

The recognition of *Caulerpa integerrima* (Zanardini) comb. et stat. nov. (Bryopsidales, Chlorophyta) from the Red Sea

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WYNNE M.J., VERBRUGGEN H. AND ANGEL D.L. 2009. The recognition of *Caulerpa integerrima* (Zanardini) comb. et stat. nov. (Bryopsidales, Chlorophyta) from the Red Sea. *Phycologia* 48: 291–301. DOI: 10.2216/08-78.1.

Evidence based on both morphological and molecular data is presented to demonstrate that *Caulerpa freycinetii* C. Agardh var. *integerrima* Zanardini, a name that has long been treated within the taxonomic synonymy of *C. serrulata* (Forsskål) J. Agardh, is to be resurrected and recognised at the level of species, *C. integerrima* (Zanardini) comb. nov., for an alga thought to be endemic to the Red Sea. Three species in the genus with which it is superficially similar, *C. bartoniae*, *C. brachypus* and *C. serrulata*, are separated from it using the *tufA* gene, complemented by morphological characters, including the entire margins and the 1.5–2.0-mm thickness of the assimilators. Another species also described originally from the Red Sea, *Herpochaeta* (*Caulerpa*) *requienii* Montagne, is also discussed and eliminated from consideration. Weber-van Bosse's assignment of this species as a forma within *C. racemosa* is accepted, namely, *C. racemosa* var. *lamourouxii* (Turner) Weber-van Bosse f. *requienii* (Montagne) Weber-van Bosse.

KEY WORDS: *Caulerpa*, *C. bartoniae*, *C. brachypus*, *C. integerrima* comb. nov., *C. serrulata*, Chlorophyta, *C. racemosa* f. *requienii*, Molecular phylogeny, Red Sea, Taxonomy

INTRODUCTION

Recent collections of a *Caulerpa* of uncertain identity in the vicinity of Eilat in the northern Red Sea caused us to search through both old and contemporary literature in the attempt to make a determination. We considered a taxon described by Zanardini (1858) as a variety of *Caulerpa freycinetii*, namely, var. *integerrima*, from the Red Sea, based on a collection made by Portier. In her monograph of the genus, Weber-van Bosse (1898) treated the name without change in status or nomenclature. The taxonomic synonymy of *C. freycinetii* C. Agardh with *C. serrulata* (Forsskål) J. Agardh (J. Agardh 1837; basionym: *Fucus serrulatus* Forsskål 1775), which was suggested by Weber-van Bosse (1898), was formally proposed by Børgesen (1932). In his catalogue of Red Sea benthic marine algae, Papenfuss (1968) accepted *C. freycinetii* var. *integerrima* within the taxonomic synonymy of *C. serrulata*. This assignment will be addressed in the present paper.

There is a strong resemblance of our unknown *Caulerpa* to *C. bartoniae* G. Murray, a species endemic to southern Africa (Murray 1896; Seagrief 1988; Stegenga *et al.* 1997). The erect fronds in *C. bartoniae* are dichotomously branched and flattened, 1.5–2.5 mm wide, with the same general habit as the Eilat alga but on a smaller scale. Weber-van Bosse (1898) assigned *C. bartoniae* to her section Thuyoideae, next to *C. freycinetii* (= *C. serrulata*), and *C. bartoniae* was placed next to *C. freycinetii* var. *integerrima*, the variety of *C. serrulata* in which the erect

frond was not twisted and had smooth margins. This close juxtaposition of these taxa by Weber-van Bosse (1898) was a sufficient reason to examine the South African species in detail, and a silica-gel sample from recently collected material was used to extract DNA for sequencing and comparison to our Red Sea material.

Another species of *Caulerpa* that has some resemblance to our Red Sea material alga is *C. brachypus* Harvey, a widely occurring species that has been assigned to Section Phyllantoideae. Sequence data of the *tufA* gene of *C. brachypus* has previously been reported by Famà *et al.* (2002) and Stam *et al.* (2006), allowing us to compare that taxon to our unknown sample.

MATERIAL AND METHODS

Study sites for the Red Sea *Caulerpa* under investigation

Gulf of Aqaba, northern Red Sea, North beach of Eilat [Eilat] (29°32.45'N, 34°58.32'E): 25 July 2007, collected by D.L. Angel, 22–27-m depth on a fine sand sediment occurring both in beds of *Halophila stipulacea* (Forsskål) Ascherson and on bare sediment. Voucher specimens have been deposited in the following herbaria: BM, C, CAT, GENT, L, LD, MCVE, MICH, PC, S, TELA, TNS, UC, and US. The herbarium abbreviations are listed on the online site <http://sciweb.nybg.org/science2/IndexHerbariorum.asp>.

9 July 2008, collected by D.L. Angel, same site and conditions as above. GENT, MICH, TELA.

Northern Red Sea. Eilat: 2 January 1966, collected by Y. Lipkin 10506, dredged started at 130-m depth, 1 km

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Table 1. Sequences used in phylogenetic analysis. Voucher numbers of the newly sequenced specimens are given in parentheses in the second column. These vouchers have been deposited in the Ghent University algal herbarium.

Species (ecad)	GenBank number	Species (ecad)	GenBank number
<i>C. ashmeadii</i>	DQ652370	<i>C. microphysa</i>	DQ652520
<i>C. bartoniae</i>	FJ810426	<i>C. paspaloides</i>	DQ652509
<i>C. brachypus (parvifolia)</i>	DQ652355	<i>C. prolifera</i>	DQ652375
<i>C. brachypus (biserrulata)</i>	AJ417934	<i>C. racemosa (laet-pelt-turb)</i>	AJ512415
<i>C. cactoides</i>	AJ417969	<i>C. racemosa (mucronata)</i>	AJ512417
<i>C. cupressoides</i>	DQ652338	<i>C. racemosa (rac-cor-lam)</i>	AJ512413
<i>C. distichophylla</i>	AJ417940	<i>C. scalpelliformis</i>	AJ417971
<i>C. filiformis</i>	AJ417964	<i>C. selago</i>	AJ417973
<i>C. flexilis</i>	AJ417970	<i>C. serrulata</i>	AJ417932
<i>C. geminata</i>	AJ417960	<i>C. sertularioides</i>	DQ652407
<i>C. integerrima</i>	FJ810424	<i>C. subserrata</i>	AJ417935
<i>C. integerrima</i>	FJ810425	<i>C. taxifolia</i>	AJ417939
<i>C. lanuginosa</i>	DQ652498	<i>C. verticillata</i>	AJ417967
<i>C. mexicana</i>	DQ652454	<i>C. webbiana</i>	AJ417966

offshore, and finished at a depth of 60 m. Bottom composed of mud and gravel. MICH.

