia et I.A.Abbott (1987: 414)
Gracilaria urvillei (Montagne) I.A. Abbott (in Abbott *et al*. 1991: 23)
TYPE LOCALITY: Toud Island (Warrior Islet), Torres Strait, off Queensland, Australia.

REMARKS: Since its original description (Montagne 1842), the genus *Hydropuntia* has been characterized morphologically and phylogenetically (e.g., Chang & Xia 1963; Fredericq & Norris 1985; Fredericq & Hommersand 1990b; Gurgel & Fredericq 2004, Conklin *et al*. 2014).

DIAGNOSIS: Thalli crassullaceous to cartilaginous, with percurrent axes, slightly compressed, constricted at the nodes. Spermatangial conceptacles of the medullary type (i.e., *Hydropuntia*-type, including other definitions such as the *Polycavernosa*-type, and the *henriquesiana*-type" *sensu* Yamamoto [1984]), scattered, embedded in the cortex and outer medulla; young conceptacles oval, in deep pits surrounded by stretched subcortical cells, becoming lobed as they extend laterally and longitudinally. Cystocarps broad-based, often coming into close contact with the outer pericarp composed of tightly packed fusiform cells bearing short carposporangial chains at periphery. Tubular nutritive cells short, fusing with cells in the inner layer of the outer pericarp that in turn fuse forming tubular pericarp fusion cells in oblique or straight series; outer pericarp thick.

Hydropuntia* subgenus *Hydropuntia

SPECIES SUBGEN. *HYDROPUNTIA*: *Hydropuntia urvillei* Montagne; and *H. eucheumatoides* (Harvey) Gurgel et Fredericq.

Hydropuntia subgenus *Polycavernosa* (C.F. Chang et B.-M. Xia) Gurgel, J.N.Norris et Fredericq, *stat. et subgen. nov.*

TYPE: *Polycavernosa* C.F. Chang et B.-M. Xia 1963: 120.
TYPE SPECIES: *Polycavernosa fastigiata* C.F. Chang et B.-M. Xia 1963: 120, pl. I: figs.1–12; pl. II: figs. 1–6. HOLOTYPE: AST 60-7240. Note: now *Hydropuntia edulis* (S.G. Gmelin) Gurgel et Fredericq 2004: 155, basionym: *Fucus edulis* S.G.Gmelin, 1763: 113.
TYPE LOCALITY: Yinggehai, SE end of Hainan Island, Hainan Province, South China Sea, China.
PERTINENT SYNONYM: *Hydropuntia fastigiata* (C.F.Chang et B.-M.Xia) M.J.Wynne 1989: 477.

DESCRIPTION: Thalli erect, attached by a rhizomatous base, terete throughout, branching without constriction at bases of branches, highest order branches usually bifid, tapered gradually to acute tips. Gonimoblast cells ovoid to fusiform, forming a spherical central mass; tubular nutritive cells issued only from gonimoblast base and fusing with cells of the inner pericarp, these in turn uniting to form a network of darkly staining stellate fusion cells; innermost cells of the pericarp not stretching during cystocarp development. Spermatangial conceptacles of the medullary type, protruding slightly from the surface at maturity; young conceptacles embedded in cortex and medulla, multicavitied, the cavities separated by thin layers of wall material, with a single opening formed above the level of the surface cortical cells, probably by the rupture of an outer cuticle; cavities enlarging in all directions displacing neighboring cortical cells and compressing them while maintaining their pit connections, sometimes surrounding a cortical cell during enlargement; breakdown of cross walls between globular portions of multi-cavitied conceptacles sometimes resulting in a single large-lobed conceptacle; spermatangia cut off inwardly into conceptacle cavity from spermatangial parent cells. Tetrasporangia subspherical, cruciately divided, slightly protruding with flattened or elongated cells present adjacent to the tetrasporangium.

REMARKS: The gonimoblast mass (placenta) in *H.* sect. *Polycavernosa* is not spherical, but characterized by a lobed morphology, and the inner gonimoblasts are usually composed of rounder and smaller cells compared to those in the genus *Crassa*.

