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Resolving phenotypic plasticity and species designation in the morphologically challenging Caulerpa racemosa peltata complex (Chlorophyta, Caulerpaceae)

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RESOLVING PHENOTYPIC PLASTICITY AND SPECIES DESIGNATION IN THE MORPHOLOGICALLY CHALLENGING *CAULERPA RACEMOSA–PELTATA* COMPLEX (CAULERPACEAE, CHLOROPHYTA)[1]

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Although recent molecular studies have indicated the presence of a number of distinct species within the *Caulerpa racemosa–peltata* complex, due to the difficulties presented by high levels of phenotypic plasticity and the large number of synonyms, infraspecific taxa, and names of uncertain affinity, taxonomic proposals are yet to be made. In this study, we aimed to resolve the taxonomy of the complex and provide an example of how historical nomenclature can best be integrated into molecular based taxonomies. We accomplished this by first determining the number of genetic species within our globally sampled data set through a combination of phylogenetic and species-delimitation approaches of partial elongation factor TU and RUBISCO large subunit gene sequences. Guided by these results, comparative morphological examinations were then undertaken to gauge the extent of phenotypic plasticity within each species, as well as any morphological overlap between them. Our results revealed the presence of 11 distinct species within the complex, five of which showed high levels of phenotypic plasticity and partial overlap with other species. On the basis of observations of a large number of specimens, including type specimens/descriptions, and geographic inferences, we were able to confidently designate names for the lineages. *Caulerpa peltata*, *C. imbricata* and *C. racemosa* vars. *laetevirens*, *occidentalis* and *turbinata* were found to represent environmentally induced forms of a single species, for which the earlier-described *C. chemnitzia*, previously regarded as a synonym of *C. racemosa* var. *turbinata*, is reinstated. *C. cylindracea*, *C. lamourouxii*, *C. macrodisca*, *C. nummularia* and *C. oligophylla* are also reinstated and two new species, *C. macra* stat. nov. and *C. megadisca* sp. nov., are proposed.

Key index words: ***Caulerpa*****;** ***chemnitzia*****; GMYC; nomenclature;** ***peltata*****; phenotypic plasticity;** ***racemosa*****;** ***rbc*****L; species delimitation; taxonomy;** ***tuf*****A**

List of Abbreviations**: BI, Bayesian inference; BP, Bootstrap percentages; *C.*, Caulerpa; GMYC, General mixed Yule coalescence; GTR, generalized time-reversible (model); ML, Maximum likelihood; PP, posterior probability; *rbc*L, RUBISCO large subunit; *tuf*A, elongation factor TU**

Phenotypic plasticity has been a long-standing source of taxonomic difficulty in many algal groups,

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frequently leading to misidentifications, nomenclatural quagmires, incorrect biodiversity estimates, and confusing classification schemes (e.g., Bacillariophyceae: Mann 2010, Chlorophyta: Leliaert et al. 2009, Phaeophyceae: Tronholm et al. 2010, Rhodophyta: Saunders 2008). Fortunately, the advent of molecular tools has provided researchers with an independent and convenient means to delimit and identify species in taxonomically challenging groups (e.g., Verbruggen et al. 2007, Saunders 2008, Leliaert et al. 2009, Mann 2010, Tronhlm et al. 2010). These tools, however, have also presented algal taxonomists with several new problems. First, considerable conflict between morphological and molecular species concepts has been uncovered (e.g., Leliaert et al. 2009, Tronholm et al. 2012) and, secondly, molecular data are revealing an overwhelming diversity of species, many cryptic, at a rate far greater than formal descriptions are being made (De Clerck et al. 2013). It is the naming of these species, especially the matching of previously described names with newly obtained molecular data, that is the greatest challenge currently faced by algal taxonomists, a task made more difficult by the overwhelming number of synonyms, infra-specific taxa, and names of uncertain affinity that plague many algal groups (De Clerck et al. 2013).

Several strategies for dealing with this challenge have been suggested. It has been proposed that newly collected and sequenced specimens (ideally topotype material similar in morphology to the type specimen) be designated as epitypes by experienced taxonomists (Tautz et al. 2003, Evans and Mann 2009, Bock et al. 2011, Zuccarello et al. 2011, Saunders and McDevit 2012). However, how can one be sure that the epitype is identical to the type specimen when the type specimen is unavailable (lost, in poor condition, based on a drawing etc. …) or if the type locality is unknown, vague (e.g., “Western Australia”), significantly altered since the original collection (e.g., Suez, Egypt) or contains a number of genetic species with similar morphology? Furthermore, how does one confidently match names and type specimens to newly collected specimens in groups where high levels of phenotypic plasticity and/or cryptic species are known to occur?

If we are to positively pinpoint the species in question, the only strategy leading to an unequivocal solution is to sequence the type material itself. It is for these reasons that Hughey and Gabrielson (2012), citing a number of examples, concluded that where possible, all type specimens, including their synonyms, should be sequenced. Although we agree with this in principle, as discussed by Saunders and McDevit (2012) and De Clerck et al. (2013), while it is feasible to obtain DNA information from older type specimens, it is a time-consuming (and partially destructive) process hampered by the large number of synonyms and infraspecific taxa. Furthermore, sequencing type specimens is also unlikely to be possible in many instances due to type specimens being unavailable (e.g., administrative controls on destructive sampling, specimens destroyed, lost or types not yet designated) or because usable DNA cannot be extracted and amplified (e.g., original specimen was formalin-preserved).

The taxonomy of the green macroalgal genus *Caulerpa* J.V. Lamouroux faces a number of the aforementioned issues. There are over 350 species and infraspecific taxon names associated with the genus, of which about 85 species are currently accepted (Guiry and Guiry 2013). Although lacking transverse cell walls (= siphonous thallus), *Caulerpa* species display a complex habit, with the thallus differentiating into stolons, rhizoids, and upright assimilators (= fronds) that usually bear ramuli (= branchlets; Fritsch 1965); the morphology of these various structures has been historically used for species delimitation. However, environmentally controlled phenotypic plasticity in all these characters has led to much confusion, a large number of synonyms, and a classification scheme involving subspecies, varieties, forms, and “*ecads*” (Peterson 1972, Calvert et al. 1976, Ohba and Enomoto 1987, Coppejans and Prud’homme van Reine 1992, de Senerpont Domis et al. 2003).

Within *Caulerpa*, the most taxonomically troublesome taxa are those currently associated with *C. racemosa* (Forsskål) J. Agardh and *C. peltata* J. V. Lamouroux, commonly referred to as the *C. racemosa–peltata* complex, which has more than 30 described varieties and forms (most given in Guiry and Guiry 2013; Fig. 1). One member of the complex, *C. racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman & Boudouresque, has recently received much scientific and public attention due to its invasion of the Mediterranean Sea, Canary Islands, and South Australia (Klein and Verlaque 2008). Although many of the *C. racemosa–peltata* complex varieties and forms were originally described as distinct species (e.g., *C. cylindracea* Sonder, *C. macrodisca* Decaisne), the subsequent discovery of apparently intermediate thalli with *C. racemosa* and *C. peltata* type morphologies resulted in these taxa being reduced to varieties or forms, mostly within *C. racemosa* (e.g., *C. racemosa* var. *macrodisca* (Decaisne) Weber-van Bosse), but with some sub-specific ranks also proposed within *C. peltata* (e.g., *C. peltata* var. *macrodisca* (Decaisne) Weber-van Bosse). However, recent molecular studies have shown the complex to consist of at least six distinct species-level entities (e.g., Sauvage et al. 2013), but as yet, no taxonomic changes have been proposed. As such, a large number of GenBank sequences (250+) remain simply labeled as either *C. racemosa* or *C. peltata*, although some sequences do include a varietal or formae epithet. This is a cause for concern as without accurately identified sequences, even with molecular sequence information available, govern-

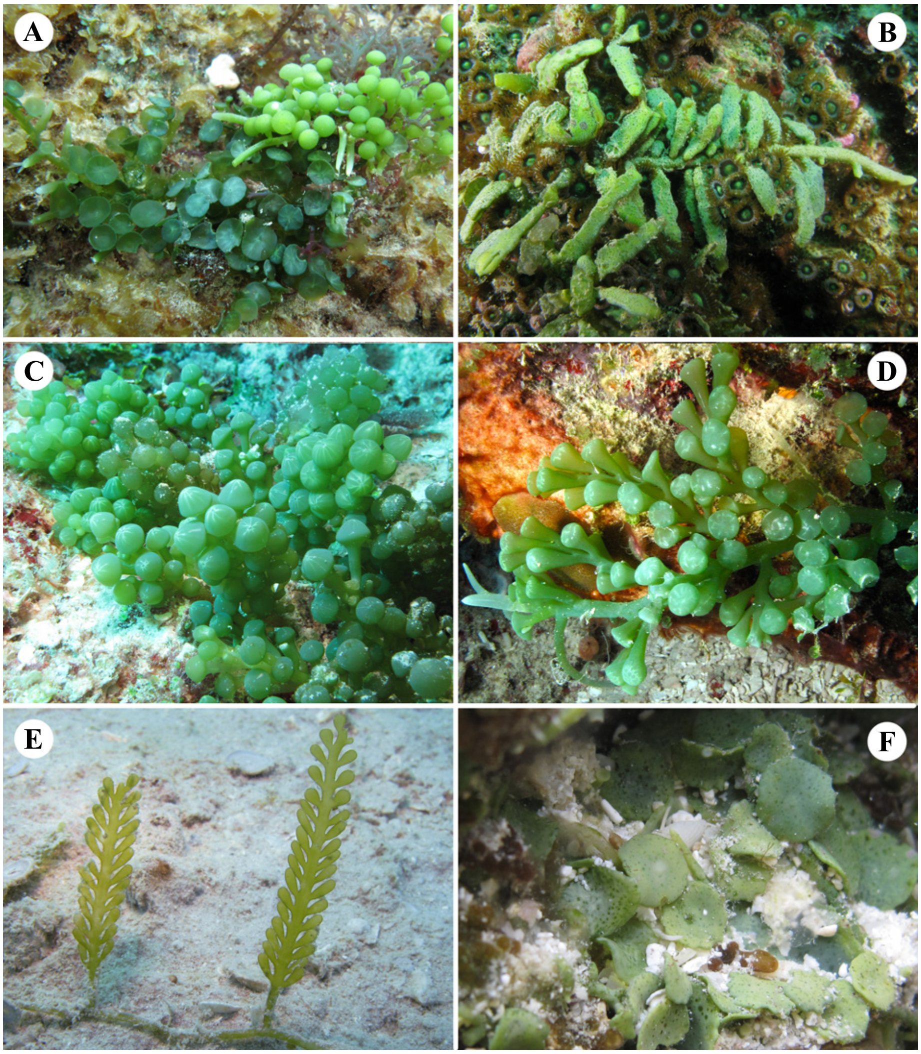

FIG. 1. Morphological variation of taxa currently assigned to the *Caulerpa racemosa-peltata* species complex. (A) *C. chemnitzia* (Esper) J.V. Lamouroux (AD-A91615) on left (previously *C. peltata* J.V. Lamouroux), growing with *C. racemosa* (Forsskål) J. Agardh (AD-A91592) on right at Ningaloo Reef, Western Australia; (B) *C. lamourouxii* (Turner) C. Agardh (PERTH 08292620) from Long Reef, north-western Australia (previously *C. racemosa* var. *lamourouxii* (Turner) Weber-van Bosse; (C) *C. chemnitzia* (AD-A92587) from Lizard Island, Great Barrier Reef (previously *C. racemosa* var. *laetevirens* (Montagne) Weber-van Bosse); (D) *C. chemnitzia* (AD-A92551) from Lizard Island, Great Barrier Reef, Australia (previously *C. racemosa* var. *turbinata* (J. Agardh) Eubank) displaying turbinate and clavate ramuli; (E) Complanate form of *C. cylindracea* Sonder (AD-A88114) from Lizard Island, Great Barrier Reef, Australia (previously *C. racemosa* f. *complanata* (J. Agardh) Weber-van Bosse); (F) *C. nummularia* Harvey ex. Agardh (AD-A91369) from Heron Island, Great Barrier Reef, Australia (previously *C. peltata*).

ment agencies and non-specialists can find it extremely difficult to correctly identify *Caulerpa* species, a factor that is becoming increasingly important as *Caulerpa* species continue to become established outside of their native ranges (e.g., Meinesz and Hesse 1991, Jousson et al. 2000, Womersley 2003, Lapointe et al. 2005, Amat et al. 2008, Jongma et al. 2013, Pérez-Estrada et al. 2013). However, designating names to sequenced *C. racemosa–peltata* complex specimens is no trivial task, as specimens can display high levels of phenotypic plasticity and in many instances crucial type specimens are lost (e.g., *C. peltata*), typification is based on illustrations only (e.g., *C. racemosa* var. *macrodisca*) or types were never designated (e.g., *C. nummularia* Harvey ex J. Agardh). Furthermore, multiple genetic species are often found at a single site (e.g., Sauvage et al. 2013).

While fully conscious of the many seemingly insurmountable problems associated with resolving the taxonomy of the complex, we feel that the current taxonomic and nomenclatural instability cannot be perpetuated. With this in mind, the present study aimed to resolve the taxonomically challenging *C. racemosa–peltata* complex and in the process provide an example of how historical nomenclature can best be integrated into molecular-based taxonomies.