Other species of *Caulerpa* examined in this work

Caulerpa bartoniae: False Bay, Western Cape Prov., South Africa: 31 May 2008, Coll. Robert Anderson G.118 (GENT). Sharks Bay, The Kowie, Eastern Cape Prov., South Africa: without date, Coll. W. Tyson, S. Afr. Exsicc. 145 (MICH).

Caulerpa brachypus: Eil. Kelapa, Thousand Islands, Indonesia: 5 October 1938, Coll. A. J. Kostermans (MICH).

Caulerpa serrulata: f. *serrulata*, Hanauma Bay, Oahu, Hawaii: March 1959, Coll. William J. Gilbert 9048 (MICH). f. *lata*, Eil. Hoorn, Bay of Batavia, Indonesia: 27 September 1938, Coll. A. J. Kostermans (MICH).

We were able to access scanned images of *Caulerpa freycineti* var. *integerrima* (a protologue specimen in L and two specimens in S) and the type specimen of *Herpochaeta requienii* in PC for our examination and inclusion in this study.

Molecular phylogenetics

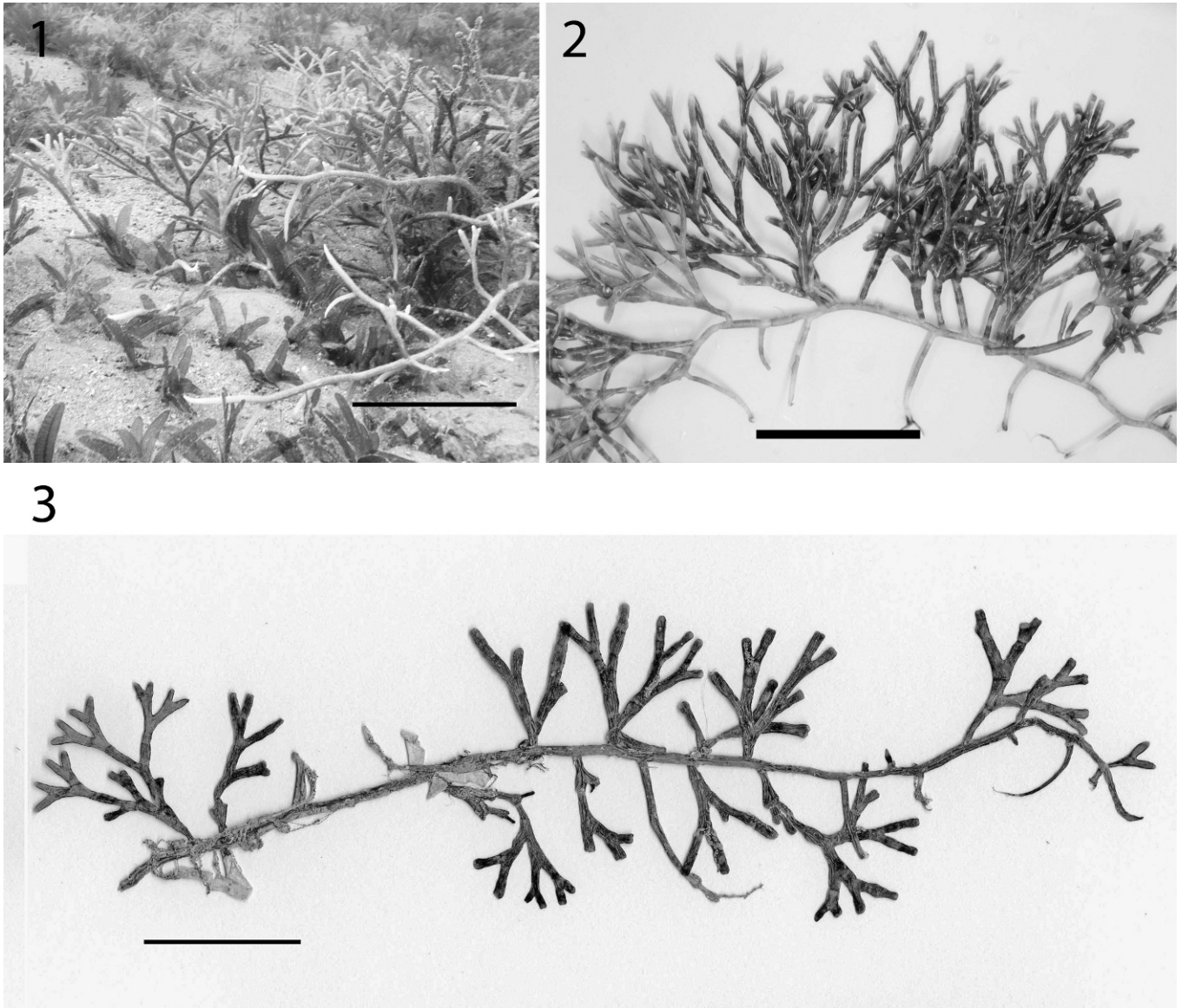
DNA was extracted from silica-gel-preserved samples of the target species from the Red Sea and the morphologically similar species *Caulerpa bartoniae* from South Africa. DNA extraction, amplification and sequencing of the *tufA* gene followed standard protocols (Fàma *et al.* 2002). Sequences were added to an alignment of previously published sequences (Table 1; Fàma *et al.* 2002; de Senerpont Domis *et al.* 2003; Stam *et al.* 2006). Because voucher specimens of Fàmà *et al.* (2002) are lacking, the identifications of these specimens cannot be checked. An appropriate model of sequence evolution was determined using the Akaike information criterion (AIC) (Posada & Buckley 2004), including partitioned models of evolution in the comparison (Verbruggen & Theriot 2008). AIC scores were calculated with TreeFinder (Jobb *et al.* 2004) using a reference topology inferred under a JC + Γ_4 model with PhyML (Guindon & Gascuel 2003). A phylogenetic tree was inferred by Bayesian inference, using MrBayes v.3.1.2 (Ronquist & Huelsenbeck 2003). Two independent MCMC runs, each consisting of four incrementally heated chains, were run for 2 million generations with default priors, chain temperature incre-

ments and other settings. Convergence of the runs was checked visually with Tracer v.1.4 (Rambaut & Drummond 2007), and an appropriate burn-in was determined with the automated method proposed by Beiko *et al.* (2006). A majority-rule consensus tree was calculated from the post-burn-in trees with MrBayes' sumt command. Based on their early-branching position in previous studies (Fàmà *et al.* 2002), *C. flexilis* and *C. verticillata* were used to root the tree.