PERTINENT SPECIES IN SUBGENUS *POLYCAVERNOSA*: ***Hydropuntia edulis*** (S.G. Gmelin) Gurgel et Fredericq; ***H. preissiana*** (Sonder) Gurgel et Fredericq; ***H. rangiferina*** (Kützing) Gurgel et Fredericq; and ***H. perplexa*** (K.Byrne et Zuccarello) Conklin in Conklin *et al*. (2014), plus the following species based on other published studies or unpublished data:

H. multifurcata (Børgesen) M.J. Wynne 1989: 477

Hydropuntia millardetii* (Montagne) Gurgel, J.N.Norris et Fredericq, *comb. nov.

BASIONYM: *Rhodymenia millardetii* Montagne (in Montagne & Millardet 1862: 9, pl. XXV: fig. 3).
PERTINENT SYNONYMS: *Gracilaria millardetii* (Montagne) J.Agardh 1885: 64
TYPE LOCALITY: La Réunion (= Réunion Island; Île Bourbon), Indian Ocean.

Crassa* Gurgel, J.N. Norris et Fredericq, *gen. nov.

TYPE SPECIES: *Crassa cornea* (J.Agardh) Gurgel, J.N.Norris et Fredericq
BASIONYM: *Gracilaria cornea* J.Agardh 1852: 598
TYPE LOCALITY: Pernambuco (?), Brazil.
LECTOTYPE: LD #29370 (ex herb. J.E. Areschoug), fig. 8 (male), Herb. Agardh, (left-hand side) (Bird *et al.* 1986: 2049).
PERTINENT SYNOMYMS: *Ceramianthemum corneum* (J.Agardh) Kuntze 1891; *Hydropuntia cornea* (J.Agardh) M.J.Wynne 1989.

DIAGNOSIS**:** Gonimoblast mass (placenta) spherical, sharp transition between gonimoblast and upper short usually dichotomously branched chains of carposporangia. Cystocarp floor flat and well defined; gametophytic fusion cells dendritic. Spermatangia of the medullary type only, forming deep conceptacles which are often confluent, giving rise to multiple cavities in the medulla when seen in transverse sections.

PERTINENT SPECIES IN *CRASSA*: ***Crassa cornea*** (J. Agardh) Gurgel, J.N. Norris et Fredericq;

Crassa changii* (B.-M. Xia et I.A.Abbott) Gurgel, J.N. Norris et Fredericq, *comb. nov.

BASIONYM: *Polycavernosa changii* B.-M. Xia et I.A. Abbott 1987: 407, 409, figs. 3, 11.
SYNONYM: *Gracilaria changii* (B-.M. Xia et I.A .Abbott) I.A. Abbott, J. Zhang et B.-M. Xia 1991: 23, figs 5, 8–9, 16–19, 21.
TYPE LOCALITY: ca. 200 m NE of beacon opposite Glugor Marine Police Jetty, Pinang, Malaysia.
HOLOTYPE: BISH, J.R. Fisher #1022.
REMARKS: *Gracilaria changii* has been subsumed in *G. firma* by Ng *et al*. (2017). We currently keep the epithet *changii* from Vietnam since type material of both species were not examined.

Crassa caudata* (J. Agardh) Gurgel, J.N.Norris et Fredericq, *comb. nov.

BASIONYM: *Gracilaria caudata* J.Agardh 1852: 598
TYPE LOCALITY: St. Croix, U.S. Virgin Islands.
LECTOTYPE: LD, -LD #29322, Rafinesque collection.

Crassa crassissima* (P. Crouan et H. Crouan) Gurgel, J.N.Norris et Fredericq, *comb. nov.

BASIONYM: *Plocaria crassissima* P. Crouan et H. Crouan, in Schramm & Mazé, 1865: 20.

PERTINENT SYNONYMS: *Gracilaria crassissima* (P.Crouan et H.Crouan) P.Crouan et H.Crouan,, in Schramm & Mazé 1866: 46; *Polycavernosa crassissima* (P.Crouan et H.Crouan) Fredericq et J.N.Norris 1985: 152; and *Hydropuntia crassíssima* M.J.Wynne 1989: 477.

TYPE LOCALITY: "Moule (récifs de ceinture du port)" (Schramm & Mazé, 1865: 20); Moule (reefs at entrance to port), Guadeloupe, F.W.I.

LECTOTYPE: BM, BM#000936166 (collected on January 16th, 1870)

Crassa truncata* (Kraft) Gurgel, J.N.Norris et Fredericq, *comb. nov.