MATERIALS AND METHODS

Overview. Due to the known phenotypic plasticity displayed by many members of the *C. racemosa–peltata* complex, we approached the present study in the following way. First, using a globally sampled DNA taxonomy (partial *tuf*A and *rbc*L sequences), including type locality or type region sequences, we determined the number of genetic species within our *C. racemosa–peltata* complex data set through a combination of phylogenetic and species-delimitation approaches. Then, guided by the molecular results, comparative morphological examinations were made to gauge the extent of both the phenotypic plasticity within each of the genetically distinct species and any morphological overlap between them. Using this information, plus geographic inferences and type specimen observations/descriptions, we then designated new, current, or previously described species names to our specimens.

Taxon sampling. *Caulerpa racemosa-peltata* specimens representing a wide range of varieties and forms were collected globally, although sampling was biased toward the Indo-Pacific region. Where possible, specimens were also collected from, or close to, the type locality for each taxon. Part of the thallus was cleaned and preserved in silica gel for DNA extraction and the remainder of the specimen either press dried onto herbarium sheets, desiccated in silica gel, or preserved in 5% formalin/seawater. Specimen vouchers were housed at AD, GENT, L, PERTH, UNB, US (abbreviations follow Holmgren et al. 1990) and the personal herbarium of C. W. Schneider. Where available, type specimens, including those of varieties and forms, were observed. When types were not available, taxon concepts were based on the protologue and any subsequent descriptions and illustrations of original material. Collection information and herbarium voucher numbers of newly collected specimens used in the present study are given in Table S1 in the Supporting Information.

DNA extraction, amplification, and sequencing. Total DNA extraction was either outsourced to AGRF (Australian Genome Research Facility, Adelaide Node, SA, Australia) or processed by hand with a DNeasy Plant mini Kit (Qiagen, Hilden, Germany). A partial section (~820 bp) of the *tuf*A gene was amplified and sequenced for all specimens using the methods of Famà et al. (2002) or Saunders and Kucera (2010). The *tufA* gene was chosen as it has been shown to have sufficient species-level resolution in the Bryopsidales, including *Caulerpa* (Verbruggen et al. 2005, Saunders and Kucera 2010, Dijoux et al. 2012, Sauvage et al. 2013). On the basis of exploratory analyses of the *tuf*A data, we selected representative specimens from each lineage to sequence a partial section of the *rbc*L gene using the methods of Saunders and Kucera (2010). Purified PCR products were sent to AGRF, Macrogen (Seoul, Korea) or First BASE Laboratories Sdn Bhd (Seri Kembangan, Malaysia) for sequencing. Additional samples were extracted, amplified, and sequenced at the Centre for Environmental and Molecular Algal Research (University of New Brunswick, Fredericton, NB, Canada) following Saunders and Kucera (2010). Individual chromatograms were assembled into contigs and edited using Sequencher v.4.8 (Gene Codes Corporation, Ann Arbor, MI, USA). Consensus sequences were compared to that of the National Centre for Biotechnology Information (NCBI) database using BLAST (http://www.ncbi.nlm.nih.gov) to check for contaminants. Newly generated sequences were submitted to GenBank and their accession numbers are given in Table S1.

Sequence alignment and phylogenetic analyses. Newly generated *tuf*A sequences from the present study were aligned with the *tuf*A alignment of Sauvage et al. (2013), which included sequences from the studies of Famà et al. (2002), de Senerpont Domis et al. (2003), Stam et al. (2006), Wynne et al. (2009), and Händeler et al. (2010). We also aligned the newly available GenBank sequences from Jongma et al. (2013), although we removed redundant sequences (i.e., 100% identical) from this data set before aligning. All available *Caulerpa rbc*L sequences were retrieved from GenBank and aligned with newly obtained *rbc*L sequences. These were from the studies of Hanyuda et al. (2000), de Senerpont Domis et al. (2003), Lam and Zechman (2006), and Maeda et al. (2012). A concatenated alignment of *tuf*A and *rbc*L sequences from de Senerpont Domis et al. (2003) and the present study was also created. GenBank sequences used in the present study are listed in Table S2 in the Supporting Information. All alignments were done using Clustal X (Larkin et al. 2007).

Alignments were analyzed using Bayesian inference (BI) and maximum likelihood (ML) with a general time-reversible substitution model incorporating a proportion of invariable sites and a gamma model of rate heterogeneity among sites (GTR+I+G) as determined by jModelTest v.1 (Posada 2008). BI was performed using BEAST v.1.7 (Drummond et al. 2006, Drummond and Rambaut 2007) with the Markov Chain Monte Carlo (MCMC) started from a random tree and run for 20 million generations, sampled every 1,000th generation, with an uncorrelated lognormal clock model. All other priors and operators were kept at their default values. A constant population size coalescent prior was used as tree prior. Tree log files were created with branch length in substitutions and MCMC runs were monitored in Tracer v.1.4.2 (Rambaut and Drummond 2007) to ensure that all final estimated sample size (ESS) values were above 200. The first 2,000 trees were removed as the burn-in before generating summary statistics and trees. Maximum-likelihood analyses were performed using RaxML (Stamatakis et al. 2008), with the reliability of each internal branch being evaluated by nonparametric bootstrapping (1,000 replicates). Final trees were edited in FigTree v.1.3.1 (Drummond and Rambaut 2007).

Species delimitation. Species were delimited using the *tuf*A data set and two different approaches. The first was to identify strongly supported clusters (i.e., bootstrap percentages (BP) ≥85, and posterior probability (PP) ≥0.95) preceded by a relatively long branch and with lower intraspecific sequence diversity (Verbruggen et al. 2005, Leliaert et al. 2009, Dijoux et al. 2012). Secondly, we used a more objective approach developed by Pons et al. (2006) and Monaghan et al. (2009) that uses a general mixed Yule coalescence (GMYC) model to define the species boundary. This method has been shown to be useful in several studies in recent years (e.g., Barraclough et al. 2009, Monaghan et al. 2009, Papadopoulou et al. 2011, Esselstyn et al. 2012, Murphy et al. 2013), including a number of macroalgal studies (e.g., Leliaert et al. 2009, Tronholm et al. 2012, Payo et al. 2013, Silberfeld et al. 2013). Using an ultrametric tree and a ML framework, the algorithm optimizes the shift in the branching patterns from interspecific branches (Yule model) to intraspecific branches (coalescent model). A threshold value is calculated such that nodes older than this threshold can be regarded as species diversification events, while younger nodes are identified as coalescence-driven clusters. The ultrametric tree was constructed using the BI methods described above, but with the tree log file being created without branch length in substitution. GMYC analysis was performed under the single-threshold model using the SPLITS package for R (R Development Core Team 2009; package available at http://r-forge.r-project.org/projects/splits/). Lineages were recognized as species if they were supported by both delimitation approaches.

Morphological observations. In order to understand the extent of phenotypic plasticity within each genetically distinct *C. racemosa–peltata* species, intra-lineage morphological variation was characterized by examining each specimen for rhizoid form, stolon width, assimilator height, and ramuli shape, size, and arrangement (Table 1). Specimens were then morphologically identified based on comparisons with type specimens, original descriptions, and numerous taxonomic references (Appendix S1 in the Supporting Information). Where available, specimen vouchers used in the studies by Famà et al. (2002), de Senerpont Domis et al. (2003), Stam et al. (2006) and Sauvage et al. (2013) were also examined. Detailed nomenclatural information of all taxa discussed in the present study is provided in Table S3 in the Supporting Information.

We based our concept of *C. racemosa* on detailed observations of the type specimen (reproduced as our Fig. 2A;

Herb. Forsskål No. 845 at C). As the type specimen of *C. peltata* is presumed lost, the illustration by Lamouroux (1809b) (reproduced as our Fig. 2B) that depicts erect assimilators bearing lateral peltate ramuli was regarded as the type form of *C. peltata*.

RESULTS

Phylogenetic analyses and species delimitation. In total, 65 *tuf*A and 20 *rbc*L sequences were newly generated (Table S1). Overall, including GenBank sequences, the final *tuf*A alignment comprised a total of 245 sequences (912 bp in length), the *rbc*L alignment 57 sequences (904 bp in length), and the concatenated data set 38 sequences (1,771 bp in length).

As the BI and ML analyses topologies were mostly congruent, only the BI topologies are shown (Figs. 3 and 4; Fig. S1 in the Supporting Information). It was difficult to compare the trees produced from the *tuf*A, *rbc*L and concatenated alignments due to data from various species not being present in all data sets. However, where *tuf*A and *rbc*L were available, the analyses produced trees with identical clades, but slightly contrasting topologies and statistical support (Figs. 3 and 4; Fig. S1). Although support in our trees was higher than in previous phylogenetic studies of *Caulerpa* (e.g., Famà et al. 2002, de Senerpont Domis et al. 2003, Sauvage et al. 2013), we still found some lack of resolution in the backbone of our single gene trees (Figs. 3 and 4). However, support was much improved in the concatenated data set analyses (Fig. S1).

We delimited 37 species with long branches and high support (PP >0.95, BS >0.85), with specimens

TABLE 1. Features of *Caulerpa* taxa that were previously assigned to either *C. racemosa* or *C. peltata*. Measurements were derived from type material and specimens collected in the present study.

	Caulerpa lamourouxii (Turner) C. Agardh	***Caulerpa oligophylla*** Montagne	***Caulerpa macra*** (Weber-van Bosse) Draisma & Prud'homme ***stat. nov.***	***Caulerpa cylindracea*** Sonder	***Caulerpa chemnitzia*** (Esper) J.V. Lamouroux
Lineage (Fig. 3)	1	2	4	5	6
Figures	1B, 5A–D	5E, F	6A, B	7A–D	1A, C, D, 8A–E
Previous accepted name(s)	*C. racemosa* var. *lamourouxii* (Turner) Weber-van Bosse	*C. racemosa* var. *lamourouxii* (Turner) Weber-van Bosse	*C. racemosa* var. *macra* Weber-van Bosse	*C. racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman & Boudouresque; *C. racemosa* f. *complanata* (J. Agardh) Weber-van Bosse	*C. racemosa* var. *turbinata* (J. Agardh) Eubank; *C. imbricata* G. Murray; *C. peltata* J.V. Lamouroux; *C. racemosa* var. *laetevirens* (Montagne) Weber-van Bosse; *C. racemosa* var. *occidentalis* (J.Agardh) Børgesen
Stolon diameter, mm	1.5–3.0	1.5–2.0	(3-)4–6	0.8–1.5(2.0)	(0.8-)2–4(-6)
Assimilator					
Height, cm	2.5–8.0(-12)	2–3	3–10+	2–7(10)	1.5–7.0(-13)
Branching	Unbranched or sparingly branched	Common but irregular	Branching not observed	Branching not observed	Uncommon
Arrangement of ramuli	The number and arrangement of ramuli is very variable: from distichous and opposite to distantly spaced or completely absent.	Usually a few distantly spaced ramuli, although some specimens completely lacking ramuli	Ramuli moderately crowded, distichously or radially arranged and usually alternating.	Crowded and radially arranged to distichous and opposite	Usually very crowded and radially arranged
Ramuli					
Shape	Clavate to sub-spherical	Clavate to sub-spherical	Oviform, pyriform, claviform to slightly bulbous	Cylindrical to clavate, often flattened	Highly variable, clavate to turbinate to peltate. Often many forms on a single assimilator
Height, mm	(3-)4–8(-10)	3–5(6)	(5-)6-10(12)	(2.5-)4.0-6.0	(1.0-)3-10(-12)
Diameter, mm	2–3	2–3	2–4(6)	1.5–2.5	(1-)2–5(-8)

(continued)

TABLE 1. (continued)

	Caulerpa nummularia Harvey ex. J. Agardh	***Caulerpa megadisca*** Belton & Gurgel ***sp. nov.***	***Caulerpa macrodisca*** Decaisne	***Caulerpa racemosa*** (Forsskål) J. Agardh
Lineage (Fig. 3)	7	8	9	11
Figures	1F, 9A, B	9E	9C, D	1A, 10A–C
Previous accepted name(s)	*C. peltata* J. V. Lamouroux; *C. peltata* var. *exigua* Weber-van Bosse; *C. peltata* var. *stellata* (Harvey ex J.Agardh) Weber-van Bosse		*C. racemosa* var. *macrodisca* (Decaisne) Weber-van Bosse	*C. racemosa* (Forsskål) J. Agardh; *C. racemosa* var. *mucronata* L.N.de Senerpont Domis
Stolon diameter, mm	0.3–0.5(-0.8)	1–2	(1.0-)1.5–3.0	1.0–2.0(2.5)
Assimilator				
Height, cm	0.4–0.5	<1	1–5	1–3(6)
Branching	Common	None	Not observed	Rarely branched but becoming very branched in specimens previously assigned to var. *mucronata*
Arrangement of ramuli	Singly, or new peltate discs arising from the margin or centre of parent disc	Single peltate discs arising from the stolon	Semi-crowded, radially arranged on an upright axis	When present, irregularly arranged and uncrowded to crowded
Ramuli				
Shape	Distinctly peltate, with smooth and/or crenulated margins	Distinctly peltate and large	Distinctly peltate and large	Spherical, pyriform on a short stalk.
Height, mm	2–5	3–6	(3-)5–8(-12)	1-3(-4)
Diameter, mm	(2-)3–4(-5)	8(10)–15(20)	(4-)5-10(-18)	1.0–2.5 (3.0)

from the *C. racemosa–peltata* complex forming 12 of these (Fig. 3). A BI phylogram of the *tuf*A data set is provided in the Supplementary data to show branch lengths (Fig. S2 in the Supporting Information). The GMYC model provided a significantly better fit than a null model driven by coalescence only (confidence interval 29–46; $L_{GMYC} = 2423.955 > L_0 = 2411.179$, $P = 0.0002$) and recovered 38 lineages, with specimens from the *C. racemosa–peltata* complex forming 13 of these (Fig. 3). The two discrepancies between the methods with regard to specimens of the *C. racemosa–peltata* complex were that the long branches and high support method recovered two separate clusters within lineage 4, and lineage 6 as a single cluster (Fig. 3 and Fig. S2), whereas the GMYC method supported three separate clusters within lineage 6, and lineage 4 as a single cluster (Fig. 3 and Fig. S2). Due to these discrepancies, we did not recognize the additional clusters within lineages 4 and 6, leaving 11 recognized *C. racemosa–peltata* lineages (Fig. 3). Two of these lineages (3 and 10) were single sequences from Sauvage et al. (2013), which lacked associated *rbc*L data, and thus consideration of these lineages will not be dealt with in the present study. The *rbc*L and concatenated trees also showed high support (PP >0.95; BS >0.85) for the nine *C. racemosa–peltata* lineages (Fig. 4 and Fig. S1, respectively).