RESULTS

Morphological characterisation of a *Caulerpa* species from the Red Sea

Creeping system (Figs 1, 2) of terete axes (= stolons) 1.5–2.0 mm in diameter, smooth, giving rise to occasional downward-oriented rhizoidal pillar-like extensions that penetrate the sandy substratum; pillars 1.2–1.5 (–2.0) mm in diameter, glabrous, arising at intervals of 1.4–2.7 mm from the stolon but without any relationship to the erect assimilators; assimilators produced sporadically from dorsal side of stolons (Figs 2, 3), that is, at distances from 1.0 to 3.0 (–6.0 cm), consisting of dark green terete to compressed erect axes, 1.8–4.0 mm in width, with somewhat fleshy, thickened texture, 1.5–2.0 mm in thickness, not thin or foliose; assimilators dichotomously or subdichotomously branched, to six orders, all orders lying in same plane (thus, not twisted); assimilators reaching 3.0–6.0 cm in height; only the most proximal 0.5 cm of assimilator is pedicellate and terete, not compressed; margins of assimilators completely devoid of teeth; assimilators both nonconstricted or occasionally constricted, especially where branching, the constrictions possibly the result of having been grazed and then regeneration from that point. Light microscopy showed the presence of small chloroplasts (*c.* 2.8–4.5 μm) without pyrenoids, thus apparently belonging to the prolifera type of Calvert *et al.* (1976). Amyloplasts are also present. Based on external morphological features, our material is attributed to J. Agardh's (1873) nomenclaturally invalid tribe Thuyoideae and to what De Toni (1889) and Weber-van Bosse (1898) referred to as Section Thuyoideae J. Agardh.



Figs 1–3. *Caulerpa integerrima* comb. nov.

Fig. 1. Wild plants occurring at 26 m depth, north beach at Eilat, Israel, occurring with the sea grass *Halophila stipulacea* (photo by Stephen Breitstein, 24 July 2007). Scale bar = 10 cm.

Fig. 2. Freshly collected specimen on 9 July 2008 (photo by Dror Angel, 25 July, 2007). Scale bar = 6 cm.

Fig. 3. Herbarium specimen collected on 25 July 2007. Scale bar = 4 cm.

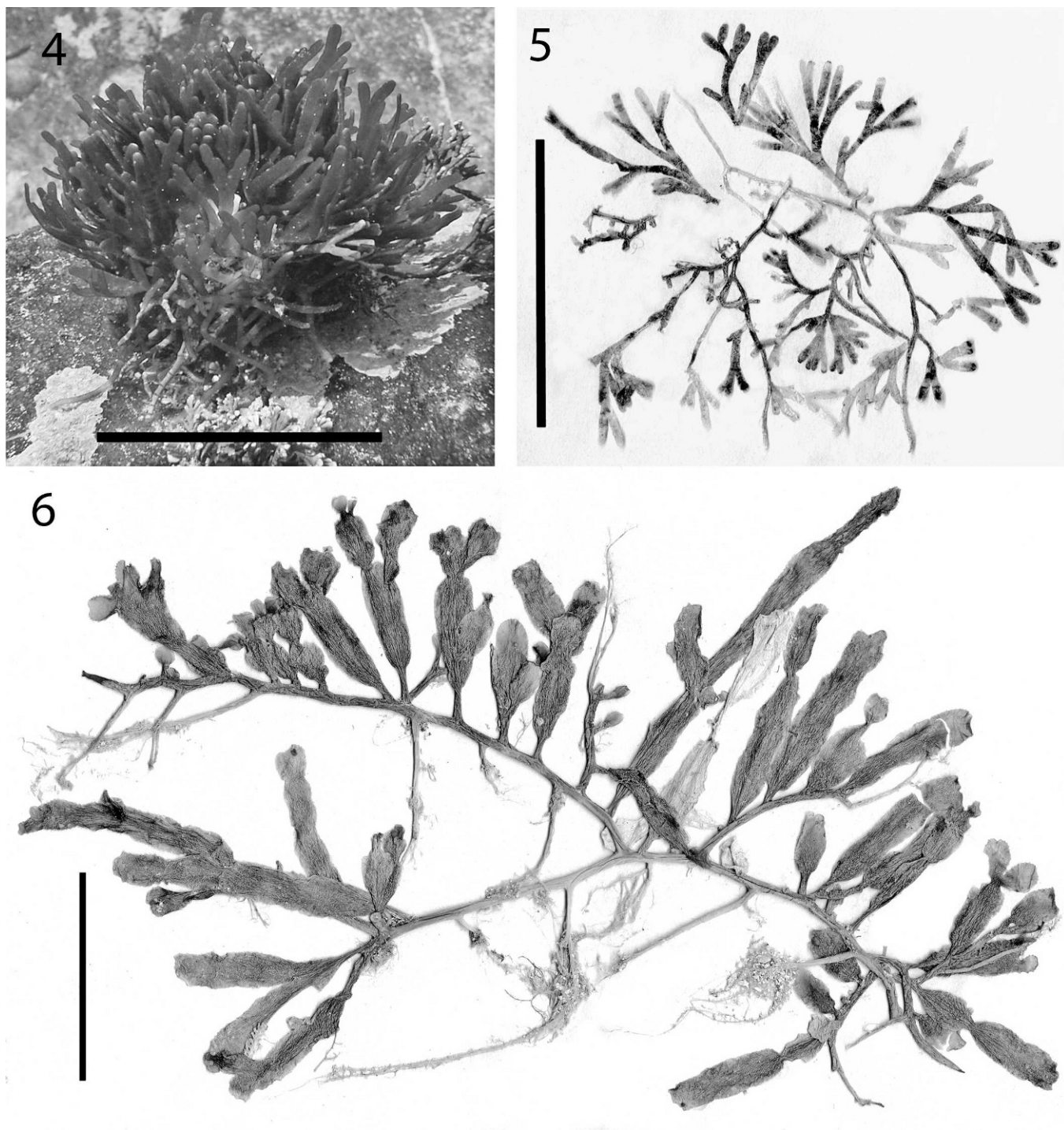
Comparison with other taxa within *Caulerpa*

In its general appearance, the *Caulerpa* under discussion bears some resemblance to several taxa in the genus: *C. bartoniae*, *C. brachypus*, a forma in *C. racemosa* and a varietas in *C. serrulata*.