BASIONYM: *Gracilaria truncata* Kraft 1977: 495

TYPE LOCALITY: Hawke's Bay, E coast of North Island, New Zealand

LECTOTYPE: TCD, TCD#00119988

REMARKS: Gurgel, unpublished data.

Crassa usneoides* (Mertens ex. C.Agardh) Gurgel, J.N.Norris et Fredericq, *comb. nov.

BASIONYM: *Sphaerococcus usneoides* C.Agardh 1823:333

PERTINENT SYNONYM: *Gracilaria usneoides* (Mertens ex. C.Agardh) J.Agardh 1852: 595

TYPE LOCALITY: Brazil

LECTOTYPE: LD, LD# 29447, leg. F.X.Mertens.

Plus the following species based on other published studies or unpublished data:

Crassa birdiae* (E.Plastino et E.C.Oliveira) Gurgel, J.N. Norris et Fredericq, *comb. nov.

BASIONYM: *Gracilaria birdiae* E.M.Plastino & E.C.Oliveira 2002: 390, figs 1–8

TYPE LOCALITY: Guajiru Beach, Trairi, Ceará, Brazil.

HOLOTYPE: SPF, SPF#54947

REMARKS: For phylogenetic evidence see Lyra *et al.* (2015)

Crassa crouaniorum* (Lyra, Nunes et Davis) Gurgel, J.N. Norris et Fredericq, *comb. nov.

BASIONYM: *Plocaria crassissima* P.Crouan & H.Crouan in Schramm & Mazé 1865: 20.

SYNONYMS: *Gracilaria crouaniorum* Lyra, J.M.C.Nunes et C.C.Davis, in Lyra et al. 2015: 364. Note: this is a new name for *Gracilaria secunda* P.Crouan et H.Crouan in Schramm & Mazé (1865: 19), which is a later homonym of the illegitimate name *G. secunda* (C.Agardh) Zanardini (1840: 240).

PERTINENT SYNONYMS: *Hydropuntia secunda* Gurgel & Fredericq 2004.

TYPE LOCALITY: Moule (Vieux-Bourg), Guadeloupe, F.W.I.

TYPE: BM, coll. No. 95, 1st series, specimen from April 1857 (cystocarpic)

REMARKS: For phylogenetic evidence see Gurgel & Fredericq (2004).

Crassa secundata* (Harvey) Gurgel, J.N.Norris et Fredericq, *comb. nov.

BASIONYM: *Gracilaria secundata* Harvey 1863: xxxv, 432

TYPE LOCALITY: Kiama, New South Wales, Australia.

HOLOTYPE: Herbarium Harvey, TCD, TCD#0012176

REMARKS: for phylogenetic evidence see Lyra *et al*. (2015).

Crassa punctata* (Okamura) Gurgel, J.N.Norris et Fredericq, *comb. nov.

BASIONYM: *Rhodymenia punctata* Okamura 1929: pl. 258

PERTINENT SYNONYM: *Gracilaria punctata* (Okamura) Yamada 1941: 203

TYPE LOCALITY: Prov. Tosa. Japan.

HOLOTYPE: SAP, SAP#84069, 8 Aug. 1933, leg. K. Okamura.

REMARKS: For phylogenetic evidence see Lin (2006), and Lyra *et al*. (2015).

Crassa firma* (C.F. Chang et B.-M. Xia) Gurgel, J.N. Norris et Fredericq, *comb. nov.

BASIONYM: *Gracilaria firma* C.F.Chang et B.M.Xia 1976

TYPE LOCALITY: Xindi, Xuwen Xian, Guangdong Province, China.

HOLOTYPE: AST, AST#66-540.

REMARKS: Although *G. firma* and *G. changii* are considered conspecific (Ng et al. 2017), we keep *G. changii* as a separate taxon, until type materials of both species can be studied (see also Remarks under *G. changii* above).

Gracilarioideae tribe Gracilariopsiseae Gurgel, J.N. Norris et Fredericq *tribus nov.*

Gracilariopsis E.Y. Dawson 1949: 40.

TYPE SPECIES: *Gracilariopsis sjoestedtii* (Kylin) E.Y. Dawson 1949: 43.