Morphological characterization of lineages. Among the genetically distinct *C. racemosa–peltata* lineages found in this study, five showed considerable levels of phenotypic plasticity and partial morphological overlap with other lineages (lineages 1, 2, 5, 6 and 11), whereas the remaining four lineages (4, 7, 8 and 9) did not.

Lineage 1 included specimens morphologically identified as *C. racemosa* var. *lamourouxii* (Turner) Weber-van Bosse (Fig. 5A) and *C. racemosa* var. *lamourouxii* f. *requienii* (Montagne) Weber-van Bosse (Figs. 1B and 5, B and C) from Western Australia and the Red Sea, although some specimens could be thought to resemble *C. racemosa* var. *cylindracea* and *C. racemosa*. Some newly collected specimens were almost identical to the type specimen of *C. racemosa* var. *lamourouxii* (BM000569449, as *Fucus lamourouxii* Turner; Fig. 5D). As with previous works on *C. racemosa* var. *lamourouxii*, specimens observed in the present study varied considerably in terms of their morphologies (Table 1), with assimilators ranging from being densely covered with clavate ramuli (Fig. 5A) to being flattened and devoid of any ramuli (Figs. 1B and 5B). Very young specimens or parts of specimens often showed a very different morphology than that of mature specimens. *Caulerpa racemosa* var. *lamourouxii* specimens that bear no (or very few) ramuli (e.g., Figs. 1B and 5, B and C) are usually referred to as *C. racemosa* var.

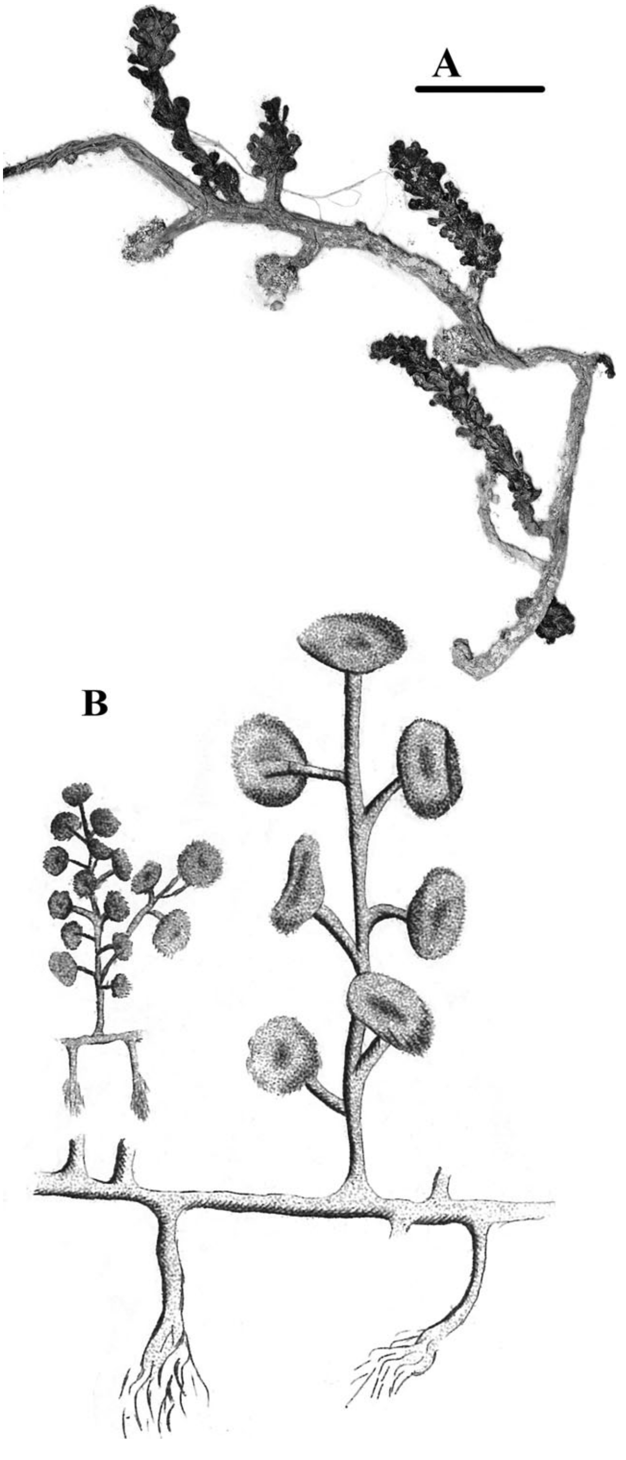

FIG. 2. (A) Photograph of the holotype of *Caulerpa racemosa* (Forsskål) J. Agardh (Herb. Forsskål No. 845 at C). Scale bar = 20 mm; (B) Illustration of *C. peltata* J.V. Lamouroux by Lamouroux (1809b). Unfortunately, as the type specimen is lost and Lamouroux's illustration does not have a scale, we were unable to provide a scale for this image.

lamourouxii f. *requienii*. However, all specimens assigned to f. *requienii* in the present study were quite different to the type specimen (see Wynne et al. 2009: 295 fig. 8, as *Herpochaeta requienii* Montagne), as well as its heterotypic synonyms *C. racemosa* var. *gracilis* (Zanardini) Weber-van Bosse (TCD0011042; Fig. S3A in the Supporting Information) and *C. clavifera* var. *nudiuscula* Zanardini (given as *nudicaulis* in herb. TCD0011044, Fig. S3B). The most notable difference was assimilator heights, with our specimens being <5 cm tall, whereas heights of the three type specimens mentioned above were up to 10–15 cm.

Lineage 2 included specimens from the Great Barrier Reef, Indonesia, Japan, New Caledonia, and the Philippines usually also attributed to *C. racemosa* var. *lamourouxii* (Fig. 5, E and F), and as with lineage 1, these specimens showed considerable morphological variation. However, these specimens were generally smaller than specimens from lineage 1 and closely resembled the type specimen of *C. oligophylla* Montagne (MA10330 at P; Fig. 5F), a species described from northeastern Australia, but currently regarded as a synonym of *C. racemosa* var. *lamourouxii* (Price 2011).

Lineage 4 included specimens from the tropical Indo-Pacific region identified as *C. racemosa* var. *macra* (Fig. 6A) based on similarity to the type specimen (Fig. 6B, L0054713 also from the Indo-Pacific region) and original description (Weber-van Bosse 1913: 107). These specimens could usually be distinguished from other *C. racemosa–peltata* complex taxa by their stolon width, large ramuli that were usually in the form of the head of a golf club, as well as elongated rhizoidal pillars (Fig. 6, A and B; Table 1). This lineage also included specimens from New Caledonia that were identified as rather similar to *C. racemosa* f. *remota* (Svedelius) Coppejans (Fig. 6C; specimens from Sauvage et al. 2013). Apart from being slightly smaller, these specimens were similar in morphology to *C. racemosa* var. *macra* specimens and also closely matched the type illustration and description by Svedelius (1906) (as *C. clavifera* f. *remota* Svedelius; reproduced in Fig. 6D) and Coppejans et al. (2009: 115, fig. 89). Unfortunately, we were unable to newly collect *C. racemosa* f. *remota* specimens from close to the type locality (Sri Lanka).

Lineage 5 included specimens collected from Australia and New Caledonia that were identified as *C. racemosa* var. *cylindracea* (Fig. 7, A and B) and *C. racemosa* f. *complanata* (J. Agardh) Weber-van Bosse (Figs. 1E and 7, C and D), although some specimens resembled *C. racemosa* var. *laetevirens* (Montagne) Weber-van Bosse. Specimens from south-western Australia (the type locality) and South Australia were identical to the type specimen of *C. racemosa* var. *cylindracea* (as *C. cylindracea*, Fig. 7B; MEL 516014), but became more varied with ramuli arrangement becoming distichous in the tropical waters of northern Australia and New Caledonia (also see Sauvage et al. 2013: 11, fig. 5), and closely resembled the type specimen of *C. racemosa* f. *com-*

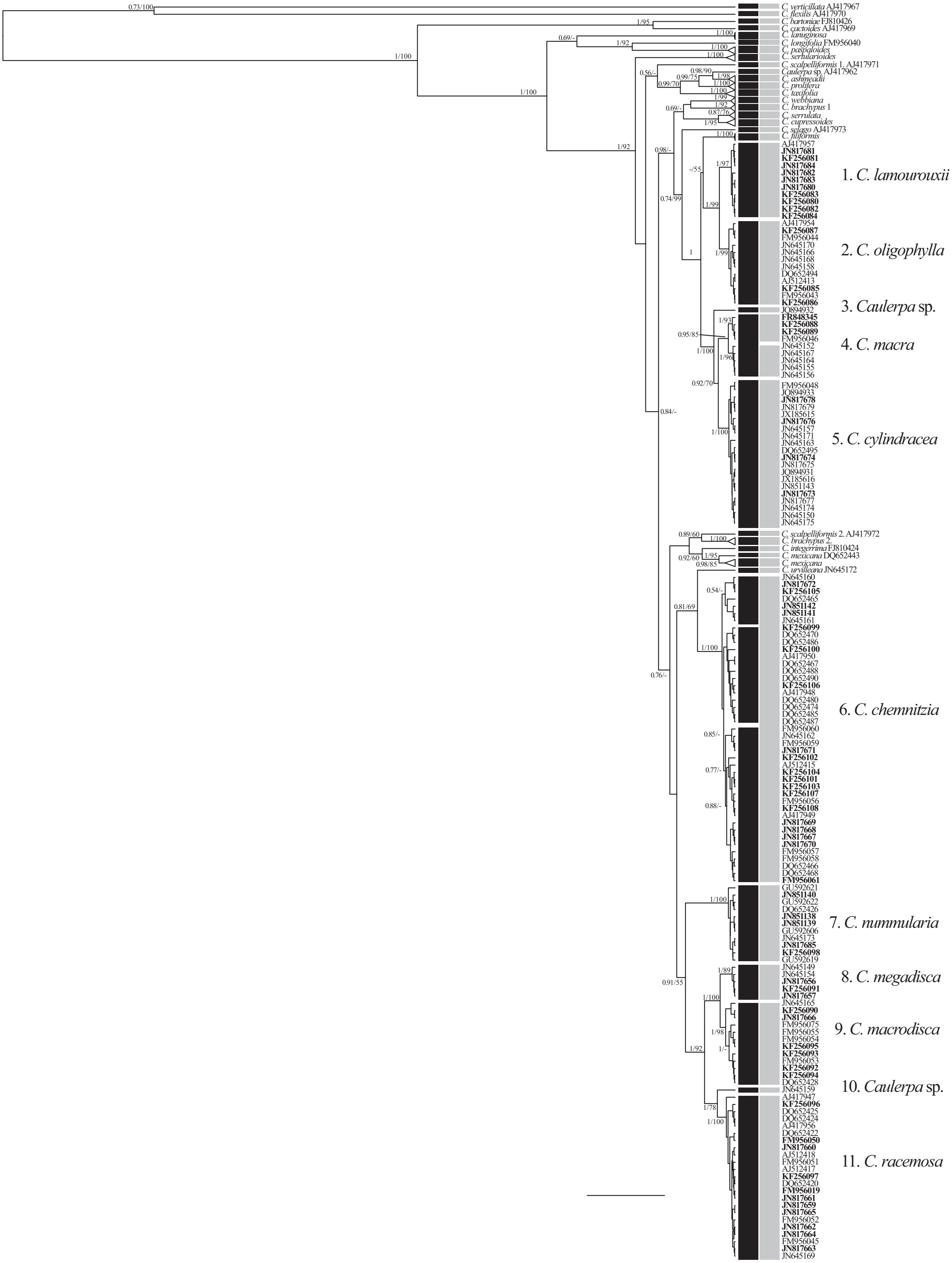

FIG. 3. Ultrametric tree of *Caulerpa* based on a Bayesian relaxed molecular clock analysis of 245 partial *tuf*A DNA sequences (912 nt, −ln = 5551.6091) with results from GMYC- and long-branch, high support species-delimitation methods. Columns to the right of the tree indicate putative species obtained under the GMYC (black) and long-branch, high support (gray) species-delimitation methods. Numbers at branch nodes correspond to BI posterior probabilities (PP) and ML bootstrap percentages (BP). PP values below 0.5 and BS values below 50% are not shown. Scale bar = 0.02 expected changes per site. Boldface = newly obtained sequences.