CAULERPA BARTONIAE: *Caulerpa bartoniae* (Figs 4, 5) has compressed erect assimilators a few times dichotomously branched. Murray (1896) described this species as having erect axes 2–4 cm in length and 1.0–1.5 mm in width; whereas, Stegenga *et al.* (1997) reported erect axes to be 1.5–2.5 mm wide and to reach 5 cm tall. Light microscopy shows chloroplasts of *c.* 5–7 μm containing a single pyrenoid, thus apparently belonging to the *microphysa* type described by Calvert *et al.* (1976). Amyloplasts are

also present. Our Red Sea *Caulerpa* has a similar appearance to this species but is more robust in overall dimensions, the assimilators 1.8–4.0 mm in width, 1.5–2.0 mm in thickness and 3.0–6.0 cm in height and with up to six orders of branches. The rhizomes of our Red Sea *Caulerpa* are also more robust, to 1.5–2.0 mm in diameter. A comparison of Figs 4 and 5 with Figs 1–3 demonstrates these differences.

CAULERPA BRACHYPUS: A distinction of our Red Sea alga with *Caulerpa brachypus* is more easily drawn. The assimilators of *C. brachypus* (Fig. 6) are thin and blade-like, ligulate or lanceolate, with smooth margins or beset with small marginal teeth (Tseng 1936; Taylor 1950; Coppejans & Prud'homme van Reine 1992). These erect blades in *C. brachypus* are 3–12 mm in width (Kraft 2007),



Figs 4–6. Comparison with other species of *Caulerpa*. Scale bar in each = 4 cm.

Figs 4–5. *C. bartoniae*.

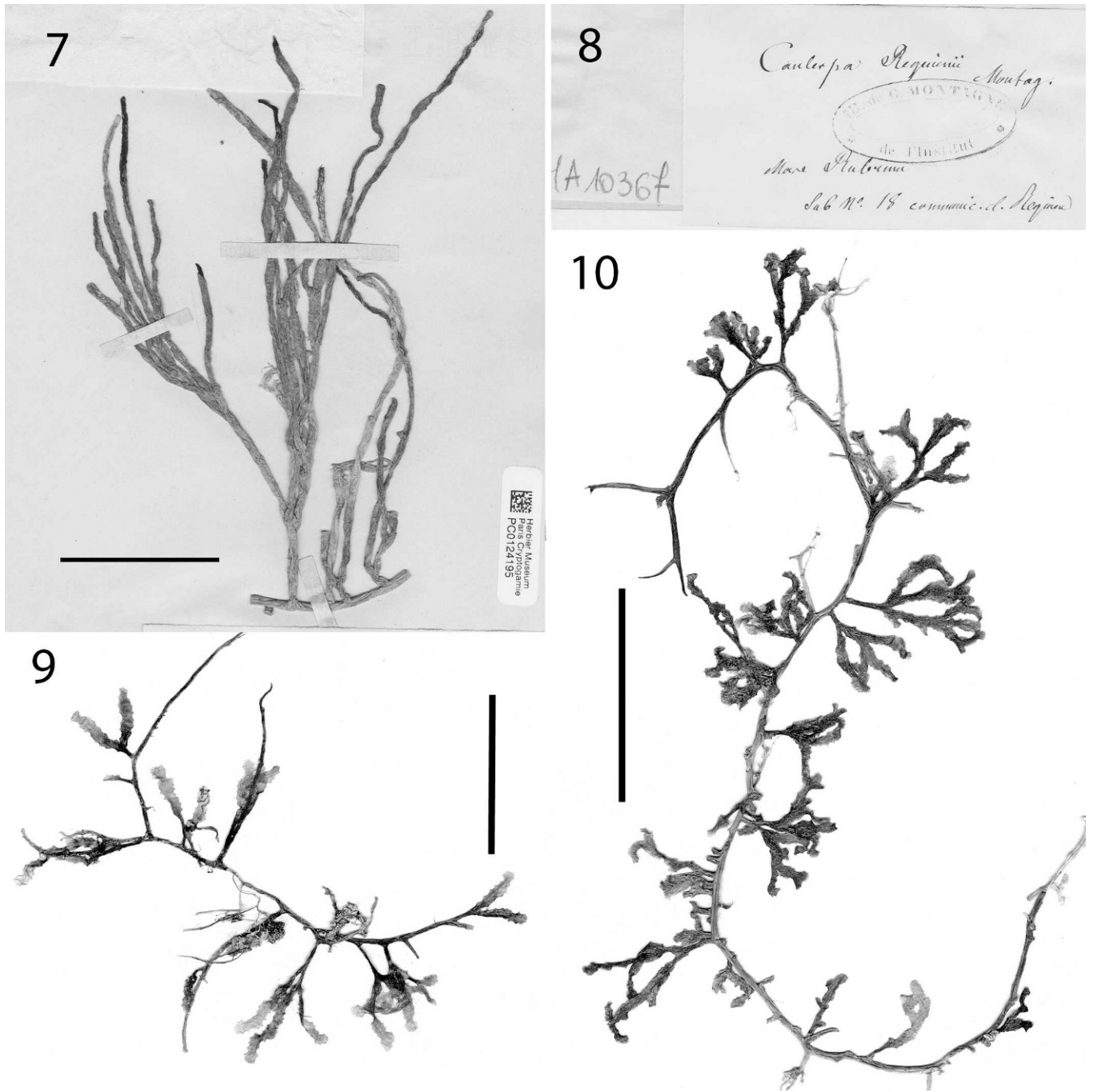
Fig. 4. Wild plant growing on rock in South Africa. (Image from Dr. Robert Anderson.)

Fig. 5. W. Tyson's South African Exsicc. No. 145 (MICH).

Fig. 6. *C. brachypus*. Collection from Thousand Islands, SW Java Sea, Indonesia (MICH).

significantly wider than the erect axes of our Red Sea *Caulerpa*. The assimilators in *C. brachypus* are not several times dichotomously branched as in the Red Sea alga under discussion.

CAULERPA RACEMOSA F. *REQUIENII*: A taxon that is being included in this survey of names being considered is *Caulerpa racemosa* (Forsskål) J. Agardh (var. *lamourouxii*) f. *requienii* (Montagne) Weber-van Bosse primarily on the



Figs 7–10. Comparison with other species of *Caulerpa*. Scale bar = 4 cm.

Figs 7–8. *Herpochaeta requienii* Montagne.

Fig. 7. Typus in PC.

Fig. 8. Label information on Typus.