BASIONYM: *Gracilaria sjoestedii* Kylin 1930: 55; which is now *Gracilariopsis andersonii* (Grunow) E.Y. Dawson 1949: 43, basionym: *Cordylecladia andersonii* Grunow (in Piccone 1886: 62).

DIAGNOSIS: Superficial spermatangia; cystocarps without tubular nutritive gonimoblast cells connecting gonimoblast mass to the pericarp; lower gonimoblast cells linking to base of cystocarp through secondary pit connections; gonimoblast mass composed of small cells with very thin cell walls.

GENUS IN TRIBE GRACILARIOPSISEAE: *Gracilariopsis* (includes *Gracilariophila*, in part)

REMARKS: Our Bayesian results together with published molecular evidence were all congruent in recognizing the genus *Gracilariopsis* as a monophyletic clade with maximum support (Figs. 1, 2). The placement of *Gracilariophila* in this tribe is based on shared morphological characters and similarities of reproductive structures characteristic *Gracilariopsis* (Fredericq *et al*. 1989). We recognize that *Gracilariophila* is congeneric with *Gracilariopsis*, and for now proposed its inclusion in that genus recognizing that further molecular data are needed to test their relationship and taxonomic status.

PERTINENT SPECIES IN GRACILARIOIDEAE TRIBE GRACILARIOPSISEAE: ***Gracilariopsis andersonii*** (Grunow) E.Y. Dawson; ***Gp. animasensis*** Gurgel et J.N. Norris; ***Gp. carolinensis*** Liao et Hommersand; ***Gp. cataluziana*** Gurgel, Fredericq et J.N. Norris; ***Gp. chiangii*** S.M. Lin; ***Gp. costaricensis*** E.Y. Dawson; ***Gp. heteroclada*** J.-F. Zhang et B.-M. Xia; ***Gp. hommersandii*** Gurgel, Fredericq et J.N. Norris; ***Gp. lemaneiformis*** (Bory de Saint-Vincent) E.Y. Dawson, Acleto et Foldvik; ***Gp. longissima*** (S.G. Gmelin) Steentoft, L.M. Irvine et Farnham; ***Gp. mclachalii*** Buriyo, Bellorin et M.C. Oliveira; ***Gp. nhatrangensis*** Nhu Hau et S.-M. Lin; ***Gp. panamensis*** (W.R. Taylor) E.Y. Dawson; ***Gp. persica*** Bellorin, Sohrabipour et E.C. Oliveria; ***Gp. silvana*** Gurgel, Fredericq et J.N. Norris; ***Gp. sjoestedtii*** (Kylin) E.Y. Dawson; ***Gp. tenuifrons*** (C.J. Bird et E.C. Oliveira) Fredericq et Hommersand

Gracilariopsis oryzoides (Setchell et H.L. Wilson) Gurgel, J.N.Norris et Fredericq, *comb. nov.*

BASIONYM: *Gracilariophila oryzoides* Setchell et H.L. Wilson, in Wilson 1910: 81.

TYPE LOCALITY: [on *Gracilariopsis andersonii*]; Fort Point (entrance to San Francisco Bay), San Francisco, San Francisco County, California, USA.

Plus the following species based on other published studies:

Gracilariopsis irregularis (I.A.Abbott) Muangmai, Chirapart et Lewmanomont in Muangmai *et al*. (2014).

Gracilariaceae subfam. Melanthalioideae Gurgel, J.N.Norris et Fredericq, *subfam. nov.*

TYPE SPECIES: *Melanthalia obtusata* (Labillardière) J. Agardh 1852: 614, basionym: *Fucus obtusatus* Labillardière 1805: 111.

DIAGNOSIS: Algae free-living, with compressed to flattened, foliose thalli; tetrasporangia and superficial spermatangia in nemathecia; gonimoblasts small, gonimoblast mass expanded and amorphous, filling the entire cystocarp cavity; gradual and wide transition between gonimoblasts and carposporangia at different stages of maturity, carposporangia formed in long straight, largely unbranched chains; mature carposporangia similar in size with later stages of gonimoblast differentiation; tubular nutritive cells absent. New filaments interpolated by gonimoblast cells deep inside fertile region. Inner pericarp is well differentiated, and gonimoblast cells fuse directly with cells of the inner pericarp without the formation of secondary pit connections. An extensive fusion network is produced in the inner pericarp in *Curdiea* in which fusion takes place alongside the broadened pit connections. Spermatangia of cortical origin, spermatangial parent cells distributed superficially, along the thallus surface. Spermatangia of *Melanthalia* have not yet been reported; but have been described in *Curdiea* (Nelson & Knight 1997).