FIG. 4. Bayesian phylogenetic tree constructed from 57 partial *rbc*L DNA sequences of *Caulerpa* (alignment = 904 bp long). Numbered lineages correspond to those of Figure 3. Numbers at branch nodes correspond to BI posterior probabilities (PP) and ML bootstrap percentages (BP). PP values below 0.5 and BS values below 50% are not shown. Numbered lineages correspond to those of Figure 3. The scale is 0.008 expected changes per site. Boldface = newly obtained sequences.

planata (Fig. 7D). Although ramuli arrangement in this lineage varied from distichous to radial, ramuli were always clavate, although they were at times slightly flattened (e.g., Fig. 1E).

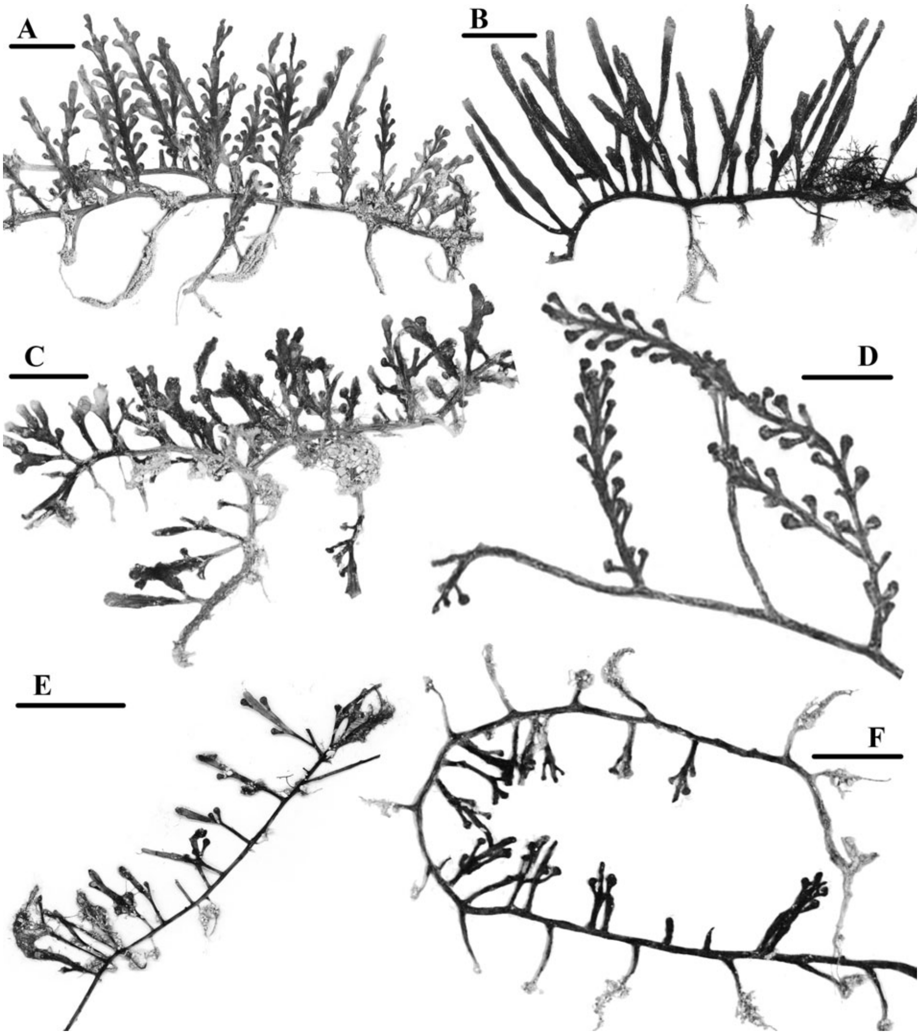

Fig. 5. Morphological variation among taxa previously assigned to the *Caulerpa racemosa* var. *lamourouxii* (Turner) Weber-van Bosse: (A) *C. lamourouxii* (Turner) C. Agardh (PERTH 08292612) from Montgomery Reef, north-western Australia; (B) *C. lamourouxii* specimen lacking ramuli (AD-A90154) from Ningaloo Reef, Western Australia; (C) *C. lamourouxii* specimen with an intermediate number of ramuli (PERTH 08428220) from Cassini Island, north-western Australia; (D) Photograph of the holotype of *C. lamourouxii* (BM000569449, as *Fucus lamourouxii* Turner); (E) Typical specimen of *C. oligophylla* Montagne (AD-A95457) from Heron Island, Great Barrier Reef, Australia; (F) Photograph of the holotype of *C. oligophylla* (MA10330 in PC) from Torres Strait, Australia. All scale bars = 20 mm.

Lineage 6 included specimens collected from the Atlantic, Indian, and Pacific Oceans and showed the largest variation in morphology (Table 1), from rather small specimens with upright assimilators bearing strictly peltate ramuli (Figs. 1A and 8A), to robust specimens with densely arranged turbinate and clavate ramuli (Figs. 1, C, D, and 8, B–D). Some specimens even bore ramuli of various forms on a single assimilator (Fig. 1D). Specimens in this lineage were identified as *C. peltata* (Figs. 1A and 8A), *C. racemosa* var. *laetevirens* (Figs. 1C and 8B), *C. racemosa* var. *occidentalis* (J. Agardh) Børgesen (Fig. 8C), *C. racemosa* var. *turbinata* (J. Agardh) Eubank (Fig. 8D), and *C. imbricata* G. Murray based on their similarity to type specimens (Figs. 2B and 8E, Figs. S4, S5 and S6A in the Supporting Information), but a myriad of intermediate specimens were also observed and some specimens were also close in morphology to *C. racemosa* var. *cylindracea* and *C. racemosa* var. *macrodisca* (Table 1). Although not from one of the Antilles Islands, a specimen from nearby Bermuda (CWS008366; Fig. 8A) was almost identical to Lamouroux's (1809b) illustration of *C. peltata* (Fig. 2B).

Lineage 7 included small, delicate, strictly peltate specimens with both crenate and entire disk margins, from which secondary peltate ramuli arose (Fig. 9A). Specimens from this lineage were only collected along the east coast of Australia (including Lord Howe Island), Micronesia, and Fiji. Although these specimens were initially identified as *C. peltata* var. *exigua* Weber-van Bosse (*sensu* Kraft 2007), *C. peltata* (*sensu* Price 2011), or *C. peltata* var. *stellata* (Harvey ex J. Agardh) Weber-van Bosse, Weber-van Bosse's (1898) illustration of the original *C. peltata* var. *exigua* concept clearly depicts secondary ramuli arising from the center of the subtending disk, not the margins. As such, these small delicate peltate plants, with secondary peltate ramuli arising from the disk margin, more accurately corresponded to *C. nummularia* (currently regarded as a heterotypic synonym of *C. peltata*, Price 2011). This identification was further confirmed by the original description of *C. nummularia* (Agardh 1873), observations

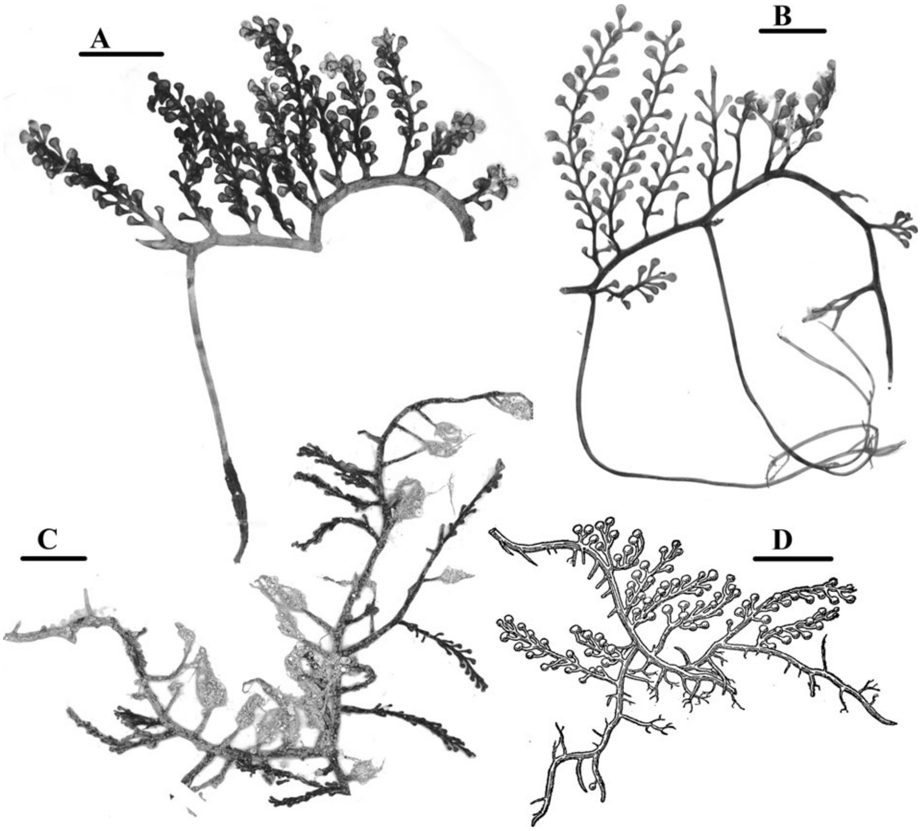

FIG. 6. Morphological variation among taxa and specimens assigned to *Caulerpa macra* (Weber-van Bosse) Draisma & Prud'homme *stat. nov.* in the present study. (A) Photograph of the holotype of *C. macra* (L 0054712 as *C. racemosa* var. *macra* Weber-van Bosse); (B) Recently collected specimen from Chuuk Island, Micronesia (L 0925909); (C) Smaller specimen from New Caledonia (= IRD5624), morphologically identified as *C. racemosa* f. *remota* (Svedelius) Coppejans); (D) Illustration of *C. racemosa* f. *remota* by Svedelius (1906) (fig. 14, as *C. clavifera* f. *remota*). All scale bars = 20 mm.

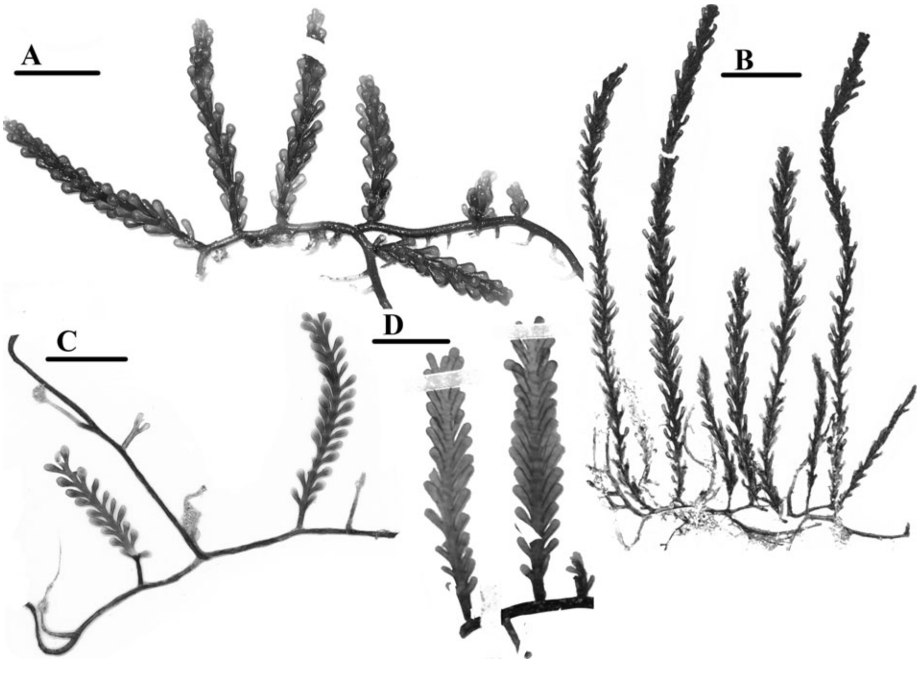

FIG. 7. Morphological variation among taxa assigned to *Caulerpa cylindracea* Sonder in the present study. (A) Specimen from south-western Australia (GWS025471); (B) Photograph of an isotype specimen (TCD001105); (C) Complanate form from Lizard Island, Great Barrier Reef, Australia (AD-A88114; previously *C. racemosa* f. *complanata* (J. Agardh) Weber-van Bosse). (D) Photograph of the holotype of *C. racemosa* f. *complanata* (originally described as *C. complanata* J. Agardh, Herb. Agardh 16718, in LD). All scale bars = 20 mm.

of syntype specimens in TCD and NSW (see Fig. 9B), and previous accounts of *Caulerpa* species from the Pacific region (i.e., Cribb and Cribb 1985, South and Skelton 2003, Abbott and Huisman 2004, Skelton and South 2007). The morphology of specimens in this lineage was unique.