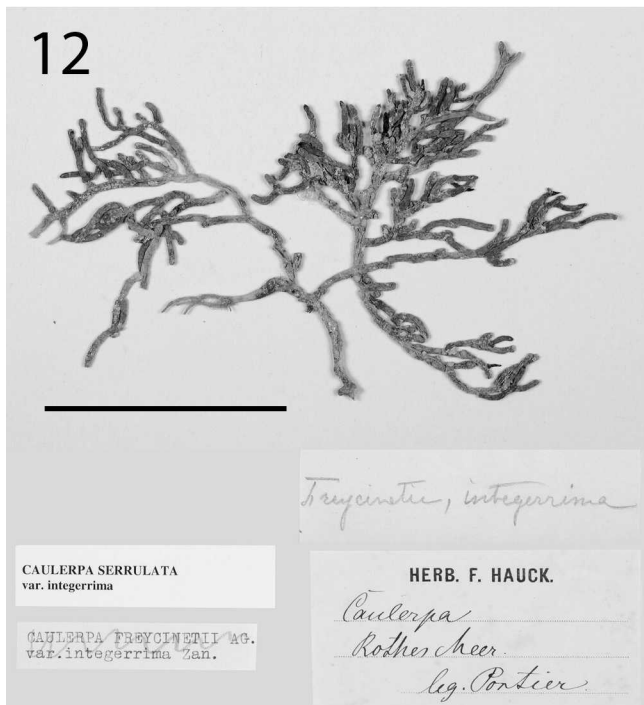
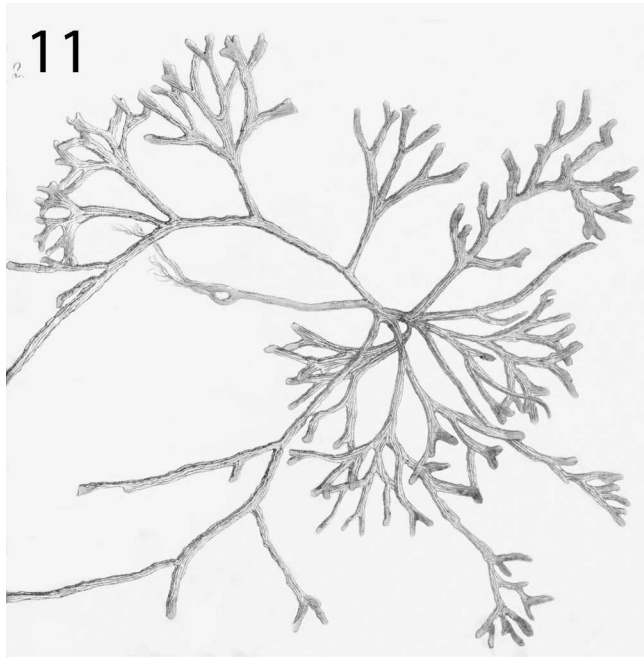
Figs 9–10. *C. serrulata*.

Fig. 9. *C. serrulata* f. *serrulata*. Collection from Hanauma Bay, Oahu, Hawaii (MICH).

Fig. 10. *C. serrulata* f. *lata* (Weber-van Bosse) C.K. Tseng. Collection from Batavia Bay NW Java, Indonesia (MICH).

basis that it was described from the Red Sea (Montagne 1856, as *Herpochaeta requienii*). An image of the Typus (in PC) was made available to us and is depicted in Fig. 7 with label data in Fig. 8. The taxon was later recognized as a species of *Caulerpa* by J. Agardh (1873) and then relegated by Weber-van Bosse (1898) to the level of a forma within *C. racemosa*. This forma was depicted by her (Weber-van

Bosse 1898, pl. 32, figs 5, 7) as having terete or slightly compressed erect axes, 2 mm in diameter, reaching up to 16 cm in height (based on Weber-van Bosse's pl. 32, fig. 7), simple or occasionally distichously branched. That account fits the Type specimen (Fig. 7). The erect fronds are entirely naked, that is, lacking any of the pyriform or clavate laterals that are present in the 'forma typica' of var.



Figs 11–12. *Caulerpa integerrima* comb. nov.
Fig. 11. Reproduction of Zanardini’s depiction of *C. freycinetii* var. *integerrima*. Magnification not stated in original.
Fig. 12. Protologue specimen of *Caulerpa freycinetii* var. *integerrima* in L. Scale bar = 5 cm.

lamourouxii. It remains recognized as a forma (Silva *et al.* 1996; Guiry & Guiry 2008) and is also reported to be present in the eastern Mediterranean (Huvé 1957; Rayss & Edelstein 1960; Verlaque *et al.* 2000). The name *Caulerpa feldmannii* Rayss & Edelstein has been used for the Mediterranean form. Within *C. racemosa*, Weber-van Bosse (1898) placed f. *requienii* next to f. *lamourouxii*, a form with compressed erect (or decumbent) axes that may

bear some (rare) opposite vesicle-like branchlets or may be completely naked (Coppejans 1992; Coppejans & Beeckman 1990; Coppejans *et al.* 2001). The erect axes of forma *requienii* are not compressed and do not exhibit the regularly and frequently dichotomous branches of our alga being compared. The inclusion of f. *requienii* within *C. racemosa* is accepted.

CAULERPA SERRULATA AND *CAULERPA FREYCINETII* VAR. *INTEGERRIMA*: There is a strong resemblance between our recent Red Sea collections and Zanardini’s var. *integerrima* (of *Caulerpa freycinetii*). Zanardini (1858) described *C. freycinetii* C. Agardh var. *integerrima* from Suez, Red Sea, based on a Portier collection. In her monograph of the genus, Weber-van Bosse (1898) maintained Zanardini’s var. *integerrima* as a variety within *C. freycinetii*. Although Børgesen (1932) and Papenfuss (1968) did not give it a distinctive status, they merged it within the taxonomic synonymy of *C. serrulata*. The fact that many infraspecific taxa have been recognized within *C. serrulata* indicates that much morphological variation is present (Weber-van Bosse 1898, 1913, both as *C. freycinetii*; Gilbert 1942); although, not all authors accepted all infraspecific taxa (Coppejans & Prud’homme van Reine 1992). Various authors have depicted *C. serrulata* (Figs 9, 10) or its varieties (e.g., Kützting 1857, as *C. freycinetii* and *C. najadiformis*; Tseng 1936; Trono & Ganzon-Fortes 1980; Coppejans & Meinesz 1988; Coppejans & Beeckman 1990; Coppejans 1992; Coppejans & Prud’homme van Reine 1992; Coppejans *et al.* 1995; Huisman 2000; Littler & Littler 2000, 2003; De Clerck *et al.* 2005; Huisman *et al.* 2007; Ohba *et al.* 2007; Kraft 2007). Assimilators of *C. serrulata* are flattened into thin, linear blades 2–3 mm wide, and they are usually slightly to greatly twisted or coiled, and only some are straight (Kraft 2007). In his study of *C. serrulata* in the area of the Dahlak Archipelago of the Red Sea, Lipkin (1987) observed plants at depths of 1.25–1.5 m as well as a community occurring at c. 100 m that consisted exclusively of a ‘low-light ecophene’ of this same species. Studying plants from this same region, Lipkin & Silva (2002) never observed plants with entire margins in the field. As the epithet alludes, the margins of the assimilators are typically serrate or toothed. The epithet ‘*integerrima*’ is Latin for ‘absolutely entire’ (Stearn 1966). We maintain that that feature is a critical distinction between our Red Sea *Caulerpa* and *C. serrulata*.