REMARKS: The geographic distribution of this subfamily is so far restricted to Antarctica, Australia, New Zealand and New Caledonia (e.g., Fredericq & Hommersand 1989c, 1990a, b; Nelson *et al.* 2013).

GENERA IN GRACILARIACEAE SUBFAM. MELANTHALIOIDEAE: *Melanthalia*, and *Curdiea*.

Melanthalia Montagne 1843: 296.

TYPE: *Melanthalia obtusata* (Labillardière) J. Agardh 1852: 614.

BASIONYM: *Fucus obtusatus* Labillardière 1805: 111; 1807: pl. 255.

TYPE LOCALITY: Southeast Tasmania.

Curdiea Harvey 1855: 333.

TYPE: *Curdiea laciniata* Harvey 1855: 333, which is now *Curdiea angustata* (Sonder) A.J.K. Millar 1990:342; basionym: *Epymenia angustata* Sonder 1853: 677.

TYPE LOCALITY: Port Fairy, Victoria, Australia.

SPECIES IN SUBFAM. MELANTHALIOIDEAE: ***Melanthalia abscissa*** (Turner) J.D. Hooker et Harvey; ***M. concinna*** J.Agardh; ***M. intermedia*** Harvey; ***M. obtusata*** (Labilardière) J. Agardh; ***M. vieillardii*** Kützing (see Nelson *et al.* 2013); and ***Curdiea codioides*** V.J. Chapman; ***C. coriacea*** (J.D. Hooker et Harvey) J. Agardh; ***C. crassa*** A.J.K. Millar; ***C. irvineae*** J. Agardh; ***C. obesa*** (Harvey) Kylin; and ***C. racovitzae*** Hariot.

- **Gracilariales Fredericq et Hommersand**
  - **Gracilariaceae Nägeli**
    - **Gracilariaceae subfam. Gracilarioideae Stizenberger, *emend.***
      - **Gracilarioideae tribe Gracilarieae Willkomm, *emend.***
        - ***Agarophyton* Gurgel, J.N.Norris et Fredericq, *gen. nov.***
        - ***Gracilaria* Greville**
          - ***Gracilaria* subgen. *Gracilaria***
          - ***Gracilaria* subgen. *Corallopsis* Gurgel, J.N.Norris et Fredericq, *stat. et comb. nov.***
        - ***Hydropuntia* Montagne**
          - ***Hydropuntia* subgen. *Hydropuntia***
          - ***Hydropuntia* subgen. *Polycavernosa* Gurgel, J.N.Norris et Fredericq, *stat. et comb. nov.***
        - ***Crassa* Gurgel, J.N.Norris et Fredericq, *gen. nov.***
      - **Gracilarioideae tribe Gracilariopsiseae Gurgel, J.N.Norris et Fredericq, *tribus nov.***
        - ***Gracilariopsis* E.Y.Dawson**
    - **Gracilariaceae subfam. Melanthalioideae Gurgel, J.N.Norris et Fredericq, *subfam. nov.***
      - ***Curdiea* Harvey**
      - ***Melanthalia* Montagne**

FIGURE 3. Diagram showing the newly proposed taxonomy and intra-ordinal classification of the Gracilariales (Rhodophyta) based on *rbc*L phylogenies and morphological evidence.

Discussion

A natural and stable classification system for the order Gracilariales recognizes major evolutionary lineages in this economically important order of red algae. In establishing a new molecular-based classification proposal for the Gracilariales we followed the topologies produced by Bayesian analyses (Figs. 1, 2). This choice was made because Bayesian results not only presented higher node support, but also corroborates morphological similarities (homologies) among higher taxonomic ranks recognized in this study. Furthermore the Bayesian estimation of phylogeny is based on the likelihood function, which corrects nucleotide sequence divergences for the presence of saturation (i.e., homoplasies), compared to MP. The implementation of maximum likelihood-based approaches to infer phylogenies has been shown to out-perform other methods such as MP and distance based algorithms, with statistical theory support (Huelsenbeck 1995; Huelsenbeck *et al*. 2002).