Lineages 8 and 9 included specimens that were identified as *C. racemosa* var. *macrodisca* that could

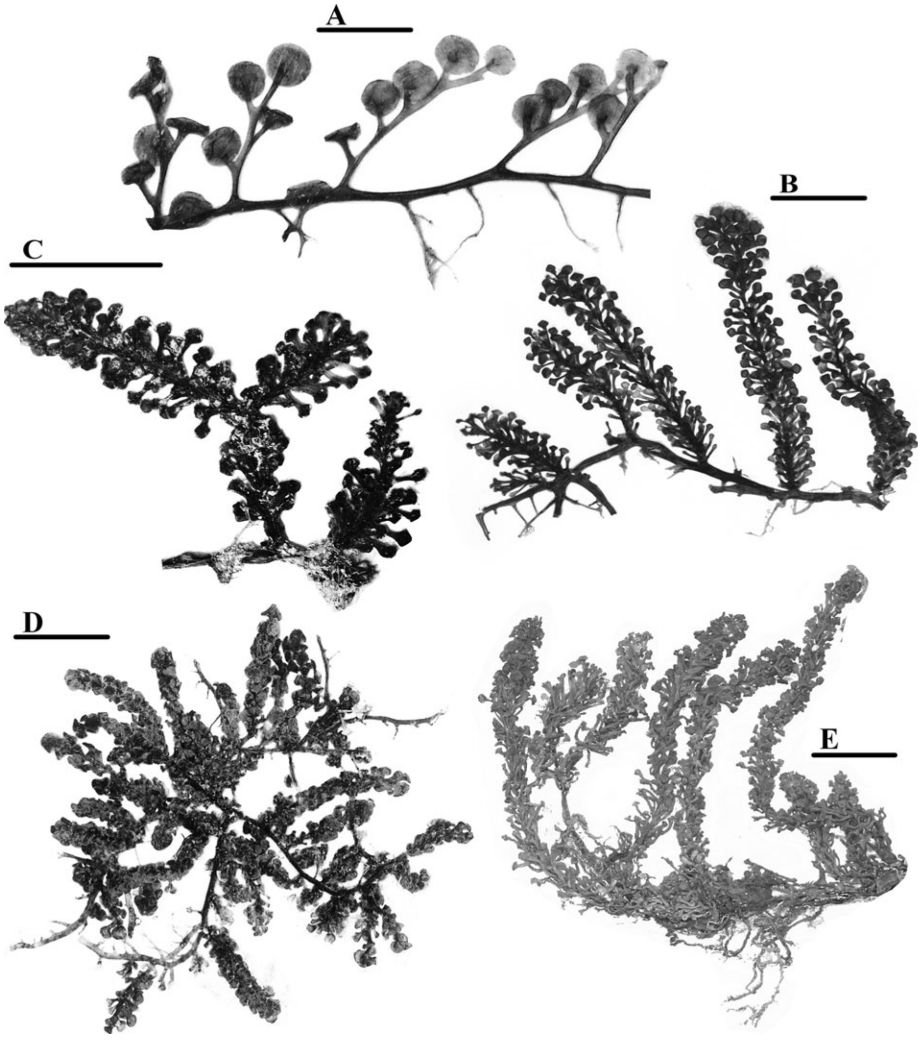

FIG. 8. Morphological variation among *Caulerpa chemnitzia* (Esper) J.V. Lamouroux taxa discussed in the present study. (A) Peltate specimen (CWS008366) from Bermuda (previously *C. peltata* J.V. Lamouroux); (B) AD-A92587 from Lizard Island, Great Barrier Reef, Australia (previously *C. racemosa* var. *laetevirens* (Montagne) Weber-van Bosse); (C) Specimen from Bermuda (= CWS008555; previously *C. racemosa* var. *occidentalis* (J. Agardh) Børgesen); (D) Pressed specimen of a recently collected individual from Sri Lanka (HEC15952); (E) Photograph of the holotype of *C. chemnitzia* (25805 in ER). Scale bars: A, E = 10 mm; B = 30 mm; C = 20 mm; D = 25 mm.

easily be morphologically distinguished from other lineages, although specimens in lineage 9 could at times resemble peltate specimens from lineage 6. Specimens in lineage 9 (Fig. 9C) closely resembled the lectotype illustration (Decaisne 1846-1864; pl. 1, fig. 1 as *C. macrodisca*; reproduced as our Fig. 9D), whereas specimens from lineage 8 had ramuli that were not arranged around an upright assimilator, but rather the assimilators consisted of a single peltate branch (Fig. 9E). No intermediates between the two forms were observed during the present study.

Lineage 11 included specimens that were collected from the Atlantic, Indian, and Pacific Ocean regions and were closest in morphology to the *C. racemosa* type morphology (compare Figs. 1A and 10A to 2A). It also included specimens that were identified as *C. racemosa* var. *macrophysa* (Sonder ex Kützing) W.R. Taylor (Fig. 10B) and *C. racemosa* var. *mucronata* L.N. de Senerpont Domis (Fig. 10C, specimen from de Senerpont Domis et al. 2003). Specimens from this lineage could usually be distinguished from other *C. racemosa–peltata* complex taxa by having ramuli that expanded abruptly from a relatively short slender stalk to a subspherical upper part, with the stalk length not being greater than the diameter of the distal regions, although some of the larger specimens could have been identified as *C. racemosa* var. *lamourouxii* (lineage 1). Unlike *C. racemosa* and *C. racemosa* var. *macrophysa, C. racemosa* var. *mucronata* showed considerable variation in ramulus form, with ramuli often completely absent from assimilators (Fig. 10C). Unfortunately, no specimens matching the type specimen of *C. racemosa* were located near the type locality (Red Sea) during the present study.

DISCUSSION

As molecular-based studies continue to show increased rates of species discovery and mismatches between molecular and morphological species concepts, the greatest challenge for algal taxonomy in the future will be how to designate names, includ-

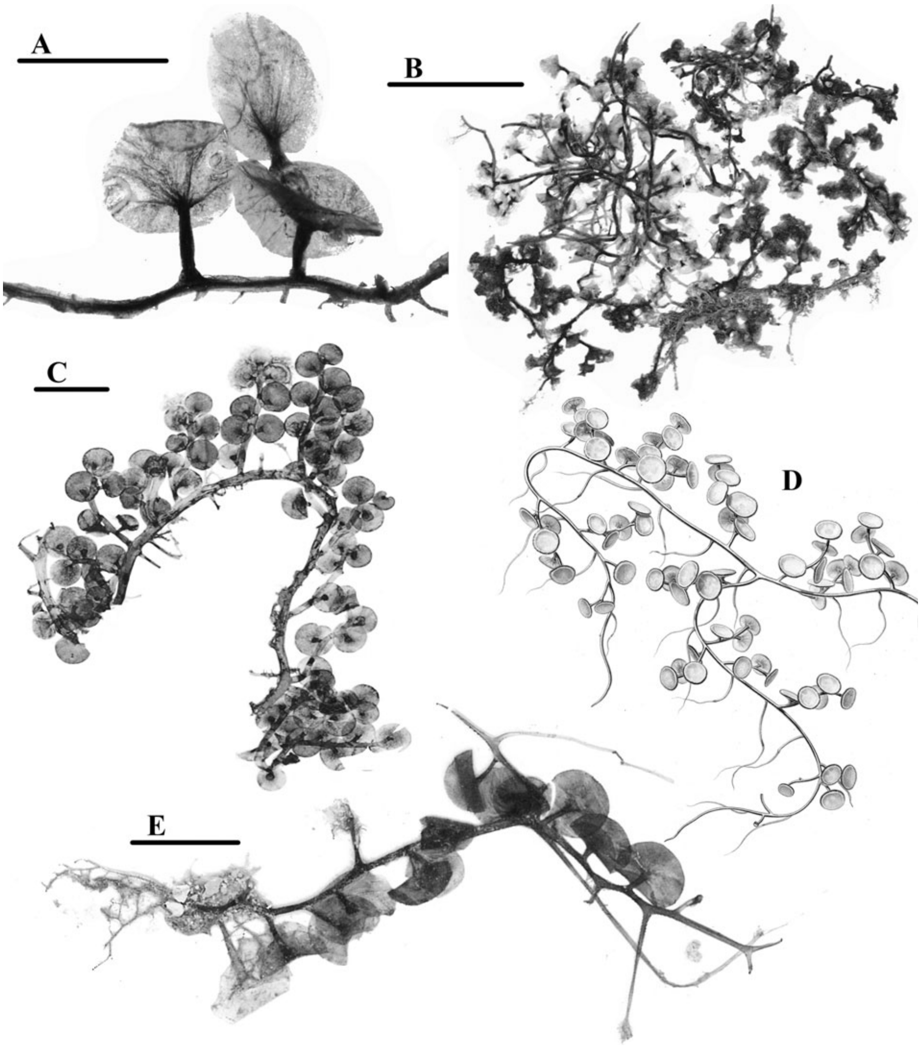

Fig. 9. Morphological variation of *Caulerpa racemosa-peltata* complex taxa discussed in the present study. (A) *C. nummularia* Harvey ex. J. Agardh (AD-A91369) from Heron Island, Great Barrier Reef, Australia, showing ramuli disk arising from margin of parent disk; (B) Syntype specimen of *C. nummularia* (TCD 00111032). (C) *C. macrodisca* Decaisne (L 0509359/FM965053) from Indonesia with characteristic upright assimilator morphology; (D) Copy of the lectotype illustration of *C. macrodisca* by Decaisne (1846 (1846-1864), pl. 1, fig. 1); (E) *C. megadisca* Belton & Gurgel *sp. nov.* (AD-A90107) from Lizard Island, Great Barrier Reef, Australia showing typical single peltate disk morphology. Scale bars: A = 0.5 mm; B = 25 mm; C, D, E = 20 mm.

ing those that have been previously described, to newly sequenced specimens (De Clerck et al. 2013). Ideally, one could aim to sequence every type specimen; however, this is a time-consuming process that may prove futile if specimens cannot be located, sequenced, or accessed. Although we acknowledge that without sequencing type specimens there may always be a level of uncertainty in the naming of lineages, including those of the present study, we are at the point in algal systematics where we need to be pragmatic and revise taxonomies to the best of our abilities. With this in mind, the primary goal in the present study was to resolve the taxonomy of the *C. racemosa–peltata* complex, one of the most taxonomically troublesome groups in the algae. The complex also has a large number of synonyms and infra-specific names that could potentially be used to name genetic lineages, and these were taken into account. We sequenced a large number of globally collected specimens to obtain a well-sampled DNA taxonomy and, for many taxa, this included sequences from type locality or regions. We then delimited species using our *tuf*A data set and two commonly used methodologies (long branch/high support and GMYC). Although the GMYC species delineation technique has its pitfalls (Lohse 2009, Papadopoulou et al. 2011, Reid and Carstens 2012, Silberfeld et al. 2013), it provides an objective tool to rapidly delimit species in large, well-sampled, single marker data sets. As our data set was large and well-sampled, the GMYC results were robust (i.e. significant difference between null model and GMYC model, and a narrow confidence interval) and results from both species-delimitation methods were largely congruent, we are confident in accepting the presence of at least 11 distinct species-level entities within the *C. racemosa–peltata* complex, although only nine of these are considered here.

We found that the morphological characterization of five of these lineages was fraught with the difficulties caused by high levels of phenotypic plasticity (Table 1), and in many instances, the morphological overlap of genetic species (e.g., lineages 1 and

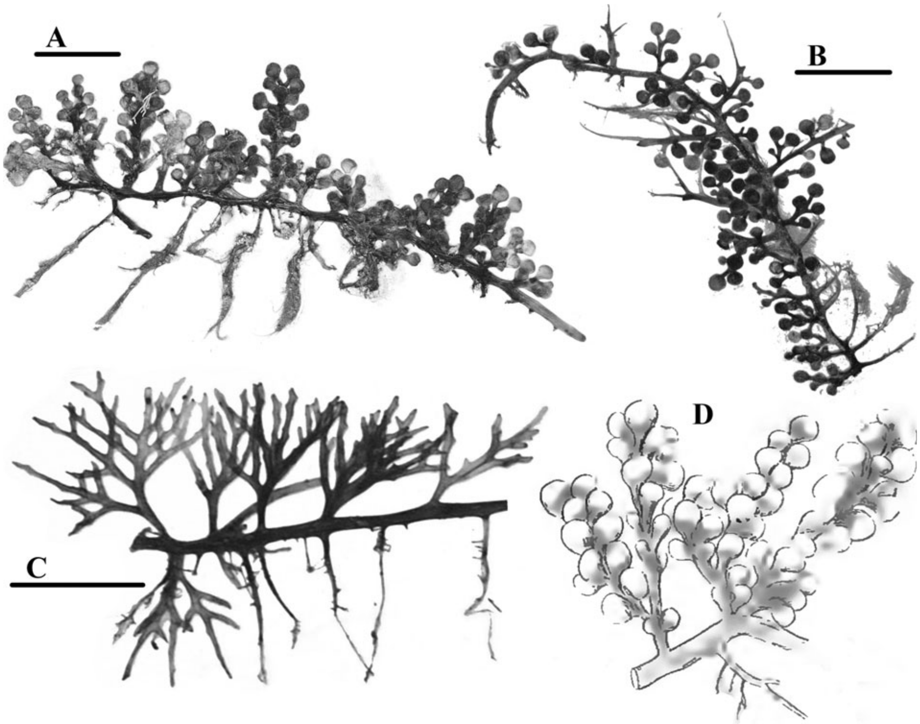

Fig. 10. Morphological variation among taxa assigned to *Caulerpa racemosa* (Forsskål) J. Agardh discussed in the present study. (A) Pressed voucher of *C. racemosa* (PERTH 08292728) from Montgomery Reef, north-western Australia; (B) *C. racemosa* var. *macrophysa* (Sonder ex Kützing) W.R. Taylor (AD-A90071) from Lizard Island, Great Barrier Reef, Australia; (C) Photograph of the holotype of *C. racemosa* var. *mucronata* L.N. de Senerpont Domis (L 0535499); (D) Illustration of *C. racemosa* var. *macrophysa* by Kützing (1857) (tab. 15 fig. II, as *Chauvinia macrophysa* Sonder ex Kützing). All scale bars = 20 mm.

2). As such, although some lineages showed distinct morphologies with minimal phenotypic plasticity (e.g., lineage 7), as an overarching conclusion for identifying our nine species, we strongly suggest the use of molecular-based identifications.