According to Weber-van Bosse’s (1898) account of var. *integerrima*, the frond is not twisted, has a cylindrical stipe, and is smooth (‘plane’) above, linear, foliose, and with entire, nondentate margins and with rare constrictions. She mentioned that Zanardini’s habit figure (Zanardini 1858, pl. 14, fig. 2) (our Fig. 11) of this variety represents a yellow shade, or gradation, at the apices. It has been noted that in the living condition the extremities of the frond of several *Caulerpa* spp. may be yellow to shades varying from very light to brilliant orange but that the lower portions are invariably a pronounced green (Weber-van Bosse 1898, citing Decaisne 1841).

The Zanardini Herbarium is now housed in the Museo Civico di Storia Naturale in Venice (MCVE), and the contents have been listed by De Toni & Levi (1888). But no specimen of *Caulerpa freycinetii* var. *integerrima* is listed. In

Table 2. Model selection based on the Akaike information criterion (AIC). The best-fitting model is in boldface. The last column (Δ AIC) shows the AIC of the condition minus the AIC of the best-fitting model.

Partitions	Model	Likelihood	Parameters	AIC	Δ AIC
Single partition	F81	-4125.8	56	8363.6	1246.5
	F81 + Γ_8	-3816.2	57	7746.5	629.4
	HKY	-4090.3	57	8294.6	1177.6
	HKY + Γ_8	-3765.5	58	7647.0	529.9
	GTR	-4080.6	61	8283.1	1166.1
	GTR + Γ_8	-3757.2	62	7638.4	521.3
Codon positions	F81	-3796.0	64	7720.0	602.9
	F81 + Γ_8	-3671.6	67	7477.1	360.1
	HKY	-3665.8	67	7465.5	348.5
	HKY + Γ_8	-3557.6	70	7255.1	138.1
	GTR	-3556.0	79	7270.0	152.9
	GTR + Γ_8	-3476.5	82	7117.1	0

fact, the only *Caulerpa* listed by De Toni & Levi is *C. cylindracea* Sonder. Dr. Luca Mizzan of MCVE has confirmed the absence of Zanardini's taxon.

In her account of *Caulerpa freycinetii* var. *integerrima*, Weber-van Bosse (1898) stated that she examined 'l'algue de Zanardini' in the Stockholm Herbarium (S). It was unclear if the material in S was part of the original protologue. We obtained electronic images of two collections of '*Caulerpa freycinetii* var. *integerrima*' in S that were examined by Weber-van Bosse. These specimens are A5863 and A5914. Sheet A5863, consisting of several specimens, bears a label with the following text: '*Caulerpa complanata*, Röda Hafvet. 1844 Maj. Fölsch misit 1850', with a second label (most likely by Weber-van Bosse) of '*Caulerpa freycinetii* var. *integerrima*' ('Röda Hafvet' = Swedish for Red Sea). *Caulerpa complanata* was described from Port Denison, western Australia, by J. Agardh (1873) and relegated to level of forma within *C. racemosa* by Weber-van Bosse (1898). A close-up of the compressed axes and the manner of branching leaves no doubt that this material is conspecific with our Eilat specimens. The herbarium material appears to have been prepared by gathering entangled masses of specimens that had been cast ashore.

The second sheet in S (A5914) has label information that it was also collected from the Red Sea in May 1844 and presumably was made by the same collector, Fölsch. It has a modern label written by N. Svedelius: '*Caulerpa Freycinetii* v. *integerrima* (Zan.), Web. v. Monogr. p. 317! Röda hafvet, gebel Tor, maj 1844. 4 fots djup. det. N. Svedelius.' There was a note in the envelope: 'Obs! A very rare form! The material should be softened in water and mounted!! Obs! Nils Svedelius 1905' (translation from Swedish by M. Hamnede). But Svedelius did not provide his sources of information, that is, locality and date of collection. It is evident that these Red Sea collections of var. *integerrima* in S closely match our recent Red Sea collections; although, the dimensions of diameter of stolons and assimilator branches of the dried specimens are somewhat smaller. It is also clear that these two collections in S are not part of the protologue.

Dr. W. F. Prud'homme van Reine, who was a reviewer of the original submission of this manuscript, kindly alerted us to the existence in Leiden of what appears to be protologue material. He arranged for an image to be made available to us (Fig. 12). This specimen is from the Hauck Herbarium and bears the original label information: '*Caulerpa* Rothes

Meer leg. Portier', as well as 'freycinetii, integerrima'. This information allows us to designate this specimen (Leiden 937.131.28) as the lectotype of *Caulerpa freycinetii* var. *integerrima* Zanardini. A modern label bears the name '*Caulerpa serrulata* var. *integerrima*'. The actual specimen shows the fairly robust axes with frequent branching that is both dichotomous and irregular. Zanardini's (1858) depiction of his new taxon (Fig. 11) shows a specimen to be more regularly dichotomous, which is more in conformity with our recent Red Sea collections.

Ecological characterisation

Populations of the *Caulerpa* under discussion have been observed in our studies to occur at depths of 22–27 m, often co-occurring with (or independent of) the sea grass *Halophila stipulacea*, on fine sand-silt (Fig. 1). Lipkin's (1974) 'peculiar form of *Caulerpa*' (which we regard as the same as our alga) was dredged between 45- and 80-m depth and the voucher specimen of that form (Y. Lipkin 10506) between 60- and 130-m depth. The alga has been persistently observed in moderate numbers at the study site described above in the northern Red Sea since 1995.

Molecular phylogenetics

The *tufA* alignment used for phylogenetic analysis included 28 sequences of 820 bases long. The model selection procedure selected a composite model in which codon positions were treated as separate partitions and GTR + Γ_8 models were applied to each partition (Table 2). The Bayesian analysis rapidly reached a likelihood plateau, and parameter estimates were consistent among runs. The burn-in was determined at 84,000 generations.