The new genus, *Agarophyton*, is proposed to accommodate three species, *A. chilensis*, *A. tenuistipitata* and *A. vermicullophylum*, which form a monophyletic group with high support. The position of *Agarophyton* is nested between the *Gracilariopsis* and the *Crassa-Hydropuntia* clades (Figs. 1, 2). Similar phylogenetic topologies also have been observed not only in other *rbc*L-based studies (Gurgel & Fredericq 2004, fig. 2A), but also in nuclear 18S rDNA and ITS rDNA sequence analyses (e.g. Bird *et al*. 1992, 1994; Bellorin *et al*. 2002). Interestingly, *rbc*L-based topologies corroborate the observations that *Agarophyton* cystocarp anatomy lies between *Gracilariopsis* and certain species of *Crassa*/*Hydropuntia*, and the external habit of *Agarophyton* resembles other cylindrical and branched species of *Gracilariopsis*. In Chile, non-reproductive specimens of *A. chilensis* may not be distinguishable from vegetative specimens of *Gracilariopsis lemaneiformis* (e.g., Bird *et al*. 1986: 2931).

Bird *et al*. (1986) and Cohen *et al*. (2004), both as *Gracilaria chilensis*, discussed the significant morphological similarities between cystocarps of *A. chilensis* and *Gp. lemaneiformis*. The general morphological similarities and comparisons between *Agarophyton* (as *G. chilensis*) and *Gracilariopsis* have also been carefully noted by Nelson & Ryan (1991) and Liao & Hommersand (2003); however, there are morphological differences in cystocarp anatomy between these two genera. In *Agarophyton* the gonimoblast cells of the cystocarps appear less dissected in organization, and the more regular homogeneous pattern of development results in a more rounded gonimoblast mass with a sparse accretion of carposporangia. See examples including: as *G. chilensis*: Bird *et al*. (1986: fig. 10), Bird *et al*. (1990; fig. 3), Liao & Hommersand (2003: fig. 11a), and Byrne *et al*. (2002: figs. 2a-e,.3a-f); as "*G. sordida*:" Nelson (1987: figs. 8, 9); and as *A. vermiculophyllum*: Gurgel & Fredericq (2004: fig. 2J, as *G. aff. tenuistipitata*). In contrast, the cystocarps in *Gracilariopsis* have gonimoblast cells in a more dissected organization usually giving rise to a lobed or pyramidal gonimoblast mass. See for example illustrations in Gurgel *et al*. (2003a): *Gp. andersonii,* fig. 5a; *Gp. carolinensis,* figs. 6a, d; *Gp. costaricensis,* figs. 7a, b; *Gp. silvana,* figs. 12, 13; *Gp. hommersandii*, figs. 26, 29; and *Gp. longissima* in Fredericq & Hommersand (1989b): figs. 44, 41, as "*Gp. lemaneiformis*"; and *Gp. animasensis* Gurgel et J.N. Norris, in Norris & Gurgel (2014): fig. 202B. Cystocarps of species of *Agarophyton* sometimes have tubular nutritive cells linking gonimoblasts and pericarp cells, a character not observed in *Gracilariopsis* species (Fredericq & Hommersand 1989b). Unfortunately, the reliability of the presence or absence of this character as a taxonomic feature to distinguish genera and subgenera within *Gracilaria sensu lato* has greatly contributed to past classification/taxonomic confusion. Although the presence of tubular nutritive cells is a polymorphic feature and can even vary among cystocarps found on the same thallus, there is a stable pattern in the tribes and between some genera. While not known in any of the species of the tribe Gracilariopsiseae, nearly all species in the tribe Gracilarieae have this character. In *Hydropuntia* and *Agarophyton* the presence of tubular nutritive cells connecting gonimoblasts and the pericarp can vary, being more often observed at the base of *Crassa/Hydropuntia* cystocarps and less so inside *Agarophyton* cystocarps.