With regard to the correct nomenclatural assignment of our nine lineages, we have based our designations and nomenclatural decisions on what we regard as "best practice": molecular data obtained from specimens collected from near the type locality, that were matched with type material, original illustrations and/or descriptions. Importantly, we found that by first grouping specimens into species using molecular data, we were able to determine the true extent of morphological variation within each species. Once this was understood, we were then able to confidently match newly collected specimens with type specimens/original descriptions/illustrations (details are listed under each species below). Unfortunately, the only lineage for which we were unable to locate specimens from the type locality or type region that resembled the type specimen was *C. racemosa* (lineage 11), and we highly recommend that future studies attempt to do so. However, we are confident in assigning this lineage to *C. racemosa* for the time being as specimens closely resembled the type specimen and were in agreement with most concepts of *C. racemosa* (e.g., Coppejans and Prud'homme van Reine 1992: 698, as *C. racemosa* ecad *racemosa*; Price 2011: 185, as *C. racemosa* var. *racemosa*). In order to reduce confusion and begin the process of solving the cumbersome nature of *Caulerpa* taxonomy, we also feel it appropriate to not recognize any infra-specific ranks (i.e., varieties and forms) within the species recognized below. However, we do suggest that the use of morphological entities without formal taxonomic status (e.g., "*ecads*") may be useful for field workers when collecting highly plastic species such as *C. chemnitzia* (e.g., *C. chemnitzia* ecad *peltata*). Arrangements have also been made with GenBank to update their *tuf*A records with the newly corrected names.

The following *C. racemosa–peltata* complex taxa were not encountered during the present study: *C. laetevirens* f. *caespitosa* Svedelius; *C. racemosa* (var. *laetevirens)* f. *compressa* W. R. Taylor; *C. racemosa* (var. *uvifera*) f. *compressa* Weber-van Bosse; *C. racemosa* f. *condensata* Weber-van Bosse; *C. laetevirens* f. *depauperata* Svedelius; *C. dichotoma* Svedelius; *C. racemosa* var. *disticha* V. J. Chapman; *C. racemosa* f. *elongata* Weber-van Bosse; *C. racemosa* f. *hypocrateriaeformis* Weber-van Bosse; *C. uvifera* f. *intermedia* Weber-van Bosse; *C. racemosa* (var. *laetevirens*) f. *laxa* (Greville) Weber-van Bosse; *C. racemosa* (var. *cylindracea*) f. *laxa* (Greville) Weber-van Bosse; *C. chemnitzia* f. *major* Weber-van Bosse; *C. chemnitzia* f. *minor* Piccone; *C. racemosa* f. *mixta* Svedelius; *C. clavifera* f. *nuda* Kützing; *C. parvula* Svedelius; *C. uvifera* f. *planiuscula* Svedelius; *C. racemosa* f. *reducta* Børgesen; *C. racemosa* f. *simplicissima* Børgesen; *C. racemosa* f. *semifalcata* V. D. Chauhan & Thivy; A.D. Zinova & N.H. Dinh; *C. clavifera* f. *vulgaris* Kützing; and *C. zeyheri* Kützing. It is hoped that future studies endeavor to collect and sequence these taxa and make comparisons to sequences from the present study in order to confirm their taxonomic status.

Lastly, our data set also showed that a number of morphologically accepted *Caulerpa* species were represented by multiple genetic species (Fig. 3; e.g., *C. brachypus* Harvey, *C. mexicana* Sonder ex Kützing and *C. scalpelliformis* (R. Brown ex Turner) C. Agardh) and the global diversity of *Caulerpa* is most likely underestimated. Taxonomic work should continue in order to resolve the taxonomy of this ecologically important and distinctive genus.

TAXONOMIC CONCLUSIONS

Lineage 1: ***Caulerpa lamourouxii*** (Turner) C. Agardh 1817: xxii (Figs. 1B and 5, A–D).

Basionym: Fucus lamourouxii Turner in *Fuci*. IV: 80, pl. 229 (1811–1819).

Type locality and specimen: Red Sea; BM000569449, in BM.

Distribution: Indian Ocean and Red Sea.

DNA barcode: KF256081, Marsa Alam, Egypt, Red Sea, voucher: HV03477.

Homotypic synonyms: C. clavifera var. *lamourouxii* (Turner) C. Agardh 1823: 438, *Ahnfeldtia lamourouxii* (Turner) Trevisan 1849: 142, *Chauvinia clavifera* var. *lamourouxii* (Turner) Kützing 1849: 498, *C. racemosa* var. *lamourouxii* (Turner) Weber-van Bosse 1898: 368, pl. XXXII, figs. 1–7, pl. XXXIII, fig. 15.

Selected illustrations: as *Fucus lamourouxii* Turner 1811-1819, pl. 229.

Remarks: The occurrence of ramuli in this taxon is extremely variable. When present, they are always marginal, but their frequency on individual assimilators differs considerably, from absent (Figs. 1B and 5B) to arising in a regular opposite pattern, with a slightly compressed rachis in the type form (Fig. 5, A and D). Molecular data from the present study found two distinct species among specimens identified as *C. racemosa* var. *lamourouxii* (Figs. 3 and 4; Fig. S1). Because the first lineage included specimens from Western Australia and the Red Sea (= type locality), and many recently collected plants closely resembled the type specimen (Fig. 5D) and illustrations thereof (Turner 1811-1819: 79, pl. 229), we feel confident in reinstating the name *C. lamourouxii* for these specimens. Unfortunately, no *C. racemosa* var. *lamourouxii* f. *requienii* or *C. racemosa* var. *gracilis* like specimens were newly collected from near their type localities in the Red Sea. Due to this, and the dissimilarity of these type specimens (Fig. S3) with *C. racemosa* var. *lamourouxii* f. *requienii* morphotype specimens collected in the present study and discussed previously, we do not list these taxa as synonyms of *C. lamourouxii* at present.

The forms displayed by *C. lamourouxii* specimens in the present study were different to specimens from the Caribbean Sea and Bermuda previously identified as *C. racemosa* var. *lamourouxii* (Littler and Littler 2000: 371). Atlantic specimens appear to be more delicate and exhibit a more uniform arrangement of clavate ramuli (e.g., Littler and Littler 2000) as opposed to the high variability in occurrence and form of ramuli from Red Sea and Indian Ocean specimens. Furthermore, specimens identified as *C. racemosa* var. *lamourouxii* from the Caribbean Sea or Bermuda fell into the *C. chemnitzia* clade, and not in the *C. lamourouxii* lineage, and *C. lamourouxii* is most likely absent from the tropical western Atlantic.

Lineage 2: ***Caulerpa oligophylla*** Montagne 1842: 14 (Fig. 5, E and F).

Type locality and specimens: Toud Island [Warrior Islet], Torres Strait, Australia; as no holotype was ever designated, MA10330 Herb. Montagne, at PC is designated here as lectotype (Fig. 5F).

Distribution: Northeastern Australia, New Caledonia, Indonesia, Japan and the Philippines. Most likely widespread throughout the Western Pacific.

DNA barcode: KF256085, Heron Island, Great Barrier Reef, Australia, voucher: AD-A95457 (Fig. 5E).

Selected illustrations: as *C. racemosa* var. *lamourouxii*: Weber-van Bosse 1898, Pl. 32, fig. 6; Coppejans and Prud'homme van Reine 1992: 694, fig. 15B; Littler and Littler 2003: 229.

Remarks: As mentioned under *C. lamourouxii* above, there was a second *Caulerpa* lineage that included specimens initially identified as *C. lamourouxii* morphotypes (Fig. 3, as *C. oligophylla*). As with *C. lamourouxii*, ramuli form and occurrence was highly variable in specimens from this lineage, with many specimens lacking ramuli completely (Fig. 5E). The most appropriate name we found for this lineage was *C. oligophylla*, a species described from Torres Strait, Australia, but currently regarded as a heterotypic synonym of *C. lamourouxii*. Indeed, newly collected specimens from close to the type locality strongly agree with the type specimen of *C. oligophylla* (compare Fig. 5, E and F). Unfortunately, we could not find any clear morphological characters to distinguish between *C. oligophylla* and smaller *C. lamourouxii* specimens and it is likely that the best means to distinguish these taxa is through DNA sequence data.

Lineage 4: ***Caulerpa macra*** (Weber-van Bosse) Draisma & Prud'homme **stat. nov.** (Fig. 6, A–C).

Basionym: C. racemosa var. *macra* Weber-van Bosse, in Liste des algues du Siboga, *Siboga-Expeditie* 59a, p. 106, fig. 26 (1913).

Updated description: Large *Caulerpa* with long thick stolons, these several decimeters long, 3–5 mm in width but often over 5 mm. Rhizoidal pillars well developed, arising from stolons at irregular distances, up to 10 cm long and several mm in diameter, often with thick terminal clumps of branched rhizoids. Erect assimilators up to 10 cm in height, with irregularly to regularly placed ramuli arranged distichously or radially and opposite or alternate. Ramuli oviform, pyriform, more rarely claviform, usually with some having a form like the head of a golf club, to 12 mm long and 6 mm in width.

Lectotypus: Designated here in L, HLB 938,7-462, Barcode L0054713 (Fig. 5A); isolectotype also in L, HLB 937, 336-70, barcode L0054712, both collected 11 August 1899.

DNA barcode: KF256089, Berau delta, North-Eastern Kalimantan, Indonesia, voucher: L 03-453.

Type locality: In the lagoon of Fau Island, close to Gebé Island, Sea of Halmahera, Indonesia (0°06′ S, 129°25′ E), Siboga Expedition, station 149, in fine mud.

Etymology: Probably from "*macro*"(Greek) = long, large, great. Note: there is also a *C. racemosa* var. *laetevirens* f. *cylindracea macra* (Harvey) Weber-van Bosse (basionym *C. cylindracea* var. *macra* Harvey 1858, where the name "*macra*" is probably a female form of the Latin word "*ma'cer*" = thin, meager).

Distribution: Fiji, Guam, Indonesia, Micronesia, New Caledonia and Papua New Guinea.

Specimens examined: Lectotype and isolectotype; #L13072A, Madang, Papua New Guinea, July 10, 1990; L03-453, Berau, N.E. Kalimantan, Indonesia, October 2003; SGAD0712207 Raja Ampat, Province West Papua, Indonesia, December 2007; L0925909, Chuuk, Micronesia, August 2008; LNR13a0109, Northern Reefs, Palau, March 2009; SGAD1012338, Silawa I., East Sabah, Borneo, December 2010; all in L. The following specimens from Sauvage et al. (2013) were also examined: IRD5626 (JN645155), IRD5625 (JN645156), IRD5640 (JN645167), IRD1878 (JN645152), IRD5624 (JN645164), FM956046 and FM956047.

Habitat: Sheltered shallow lagoons with a sandy or muddy substratum; the alga is always submerged.

Selected illustrations: as *C. racemosa* var. *macra*: Weber-van Bosse 1913: 107, fig. 26.

Remarks: Weber-van Bosse described *C. racemosa* var. *macra* (now *C. macra*) from specimens collected in Indonesia. Although she thought that her new variety was closely related to *C. racemosa* vars. *lamourouxii* and *laetevirens*, she regarded it as distinct due to its larger ramuli that were regularly spaced. Specimens that were almost identical to the type specimens (designated above) and the original illustration (Weber-van Bosse 1913: fig. 26) were newly collected from a number of localities around Indonesia and nearby in Micronesia and Papua New Guinea during the present study. In agreement with Weber-van Bosse, these specimens could also be distinguished from other *C. racemosa–peltata* complex taxa by their morphology (Table 1) and molecular sequence data (Figs. 3 and 4; Fig. S1), thus justifying their status as a distinct species.

It should be noted that specimens from Sauvage et al. (2013) that were morphologically identified as *C. racemosa* f. *remota* from New Caledonia (JN645155, -56, -64, - 67; details in Table S1) and Fiji (JN645152) formed a well-supported clade preceded by a relatively long branch (Fig. 3). However, its independence from *C. macra* was not supported by the GMYC analyses (Fig. 3) and, as such, they were not recognized as a distinct species in the present study. Morphologically these specimens were very similar to *C. macra*, but slightly smaller (Fig. 6C). As *C. racemosa* f. *remota* specimens from the type locality in Sri Lanka were neither available nor analyzed during the current study, we hesitate at present to list *C. racemosa* f. *remota* or *C. clavifera* f. *remota* as synonyms of *C. macra*.

Lineage 5: ***Caulerpa cylindracea*** Sonder 1845: 49-57 (Figs. 1E and 7, A–D).

Type locality and specimen: Western Australia; holotype: 516014 in MEL.

Distribution: Australia, Indonesia, New Caledonia, Canary Islands and the Mediterranean Sea.

DNA barcode: JN851143, Point Peron, Western Australia, voucher: GWS025471 (Fig. 7A).

Homotypic synonyms: *C. racemosa* [var. *laetevirens*] f. *cylindracea* (Sonder) Weber-van Bosse 1898: 366, pl. XXXIII: figs. 17, 19, 20; *C. racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman & Boudouresque, in Verlaque et al. 2003: 336.

Heterotypic synonym: C. complanata J. Agardh 1873: 33, *C. racemosa* f. *complanata* (J. Agardh) Weber-van Bosse 1898: 364-365, pl. XXXIII: figs. 13, 14; *C. cylindracea* var. *macra* Harvey 1858, pl. XXX, fig. 2.