The phylogenetic tree shows that the Red Sea specimens (*C. integerrima* G.086 and G.088) form a clade within a cluster of *Caulerpa* species that is poorly resolved, with *C. mexicana* as its closest relative in our taxon sampling (Fig. 13). The South African species *C. bartoniae*, which is similar in morphology to the specimens from the Red Sea, is part of an early-branching *Caulerpa* lineage consisting of *C. geminata*, *C. cactoides* and *C. microphysa*, whose chloroplasts have a pyrenoid. Sequences assigned to *Caulerpa brachypus*, another look-alike of our Red Sea entity, come out in two places of the phylogenetic tree. There is considerable confusion about the identity of these sequences

13

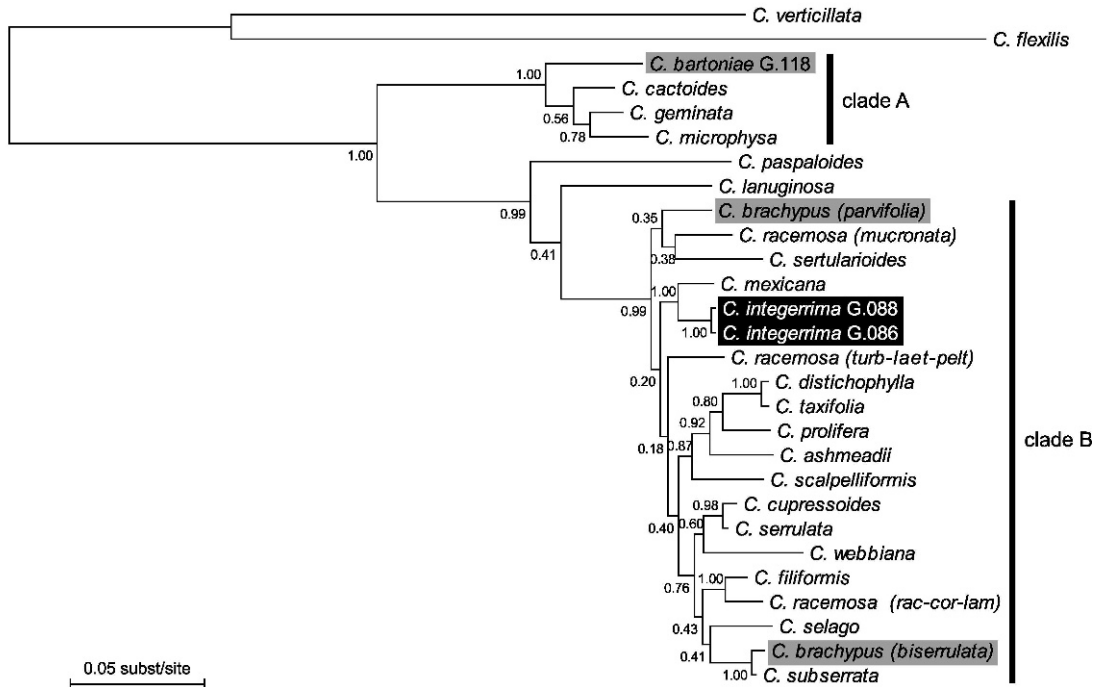


Fig. 13. Phylogenetic tree showing the relationship of *Caulerpa integerrima* with other *Caulerpa* species. The tree was reconstructed from *tufA* sequence data using Bayesian inference. Numbers at nodes represent Bayesian posterior probabilities.

from GenBank. The first clade, represented in our tree by sequence DQ652355, represents the *parvifolia* form, which is presently regarded as a form within *C. brachypus* but may deserve reinstatement at the species level (Willem Prud'homme van Reine, personal communication). The second clade consists of sequence AJ417934, which was listed as *C. brachypus* by Famà *et al.* (2002), but reexamination of the material indicates that it is *C. biserrulata* (Willem Prud'homme van Reine, personal communication). Nonetheless, the clade to which sequence AJ417934 belongs also contains typical *C. brachypus* (Stefano Draisma & Willem Prud'homme van Reine, unpublished results), adding to the confusion surrounding the phylogenetic position of this species. Despite the confusion about *C. brachypus*, however, the phylogenetic results unambiguously show that the Red Sea population is distinct from morphologically similar species like *C. bartoniae* and *C. brachypus* and deserves recognition at the species level.

The results of the gene sequencing analyses, as depicted in Fig. 13, and the morphological distinctions from several species somewhat similar in appearance as delineated above all lead us to the conclusion that this taxon should be recognized at the species level.

***Caulerpa integerrima* (Zanardini) M.J. Wynne, Verbruggen & D.L. Angel comb. nov. et stat. nov.**

BASIONYM: *Caulerpa freycinetii* var. *integerrima* Zanardini, 283, pl. XIII, fig. 2: 1858. Type locality is Suez, the Red Sea.

LECTOTYPE: In Leiden (937.131.28).

OCCURRENCE: Marine. Known from the Red Sea.

DISCUSSION

Caulerpa Lamouroux (1809) is a large genus of tropical green algae, with approximately 75 species now recognized (Weber-van Bosse 1898; Famà *et al.* 2002; Silva 2003). That number reflects the segregation of *Caulerpa ambigua* Okamura (and its taxonomic synonyms *C. vickersiae* Børgesen and *C. biloba* Kempermann & Stengena) into the genus *Caulerpella* (Prud'homme van Reine & Lokhorst 1992). A relatively small number of species has been recognised as occurring in the Red Sea. In his catalogue of Red Sea benthic marine algae, Papenfuss (1968) recognized 10 species of *Caulerpa*, which included additional subspecific taxa; whereas, Lipkin (1974) counted 13 species in total. In their account of algae and sea grasses of the Dahlak Archipelago in the southern Red Sea, Lipkin & Silva (2002) listed eight species of *Caulerpa*.

J. Agardh (1873) was the first to establish a number of subdivisions within the genus *Caulerpa* that he referred to as 13 tribes: Vaucherioideae, Charoideae, Bryoidae, Zosterioideae, Phyllathoideae, Filicoideae, Hippuroideae, Thuyoideae, Lycopodioidae, Araucarioideae, Paspaloideae, Sedoideae and Opuntioideae. These are all illegitimate because of Article 33.9 of the Vienna code. De Toni (1889) changed the rank of all J. Agardh's tribi to sections. The J. Agardh names are now valid sections, author's citation J. Agardh *ex* De Toni. In her monographic treatment of the genus, Weber-van Bosse (1898) essentially accepted all of J. Agardh's tribes (except for the Opuntioideae), again referring to them as sections of the genus. J. Agardh's tribe Opuntioideae was treated by Weber-van Bosse as one of four subsections (Claviferae, Opuntioidae, Vesiculiferae and Pedicellatae) within her section Sedoideae.