Agarophyton vermiculophyllum, a species originally described from Japan in the warm temperate western Pacific, is a highly invasive species that has recently spread. It has been found in: Europe (including the Baltic Sea, Denmark, Atlantic France, Ireland.Italy, The Netherlands, Portugal, Spain, Canary Islands, Norway, and Sweden), north Adriatic, the Mediterranean, Morroco, Gulf of California and Pacific coast of Baja California, Mexico, and on both the eastern Pacific and western Atlantic coasts of the United States and Canada (Gulbransen *et al*. 2012; Guiry & Guiry, 2018). All species of *Agarophyton* possess an optimum combination of ecological and biochemical features as the best species for aquaculture and mariculture farming for the production of agar, hence the generic name, "agar-plant." These three species are also typical of estuarine habitats hence displaying euryhaline and ectothermic physiologies, which allow them to survive across a wide range of environmental conditions (e.g., Thomsen *et al*. 2006).

According to our classification, *Gracilaria* encompasses lineages characterized by cortical conceptacles of either the *verrucosa*-type or the *textorii*-type of spermatangial conceptacles *sensu* Yamamoto (1978). *Hydropuntia* and *Crassa* are characterized by spermatangial medullary conceptacles of the *Polycavernosa*-type (also known as *Henriquesiana*- or *Hydropuntia*-type), with only one known exception, *Crassa caudata*. *C. caudata* has spermatangial medullary conceptacles that can originate as *verrucosa*-type conceptacles, and herein considered as special case of paedomorphism (the retention of the ancestral juvenile shape in the descendent adult), missing the secondary linking of spermatangial parent cells to medullary cells as in most species of *Hydropuntia* and *Crassa* (see the discussion of paedogenesis in *Besa*, Phyllophoraceae, Fredericq & Lopez-Bautista 2002). Character evolution of spermatangial reproductive structures in *Gracilaria sensu lato* has a more complex history than has been appreciated, and it is more plastic in the genus *Agarophyton* than in any other genus of the Gracilariales. Regardless of how deep into the thallus the spermatangial conceptacles of *Agarophyton* reach, spermatangial parent cells in this genus seem to have a cortical cell origin and do not interact with medullary cells as they mature to form confluent, fused, ramified and complex medullary spermatangial conceptacles as seen in *Hydropuntia* and *Crassa*. When deeper conceptacles develop, an initial *chilensis*-type pit expands to give rise to a circular to oval-shaped and deeper conceptacle resembling a *verrucosa*-type (e.g., Rueness 2005).

Depending on the species being compared, examination of spermatangial conceptacles in *Agarophyton* (e.g., *A. vermiculophyllum*), *Crassa (*e.g., *C. caudata*) and *Hydropuntia* could mistakenly interpret them to be the same kind, i.e. of the *verrucosa*-type. However, spermatangial development in these three genera is in fact distinct (Table 1). Ontological differences between *Gracilaria* and *Hydropuntia/Crassa* spermatangial conceptacles are subtle. For example, in *Gracilaria*, the "*verrucosa*-type" is of cortical origin and development, and does not interact with medullary cells, and growth of adjacent vegetative cortical cells follows the radial expansion of the spermatangial conceptacles. Under this proposed taxonomic revision, the taxonomic spermatangial feature that should be considered to define a genus is whether or not spermatangial parent cells and cells of the spermatangial conceptacle floor extensively interact with medullary cells by means of secondary pit connections, and whether the regular cortical cells continue to divide to produce an increased number of cortical cell layers. Therefore, the sole shape of the mature conceptacles alone as viewed in transverse sections of the thallus may not always be diagnostic enough to interpret spermatangial homology nor define genera in the tribe Gracilarieae if collection of voucher specimens is inadequate, their preservation is poor, and the cells are not stained with Wittman hematoxylin (Wittman 1965, Fredericq & Hommersand 1990b, Hommersand & Fredericq 1990).

The genus *Crassa* comprises all species that were previously referred to as *Hydropuntia* known for the western Atlantic, plus three other Pacific species, i.e., *C. secundata,* and two species referred to as *C. firma* and *C. changii* (but note Ng *et al*. 2017). These results suggest that all western Atlantic *Crassa* species originated locally from a single common ancestor most likely of an Indo-Pacific origin.

Hydropuntia is so far strictly composed of Indo-Pacific species. The deepest node in the *Hydropuntia* clade separates two newly proposed subgenera, i.e., *H.* subgen. *Hydropuntia* and *H.* subgen. *Polycavernosa*. Thus far, *H.* subgen. *Hydropuntia* is unique in being composed of compressed, cartilaginous to crassullacean species with prostrate thalli, including the generitype *H. urvillei* and *H. eucheumatoides*. *Hydropuntia* subgen. *Polycavernosa*, was here named because it contains the generitype '*Polycavernosa fastigiata*' (which is now known as *Hydropuntia edulis*; Gurgel & Fredericq 2004).