Selected illustrations: as *C. cylindracea*: Harvey 1858, Pl. XXX. As *C. racemosa* var. *laetevirens* f. *cylindracea.* Womersley 1984, fig. 91B, 92D; Huisman 2000: 255. As *C. racemosa* var. *cylindracea*: Sauvage et al. 2013: 11, fig. 4.

Remarks: Although described as an independent species by Sonder (1845), *C. cylindracea* has mostly been considered a form of *C. racemosa* var. *laetevirens* (Weber-van Bosse 1898, Womersley 1956, 1984, Huisman 2000). Verlaque et al. (2003) raised this forma to varietal status (*C. racemosa* var. *cylindracea*) while investigating the source of the introduced *C. racemosa* in the Mediterranean Sea, citing the lack of distributional overlap with *C. racemosa* var. *laetevirens*, lack of rhizoidal pillars, its more slender thallus, the slight inflation of the basal part of the frond axis, clavate to cylindrical ramuli (never peltate or turbinate) and by its molecular distinction from other *C. racemosa* infraspecific taxa based on ITS1, 5.8S and ITS2 sequence data. Although Verlaque et al. (2003: 331) mentioned thin rhizoids (and no rhizoidal pillars) as characteristic of *C. cylindracea*, inspection of the type (MEL 516014, Fig. 7B) shows the occurrence of distinct rhizoidal pillars, which can also be observed in Sauvage et al. (2013, fig. 4). Sauvage et al. (2013) also showed the genetic independence of *C. racemosa* var. *cylindracea* as a species-level entity, but did not make the taxonomic change. On the basis of their results as well as those from Verlaque et al. (2003) and the present study, we propose the reinstatement of *C. cylindracea*.

Although extensive collections were made in the present study, no *Caulerpa* sequences other than those from Australia, New Caledonia, Canary Islands, and the Mediterranean Sea clustered with *C. cylindracea* and, as noted by Sauvage et al. (2013), reports of *C. cylindracea* outside of these regions should be interpreted carefully, and will require molecular confirmation for clarification (as *C. cylindracea*: Guadalupe in Setchell and Gardner 1930, Mexico in Pedroche et al. 2005, India, Kenya, and Sri Lanka in Silva et al. 1996, as *C. cylindracea* f. *laxa* (Greville) Weber-van Bosse: Sri Lanka in Silva et al. 1996 and Coppejans et al. 2009).

Molecular data from Sauvage et al. (2013) and the present study (Fig. 3) also showed *C. racemosa* f. *complanata* (Figs. 7, C and D) to be genetically identical to *C. cylindracea* (it should be noted that *C. racemosa* f. *complanata* was recently synonymized with *C. racemosa* var. *laetevirens* by Price 2011). As such, we propose synonymizing *C. racemosa* f. *complanata* with *C. cylindracea*.

Lastly, some forms of *C. chemnitzia* (especially those previously assigned to *C. racemosa* var. *laetevirens*) were found to closely resemble *C. cylindracea*, but the latter could usually be distinguished by the smaller size of both stolon and ramulus form, and by its often distichously, or partly distichously, arranged ramuli (Table 1). However, identification may prove difficult in some specimens, especially young plants, and we suggest that molecular sequence data always be used to confirm identifications.

Lineage 6: ***Caulerpa chemnitzia*** (Esper) J. V. Lamouroux 1809a: 332 (Figs. 1, A, C, D; 8, A–E).

Basionym: Fucus chemnitzia Esper, *Icones Fucorum …* Vol. 1, Part 4: 167, pl. LXXXVIII, figs. 1, 4–6 (1800).

Type locality and specimen: aus den Malabarische Küsten [Malabar Coast], India; holotype: 25805 in ER (Fig. 8E); isotypes: 690468 in MEL and 937.336-82 in L.

Distribution: Pantropical.

DNA barcode: KF256101, Matara, Sri Lanka, voucher: HEC15952 (Fig. 8D).

Heterotypic synonyms: Lamouroux 1809a: 332-333; C. peltata J.V. Lamouroux 1809b, 145 & pl.3, fig. 2a, 2b; *C. clavifera* (Turner) C. Agardh var. *turbinata* J. Agardh 1837: 173, *C. laetevirens* Montagne 1842: 13, *C. chemnitzia* var. *peltata* (J.V. Lamouroux) Zanardini 1858: 287, *C. chemnitzia* var. *occidentalis* Agardh 1873: 37, *C. imbricata* G. Murray 1887: 37-38; *C. racemosa* f. *turbinata* (J. Agardh) Weber-van Bosse 1898: 370-371, pl. XXXI: fig. 8; *C. racemosa* var. *laetevirens* (Montagne) Weber-van Bosse 1898: 366, *C. peltata* f. *imbricata* (G. Murray) Weber-van Bosse 1898: 375, *C. racemosa* var. *chemnitzia* (Esper) Weber-van Bosse 1898: 376, pl. XXXI: figs 5–7; *C. racemosa* var. *occidentalis* (J. Agardh) Børgesen 1907: 379, figs 28, 29; *C. racemosa* var. *imbricata* (Kjellman) Eubank 1946: 423, fig. 2w; *C. racemosa* var. *peltata* (Lamouroux) Eubank 1946 421-422, fig. 2, r-s; *C. racemosa* var. *turbinata* (J. Agardh) Eubank 1946: 420–421, fig. 2o; *C. racemosa* f. *occidentalis* (J. Agardh) Nizamuddin 1964: 207, figs. 5, 5a, pl. 2b

Selected illustrations: as *Fucus chemnitzia*: Esper 1800: 127, Pl. LXXXVIII, figs. 1, 4–6; Turner 1811-1819: pl. 200. As *C. chemnitzia* Svedelius 1906: 129, figs. 26–30; As *C. racemosa* var. *chemnitzia*: Weber-van Bosse 1898, Pl. 31, figs. 5–8; Reinke 1899: 38, fig. 57. As *C. racemosa* var. *turbinata*: Eubank 1946: 420, fig. 2, o–q; Price 2011: 181, fig. 9E. As *C. peltata*: Lamouroux 1809b, Pl. 3 fig. 2, a–b; Weber-van Bosse 1898 Pl. 31, fig. 9. As *C. racemosa* var. *peltata*: Coppejans and Prud'homme van Reine 1992: 697 fig. 16, A–B; Littler and Littler 2000: 373, Kraft 2007: 185, fig. 68G. As *C. racemosa* var. *laetevirens*: Coppejans and Prud'homme van Reine 1992: 695, fig. 16, A–C; Kraft 2007: 185, fig. 68F; Price 2011: 182, fig. 10C. As *C. racemosa* var. *occidentalis*: Børgesen 1907: 379, figs. 28–29; Taylor 1960: 696, fig. 6; Littler and Littler 2000: 371. As *C. imbricata*: Coppejans et al. 2009: 106-107, fig. 81.

Remarks: Specimens in this lineage were morphologically identified as *C. racemosa* vars. *turbinata*, *laetevirens*, and *occidentalis*, *C. imbricata* and *C. peltata*. Comparative morphological observations of these taxa show a continuous morphological gradient between them. When regarding this lineage as an independent species, the earliest available name is *C. chemnitzia* (Esper) J.V. Lamouroux, based on *F. chemnitzia* Esper, a species described from southern India by Esper in 1800, but which is currently considered a heterotypic synonym of *C. racemosa* var. *turbinata* (Price 2011). A sequence from a specimen (HEC15952, from Sri Lanka; Fig. 8D) that was almost identical to the type specimen of *C. chemnitzia* (Fig. 8E) clustered with sequences of *C. racemosa* vars. *laetevirens*, *occidentalis,* *turbinata*, *C. imbricata,* and *C. peltata* (Figs. 3 and 4; Fig. S1), giving further support to the use of the *C. chemnitzia* name for this lineage.

There is considerable historical precedence for our proposed taxonomy, with many studies suggesting that these taxa were environmentally induced forms of the same entity (Peterson 1972, Ohba and Enomoto 1987, Coppejans and Prud'homme van Reine 1992, de Senerpont Domis et al. 2003, Price 2011). Furthermore, *C. peltata* was treated as a variety of *C. chemnitzia* by Turner (1811-1819: 8), a move that, according to Turner, even Lamouroux acknowledged "*may probably be the case*." Central to this debate was the uncertain placement of *C. peltata*, with some authors accepting it as distinct from *C. racemosa* (e.g., Silva et al. 1996, Littler and Littler 2000, Price 2011), while others have treated it at various infraspecific levels within *C. racemosa* (e.g., Weber-van Bosse 1898, Coppejans and Prud'homme van Reine 1992, Huisman 2000), while still others accepted both *C. peltata* and *C. racemosa* var. *peltata*

Eubank (Kraft 2007). This debate is further confounded by the presumed loss of the *C. peltata* type specimen, and thus our concept of the species is by necessity based on Lamouroux's (1809b) illustrations (Fig. 2B) and description (Lamouroux 1809a). Although it has been suggested that Lamouroux wrongly interpreted the stolon branches as erect axes (Price 2011: 179), our observations of material from the same region as the probable type locality (Antilles Islands) suggest that Lamouroux was indeed depicting erect assimilators bearing radially arranged peltate ramuli.

However, clarifying the concept of *C. peltata* has minimal impact on establishing an accurate taxonomy, as by far the greatest confusion stems from the occurrence of peltate ramuli in three other species within the *C. racemosa–peltata* complex (viz. *C. macrodisca*, *C. megadisca* sp. nov. and *C. nummularia*). Fortunately, these taxa can be distinguished from *C. chemnitzia* by their much larger peltate disks (*C. macrodisca* and *C. megadisca*) and branching pattern (*C. nummularia*). Furthermore, *C. chemnitzia* is pantropically distributed, whereas *C. macrodisca*, *C. megadisca,* and *C. nummularia* appear to be restricted to the central Indo-Pacific region.

It should be noted that there remains some confusion over the type locality of *C. peltata,* as although Lamouroux (1809a) gave "*Antilles*" as its (type) locality, in the paper where *C. peltata* is illustrated (1809b), he did not name any locality, only "*ded. Thuillier.*" Later, Lamouroux (1813) cited "*Oris Amer. Merid. Orient.*" and in 1823 he cited "*côtes occidentales de l'Afrique.*" Until the type specimen is located, we suggest that the eldest listed locality, the Antilles Islands, should be regarded as the probable type locality of *C. peltata.*

Interestingly, our *C. chemnitzia* sensu stricto specimen (HEC 15952) would have been identified as *C. imbricata* based on the description of Coppejans et al. (2009). However, on the basis of observations of a large number of specimens including type specimens, we concluded that *C. chemnitzia* and *C. imbricata* were the same entity. Furthermore, Coppejans et al. (2009) also suggested that *C. imbricata* specimens from Sri Lanka closely resembled *C. chemnitzia* (as *C. racemosa* var. *chemnitzia* (Esper) Weber-van Bosse. As such, we are confident of listing *C. imbricata* as a heterotypic synonym of *C. chemnitzia.*

Lastly, it should be noted that there were three *C. chemnitzia* lineages supported as distinct species in the GMYC analyses of the *tuf*A data set. However, as these lineages had poor BP and PP support and their relationships varied between the *tuf*A and *rbc*L/concatenated data sets, we do not recognize them as separate taxa, but suggest that further work be undertaken to better resolve and understand these relationships.

Lineage 7: ***Caulerpa nummularia*** Harvey ex. J. Agardh 1873: 38 (Figs. 1F and 9, A and B).

Type locality: Friendly Islands, Tonga; Nukahiva, Marquesas Islands.

Syntypes: Herb. Agardh 16809, 16811 (in part), in LD; BM; 287054, in NSW; DSC01032, in TCD. *Note*: as type material was never designated by J. Agardh, the specimen marked 77 Friendly Isl. *C. nummularia* in TCD (TCD 0011105) is designated here as the lectotype (reproduced in Fig. 9B).

Distribution: Tropical Pacific.

DNA barcode: JN817685, Heron Island, Great Barrier Reef, Australia, voucher: AD-A91369 (Figs. 1F and 9A).

Heterotypic synonyms: *C. peltata* var. *exigua* Weber-van Bosse 1898: 377, pl. XXXI, fig. 11 (Fig. S6B); *C. peltata* var. *stellata* (Harvey ex J. Agardh) Weber-van Bosse 1898: 377 (Fig. S6C).

Selected illustrations: as *C. nummularia*: Abbott and Huisman 2000: 121, fig. 44A. As *C. peltata* var. *exigua*: Weber-van Bosse 1898, Pl. 31 fig. 11; Littler and Littler 2003: 225, Kraft 2007: 173, fig. 64, D–E.

Remarks: Many authors have overlooked *C. nummularia,* treating it as a heterotypic synonym of *C. peltata* (Coppejans and Prud'homme van Reine 1992, Price 2011). However, as mentioned previously, the illustration of *C. peltata* by Lamouroux (1809b) clearly depicts a specimen with erect assimilators bearing radially arranged peltate ramuli. This morphology differs greatly from the original diagnosis of *C. nummularia* by J. Agardh (1873) who, although considering *C. nummularia* to be closely related to *C. peltata*, described the ramuli as shield like, 4–5 mm in diameter with crenulated margins and peltate branches arising from the margin of the ramulus below. The distinction between *C. nummularia* and *C. peltata*, as well as other *C. racemosa–peltata* taxa, is supported by our molecular data including sequences from close to the type locality (KF256098, Fiji), and thus *C. nummularia* warrants recognition as an independent species, a view also held by Cribb and Cribb (1985), South and Skelton (2003), Abbott and Huisman (2004), Hodgson et al. (2004), N'Yeurt and Payri (2004), and Skelton and South (2007). Many of these authors distinguished *C. nummularia* from *C. peltata* var. *exigua* (Fig. S6B), a variety originally described from Samoa and the Cook Islands, by secondary ramuli arising from the center of the disk of subtending ramuli in the latter. However, Abbott and Huisman (2004), as well as Kraft (2007), when commenting on *C. nummularia* and *C. peltata* var. *exigua* respectively, noted that secondary peltate ramuli arose either from the margin or from the center of the ramulus below, thus also removing the distinction between the *C. peltata* varieties *exigua* and *stellata.* This casts some doubt on the independence of *C. peltata* var. *exigua* and *C. peltata* var. *stellata* from *C. nummularia,* a view also shared by Price (2011). On the basis of this, the close proximity of their type localities and the variability observed in material from various regions, we synonymize both *C. pel-*

tata var. *exigua* and *C. peltata* var. *stellata* with *C. nummularia.*

Lineage 8: ***Caulerpa megadisca*** Belton & Gurgel **sp. nov.** (Fig. 9E).