Much has been published on the impact of gradients or variations in various ecological parameters, such as light, depth, substrate, and water turbulence, on the morphological appearance seen in the assimilators (Svedelius 1906; Børgesen 1907; Nasr 1947; Peterson 1972; Calvert 1976; Enomoto & Ohba 1987; Ohba & Enomoto 1987; Ohba *et al.* 1992; Prud'homme van Reine *et al.* 1996). This great plasticity in morphological expression has always impeded confidence in the species-level taxonomy of the genus. DNA sequence analysis has enabled a new focus to be put on the delineation of species within the genus and has been used to evaluate sections within the genus (Lehman & Manhart 1997; Famà *et al.* 2002; de Senerpont Domis *et al.* 2003; Stam *et al.* 2006). Famà *et al.* (2002) found that the clades obtained in their analysis did not support Weber-van Bosse's (1898) morphologically defined sections, which are, in fact, the infrageneric groups J. Agardh had proposed in 1873. All sections that contained more than one species turned out to be nonmonophyletic. This is explicitly confirmed by our study, where the species of section Thuyoideae (*C. integerrima*, *C. bartoniae*, *C. cupressoides*, *C. freycinetii* = *C. serrulata* and so on) come out in very different places of the molecular phylogenetic tree. The failure of the classical sectional subdivision based on external morphology calls for a revision of the higher-level taxonomy of *Caulerpa* based on characters that show a strong phylogenetic imprint. Famà *et al.* (2002) have shown that some of the chloroplast features correlate well with phylogenetic structure. Our observations on *C. bartoniae* and *C. integerrima* confirm this correlation (Fig. 13). Like other species in clade A, *C. bartoniae* has microphysa-type chloroplasts with a pyrenoid, and, like other species in clade B, *C. integerrima* has a prolifera-type chloroplast without a pyrenoid. *Caulerpa paspaloides* and *C. lanuginosa*, separate lineages most closely related to clade B, also have characteristic chloroplast features (Calvert *et al.* 1976). The generality of the utility of chloroplast structure for clade delimitation remains to be evaluated with expanded taxon sampling.

Nasr (1947) recognised seven species of *Caulerpa*, including *C. serrulata*, in his treatment of the algae of the Egyptian Red Sea coast, but he clearly stated that he did not recognise the several distinct varieties of *C. serrulata* that Weber-van Bosse had listed in her monograph (as *C. freycinetii*). He offered as evidence his observations from transplant studies that plants with the dentate and spirally twisted form, when moved from the open sea to being grown in aquaria, became scarcely dentate and lost the spirally twisted form. He also noted that plants collected at 10 fathoms (i.e. in weak-light and calm-water conditions) lacked the spirally twisted form, and teeth were not well developed.

In his study of the ecological distribution of *Caulerpa* in the Red Sea, Lipkin (1974) referred to *C. serrulata* and *C. racemosa* (Forsskål) J. Agardh as the most common among the species of *Caulerpa* in the Red Sea. He also stated that those two species could occur on a variety of substrates but that they prefer soft substrates. He went on to discuss a 'peculiar form of *Caulerpa*' that was dredged from depths between 45 m and 80 m at the northern end of the Gulf of Eilat and indicated that the plants were closely comparable

to what was considered *C. freycinetii* var. *integerrima* Zanardini. He stated them to be '(= *C. serrulata* var. *integerrima*)' (but that name has never been validated). Interestingly, he thought that this peculiar form could not be considered as belonging to *C. serrulata*, 'as they do not exhibit the "depth form" attained by *C. serrulata* in the same and even in greater depths; though the assimilators of both branch similarly.' He concluded his discussion by saying that 'it may be a form of a known species, simplified due to the deficiency of light, but it still may be a new species of *Caulerpa*.' It is clear that a specimen dredged by him at Eilat in early 1966 and sent to Dr. W.R. Taylor at MICH that Lipkin was dealing with the alga that we now identify as *Caulerpa integerrima* (Zanardini) comb. nov. In a letter (dated 19.x.1966) sent by W.R. Taylor to Y. Lipkin, Taylor wrote, 'It is entirely possible that you have a "new species" here. On the other hand, it is quite possible that it is a very tall form of *C. freycinetii* v. *integerrima* Zan.'

Lipkin & Silva (2002) discussed the 'considerable morphological variation' that they observed in *Caulerpa serrulata* from the Dahlak Archipelago in the southern Red Sea, pointing to light intensity as the most important factor influencing the morphology. They referred to *C. serrulata* var. *boryana* (J. Agardh) W.J. Gilbert as the 'low-light ecophene', with assimilators still dichotomously branched and serrulate but the ramuli becoming flattened and band-shaped rather than terete and losing the spiral twisting. They never observed plants with entire margins in the field. According to their conclusion, this 'boryana-ecophene' could occur in deep, presumably still water (100–120-m depth) or on mudflats at c. 10 m, where some water movement may occur.

In conclusion, our study, supported by both morphological and molecular evidence, has led us to propose the reinstatement of Zanardini's *Caulerpa freycinetii* var. *integerrima* rather than to subsume it with *C. serrulata* but to recognize it as a distinct species. This somewhat rarely reported taxon of green algae is at present regarded to be endemic to the Red Sea.

ACKNOWLEDGEMENTS

We are grateful to Dr. Willem F. Prud'homme van Reine of the Nationaal Herbarium Nederland for his constructive review of the original submission and for informing us of the existence of the protologue material of *Caulerpa freycinetii* var. *integerrima* in L and for arranging for a scan to be made. We are also grateful to Dr. Bruno de Reviers and Mr. Lionel Kervran of the Museum National d'Histoire Naturelle, Paris, as well as Dr. Marianne Hamnede and Ms. Ramona Ubral-Hedenberg of the Swedish Museum of Natural History, Stockholm, for information from their holdings and also for providing us with scanned images. We thank Dr. Luca Mizzan of the Museo Civico di Storia Naturale of Venice for his assistance. We thank Dr. Robert Anderson of the Seaweed Unit, Marine & Coastal Management, University of Cape Town, for the sample of *Caulerpa bartoniae*. We acknowledge the helpful advice from Dr. Gianfranco Sartoni of the

University of Florence, Italy, and Dr. Hideo Ohba of the Tokyo University of Marine Science and Technology. Thanks also to Stephen Breitstein and to Amir Yurman for their assistance in the field and for underwater photographs of the algae. Funding was provided by the Research Foundation Flanders (postdoctoral fellowship and grants G.0142.05 and 1.5.218.08 to HV) and NATO Science for Peace (Grant 982381 to DLA). Phylogenetic analyses were carried out on the KERMIT computing cluster (Ghent University).

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Received 1 October 2008; accepted 10 February 2009
Associate editor: Alan Millar