In recent molecular phylogenetic studies, Lyra *et al.* (2015) using a multi-marker concatenated dataset based on *rbc*L, UPA and *cox*1 DNA sequences, and Iha *et al*. (2018), using a phylogenomic approach, concluded that there was no phylogenetic basis for recognizing *Hydropuntia* and *Agarophyton* (as '*G. chilensis'*) as genera distinct from *Gracilaria*. We disagree with their interpretation. In rejecting *Hydropuntia* as a distinct genus, Lyra *et al*. (2015) placed strong emphasis on two molecular results: the paraphyletic position of a single species, *H. rangiferina* (note: not the generitype), in relation to all other species of Gracilarieae in their concatenated phylogenetic tree, and results from the approximate unbiased test of Shimodaira (2002). Our results (Fig. 1) and those of Lyra *et al*. (2015: fig. 2) clearly place *H. rangiferina* in the genus *Hydropuntia*. Under the taxonomy herein presented, all topologies proposed in Lyra *et al*. (2015) and Iha *et al*. (2018) agree with our new generic concepts in the Gracilariaceae. Our new proposed taxonomic scheme for the Gracilariales will serve as both a natural classification of the order and a nomenclatural framework upon which intra-familial taxa are recognized.

TABLE 1. Comparative table of distinct morphological characters among Gracilariales (Rhodophyta) genera.

Genera	Interaction of spermatangial parent cells with medullary cells	Cortical growth following spermatangial maturation	Shape of shallow spermatangial conceptacles	Club-shaped cortical cells flanking spermatangial conceptacles
Agarophyton	present	absent	flattened bottom	present
Crassa	extensive	absent	concave bottom*	absent
Gracilaria	absent	conspicuous	concave bottom	absent
Gracilariopsis	absent	n.a.	n.a.	absent
Hydropuntia	extensive	absent	concave bottom*	absent

n.a. = Not applicable

* = mature spermatangial conceptacles can become confluent and deeply inbeded in the medulla or thallus.

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Appendix 1. List of species identification, collection information, *rbc*L GenBank accession numbers for newly generated and published rbcL DNA sequences.

Newly generated sequences:
Agarophyton chilensis (Isla Mancera, Chile; MH760419), *A. vermiculophyllum* 1 (Vietnam; coll. L.N. Hau, *LAF#:*719; MH760424), A. *vermiculophyllum* (Vietnam; coll. L.N. Hau, LAF#:739; MH760423), *A. vermiculophyllum* (Vietnam; coll. L.N. Hau, LAF#:722; MH760425), (Vietnam; coll. L.N. Hau, *LAF#:*723; MH760426), *A. vermiculophyllum* (Vietnam; coll. L.N. Hau, *LAF#:*736; MH760422), *Crassa firma* (Vietnam; coll. L.N. Hau, det. C.F.D. Gurgel, *LAF#:734*; MH760421), *Hydropuntia millardetii* (Sodwana Bay, 2 mile reef, South Africa; coll. S. Fredericq, Feb 1st, 2001; MH760420)

GenBank sequences:
*Agarophyton chilensis (*AY049396), *A. vermiculophyllum* (Japan: AY049324), A. *vermiculophylum* (USA: AY049312), *Gracilaria beckeri* (AY049377), *G. bursa-pastoris* (AY049376), *G. canaliculata* (AY049390), *G. cervicornis* (AY049365), *G. gracilis* (AY049400), *G. mammillaris* (AY049323), *G. ornata* (AY049318), *G. pacifica* (AY049397), *G. salicornia* (AY049385), *G. textorii* (AY049325), *G. tikvahiae* (AY049432), *Gracilariopsis heteroclada* (AY049411)*, Gp. hommersandii* (AY049407)*, Crassa caudata* (AY049359)*, C. cornea* (AY049339)*, C. crassissima* (AY049351)*, C. cornea* (AY049338), *Hydropuntia edulis* (AY049387), *H. eucheumatoides* (AY049389), *H. perplexa* (AY112677), *H. preissiana* (AY049403), *H. rangiferina* (AY049379), *H. urvillei* (AY049402).