Diagnosis: Thallus medium to dark green, low growing, spreading laterally to 50 cm; stolon smooth, 1–2 mm in diameter, sparsely branched; rhizoidal system well developed with rhizoidal pillars, 1.5–8 cm long, 0.8–1.5 mm wide, branching to slender apices; individual assimilators consisting of a single peltate disk attached to stolon by a terete stalk, 3–6 mm long, 0.5–1.0 mm wide, expanding abruptly into a circular, flat disk; disk fleshy to thin (8) 10–15 (20) mm wide, margin of disk entire.

Holotypus: AD-A90107a, in AD. Collected by C.F.D. Gurgel and R.R.M. Dixon, February 17, 2009 at 11 m depth from Lizard Island, Australia (Fig. 9E).

Holotype DNA barcode: JN817657 (collection details as above).

Type locality: North Direction Island, Lizard Island group, Queensland, Australia.

Etymology: This species is named after the large peltate disks born directly from the stolon.

Distribution: northeastern Australia, New Caledonia and Fiji, but most likely also in the Indonesian region (based on various samples in L).

Specimens examined: AD-A90107 b-d, North Direction Island, Lizard Island group, Queensland, Australia, at 11 m depth, collected by C.F.D. Gurgel and R.R.M. Dixon, February 17, 2009; AD-A92609, "Bommie Bay," North-side of Lizard Island, Queensland, Australia, at 12 m depth, collected by G.S. Belton and M.H.K. Marklund, September 07, 2010; DML40342, Yaukuvelailai Island, Fiji. Collected by M.M. Littler, D.M. Littler and B.L. Brooks, March 09, 1996.

Habitat: Plants were found growing over sandy substrata and coral rubble at 5–12 m depth.

Selected illustrations: as *C. peltata*: Kraft 2007: 173, fig. 64A.

Remarks: C. megadisca can be distinguished from *C. macrodisca* by its single large peltate disk assimilator and much thinner stolon (Fig. 9, C and E; Table 1). Based on these morphological observations, as well as molecular data that distinguished *C. megadisca* from *C. macrodisca* and other *Caulerpa* species (Figs. 3 and 4), its status as a distinct species is fully warranted.

Lineage 9: ***Caulerpa macrodisca*** Decaisne 1842: 336 (Fig. 9, C and D).

Type locality and specimen: Îles Anambas (Anambas Islands), Indonesia; lectotype illustration: Decaisne [1846 (1846-1864), pl. 1, fig. 1], designated by Price (2011, p. 190).

Distribution: Central Indo-Pacific.

DNA barcode: FM956053, Thousand Islands, Java Sea, Indonesia, voucher: L 0509359 (Fig. 9C).

Homotypic synonyms: C. racemosa (Forsskål) J. Agardh var. *macrodisca* (Decaisne) Weber-van Bosse 1898: 376, pl. XXXI, fig. 10. *C. peltata* J.V. Lamouroux var. *macrodisca* (Decaisne) Weber-van Bosse 1898: 376, XXVIII.

Selected illustrations: as *C. macrodisca:* Decaisne 1846-1864; Pl. 1. fig. 1; Reinke 1899: fig. 61. As *C. racemosa* ecad *peltata-macrodisca*: Coppejans and Prud'homme van Reine 1992: 697, fig. 17C.

Remarks: As *C. macrodisca* could be easily identified and distinguished from other *C. racemosa–peltata* complex taxa by molecular data and its large peltate ramuli arranged around an upright axis, its recognition as an independent species is fully justified. Most of our specimens (Fig. 9C) closely resembled the lectotype illustration (Fig. 9D); however, there was some variation, with the ramuli of some specimens (AD-A88056) having a gradual widening toward the peltate disk and others (PERTH 08292663) being slightly mushroom-like. This latter morphology is in agreement with a remark by Weber-van Bosse (1898, p. 253) who noted that after only a few minutes outside the water, the fresh ramuli become flaccid and these ramuli take different flattened forms. However, in comparison to *C. chemnitzia* specimens, the widening was always quite abrupt and the disk (including those that were slightly mushroom shaped) was always larger, 6–10 mm in diameter.

Lineage 11: ***Caulerpa racemosa*** (Forrskål) J. Agardh 1873: 35-36 (Figs. 1A and 10, A–C)

Basionym: *Fucus racemosus* Forsskål 1775: 191.

Type locality and specimen: Suez, Egypt; Herb. Forsskål No. 845 at C.

Distribution: Pantropical.

DNA barcode: JN817665, Kimberley, northwestern Australia, voucher: PERTH 08292728 (Fig. 10A).

Heterotypic synonyms: *Fucus clavifer* Turner 1807-1808: 126-127, pl. 57 *nom. illeg.* (*Fucus clavifer* Turner is a later homonym of *Fucus clavifer* Forsskål 1775, currently *Laurencia uvifera* (Forsskål) Børgesen); *Fucus uvifer* Turner 1817: 81-82, pl. 230, nom. illeg. (*Fucus uvifer* Turner is a later homonym of *Fucus uvifer* Forsskål 1775); *C. uvifera* C. Agardh 1817: xxiii; *Chauvinia clavifera* (C. Agardh) Bory de Saint-Vincent 1826–1829: 207, ; *Chauvinia clavifera* var. *uvifera* (C. Agardh) Kützing 1849, *C. racemosa* var. *clavifera* (C. Agardh) Weber-van Bosse 1898: 361-362, pl. XXXIII: figs. 1–3; *C. racemosa* var. *mucronata* L.N. de Senerpont Domis in de Senerpont Domis et al. 2003: 1035, fig. 2.

Selected illustrations: as *C. racemosa*: Littler and Littler 2003: 227, Price 2011: 176, fig. 8B. As *Fucus uvifer*: Turner 1811-1819: Pl. 230. As *C. uvifera*: Svedelius 1906: 122, fig. 15. As *C. racemosa* var. *clavifera*: Weber-van Bosse 1898, Pl. 33, figs. 1, 4–5.

Remarks: Although it has been widely accepted that *C. racemosa* exhibits considerable morphological variation, the majority of specimens from this lineage in the present study were comparatively uniform and could usually be distinguished from other *C. racemosa–peltata* taxa by their more or less pyriform ramuli that abruptly expanded above a short, stalk-like proximal region whose length was not greater than the diameter of the distal region. However, our results show *C. racemosa* var. *mucronata* (Fig. 10C) to cluster with *C. racemosa* specimens in both the *tuf*A and *rbc*L trees (Figs. 3 and 4) proving that *C. racemosa* can display quite substantial morphological variation, supporting the findings of Peterson (1972), Calvert (1976) and de Senerpont Domis et al. (2003).

We could not detect any clear morphological or genetic boundary between *C. racemosa* and specimens identified as *C. racemosa* var. *macrophysa*. It is therefore quite likely that *C. racemosa* var. *macrophysa* should be synonymized with *C. racemosa*. Unfortunately, the type specimen of *C. racemosa* var. *macrophysa* is presumed lost and no physical comparisons with the type specimen of *C. racemosa* could be made. However, the illustration of *C. racemosa* var. *macrophysa* (as *Chauvinia macrophysa* Sonder ex Kützing) by Kützing 1857: Tab. 15, fig. II; reproduced as our Fig. 10D) was detailed, clear, and accurate enough to help distinguish this morphotype and secure a correct identification of the specimens herein assigned to this taxon (e.g., Fig. 10B). But as we were unable to obtain sequences from the Pacific coast of Central America (= type locality), we suggest further work be undertaken before this synonymy is adopted.

Observations of the type material of *C. racemosa* var. *uvifera* (as *Fucus uvifer* Turner *nom. illeg.* BM000569472, Fig. S7 in the Supporting Information) and *C. racemosa* var. *clavifera* Weber-van Bosse (as *Fucus clavifer* Turner BM000569148, Fig. S8 in the Supporting Information), both originally described from the Red Sea (also the type locality for *C. racemosa*) and currently regarded as synonyms of *C. racemosa*, led us to conclude that their synonymy with *C. racemosa*, as proposed by Papenfuss and Egerod (1957), was most likely correct.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1. Bayesian inference results derived from the combined *tuf*A and *rbc*L DNA sequence data set (38 taxa, 1,771 nt) for *Caulerpa*. Numbered lineages correspond to those of Figure 3. Values at internal nodes are BI posterior probabilities (PP) and ML bootstrap percentages (BP), respectively. PP values below 0.5 and BS values below 50 are not shown. The scale is 0.02 expected changes per site.

Figure S2. Phylogram of taxa belonging to *Caulerpa* based on Bayesian relaxed molecular clock analyses of the same *tuf*A data set as Figure 3. *Caulerpa racemosa-peltata* complex taxa are in boldface. Lineage 6 (*C. chemnitzia*) represents three GMYC lineages and Lineage 4 (*C. macra*) represents two "long branches and high support" lineages. Numbers at branch nodes correspond to BI posterior probabilities (PP) and ML bootstrap percentages (BP). PP values below 0.5 and BS values below 50 are not shown. The scale is 0.03 expected changes per site.

Figure S3. (A) Type specimen of *Caulerpa racemosa* var. *gracilis* (Zanardini) Weber-van Bosse from Tor, Sinai Peninsula, Egypt (originally described as *C. clavifera* var. *gracilis* Zanardini), currently regarded as a heterotypic synonym of *C. racemosa* var. *lamourouxii* f. *requienii* (Montagne) Weber-van Bosse. Specimen TCD0011042. (B) Type specimen of *Caulerpa clavifera* var. *nudiuscula* Zanardini (given as *nudicaulis*), from Red Sea, Egypt. This taxon is currently regarded as a heterotypic synonym of *C. racemosa* var. *lamourouxii* f. *requienii* (Montagne) Weber-van Bosse. Specimen TCD0011044. Both scale bars = 40 mm.

Figure S4. (A) Type specimen of *Caulerpa racemosa* var. *laetevirens* (Montagne) Weber-van Bosse from Toud Island, Torres Strait, Australia (MA10323 in PC, originally described as *C. laetevirens* Montagne but now regarded as *C. chemnitzia* (Esper) J. V. Lamouroux). (B) Specimen of *Caulerpa racemosa* var. *occidentalis* (J. Agardh) Børgesen (originally described as *C. chemnitzia* var. *occidentalis* J. Agardh, but now regarded as *C. chemnitzia* (Esper) J. V. Lamouroux) from a folder in Herbarium Agardh (LD) labeled: "*syntypes of β occidentalis*". Specimen collected from Vera Cruz (16789). Scale bars: A = 50 mm; B = 40 mm.

Figure S5. Syntype specimen of *Caulerpa imbricata* G. Murray from Sri Lanka, now regarded as a heterotypic synonym of *C. chemnitzia* (Esper) J. V. Lamouroux. Specimen: BM000569448.

Figure S6. (A) A supposed lectotype specimen of *Caulerpa racemosa* var. *turbinata* (J. Agardh) Eubank from the Red Sea, Egypt (originally described as *C. clavifera* var. *turbinata* J. Agardh, but now regarded as *C. chemnitzia* (Esper) J. V. Lamouroux). As J. Agardh did not annotate which specimens he used when describing new taxa, we cannot be sure that this is the true lectotype specimen (specimens 16753a from LD). (B) Syntype specimen of *C. peltata* var. *exigua* Weber-van Bosse (BM000841593) collected from the Cooks Islands. (C) One of the syntype specimens of *C. peltata* var. *stellata* (Harvey ex J. Agardh) Weber-van Bosse (BM001044725) collected from Tonga. Scale bar: A = 20 mm; C = 30 mm.

Figure S7. Holotype specimen of *Caulerpa racemosa* var. *uvifera* (Turner) Weber-van Bosse (as *Fucus uvifer* Turner *nom. illeg.*) from the Red Sea, currently regarded as a heterotypic synonym of *C. racemosa* (Forsskål) J. Agardh. Specimen: BM000569472. Scale bar = 50 mm.

Figure S8. Holotype specimen of *Caulerpa racemosa* var. *clavifera* Weber-van Bosse (as *Fucus clavifer* Turner) from the Red Sea, currently regarded as a heterotypic synonym of *C. racemosa* (Forsskål) J. Agardh. Specimen: BM000569148.

Table S1. GenBank accessions, herbarium accessions and collection details of newly sequenced *Caulerpa* specimens.

Table S2. GenBank sequences used in the *tuf*A and *rbc*L alignments. Updated names are only provided for taxa previously assigned to the *Caulerpa racemosa*–*C. peltata* complex.

Table S3. Nomenclature details of taxa discussed in the present study.

Appendix S1. References used to morphologically identify newly collected specimens.