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Historical overview of the genus *Caulerpa*[1]

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Abstract — The distinctive habit of *Caulerpa* – a nonseptate siphonous thallus consisting of a creeping rhizome that produces tufts of colorless rhizoids downward and photosynthetic branches upward – was recognized as a generic character by Lamouroux in 1809. The uniqueness of this habit is supported by a suite of cytological, structural, and biochemical characters: the presence of trabeculae (struts of wall material), first demonstrated by Montagne in 1837; heteroplastidy (the presence of amyloplasts as well as chloroplasts), first demonstrated by Nägeli in 1844; holocarpic sexual reproduction involving anisogametes, first demonstrated by Dostál as well as by Schussnig in 1929; the presence of carotenoids (siphonaxanthin and siphonein) characteristic of siphonous green algae, first demonstrated by Strain in 1949; and the replacement of cellulose by xylan as a major wall constituent, first demonstrated by Mackie & Percival in 1959. The invasion of the Mediterranean, and subsequently other areas, by weedy strains of *C. taxifolia* and *C. racemosa* has stimulated research in numerous laboratories, resulting in hundreds of publications dealing with various aspects of biology in these species and other species of *Caulerpa*.

***Caulerpa* / Caulerpaceae / Caulerpales / invasive marine algae / trabeculae**

Résumé — Revue historique du genre *Caulerpa*. La morphologie distinctive de *Caulerpa* – un thalle siphoné sans cloisons, comprenant un rhizome rampant qui émet vers le bas des touffes de rhizoïdes incolores et vers le haut des frondes dressées photosynthétiques – fut reconnue comme un caractère générique par Lamouroux en 1809. Ce caractère unique est renforcé par un ensemble d'autres caractères, cytologiques, structuraux et biochimiques : la présence de trabécules (composées de la même substance chimique que la paroi), démontrée pour la première fois par Montagne en 1837 ; l'hétéroplastidie (la présence d'amyloplastes en plus des chloroplastes), démontrée pour la première fois par Nägeli en 1844 ; la reproduction sexuelle holocarpique, exécutée par des anisogamètes, démontrée pour la première fois par Dostál et aussi par Schussnig en 1929 ; la présence de siphonaxanthine et de siphonéine, deux caroténoïdes caractéristiques des algues siphonales, démontrée pour la première fois par Strain en 1949 ; et le remplacement de la cellulose de la paroi par des xylanes, démontré pour la première fois par Mackie & Percival en 1959. L'envahissement récent de Méditerranée par des souches vigoureuses de *C. taxifolia* et *C. racemosa* a stimulé la recherche de nombreux laboratoires, conduisant a des centaines de publications ayant pour objet une grande variété de problèmes biologiques concernant ces espèces et autres espèces du genre *Caulerpa*.

algues marines envahissantes / *Caulerpa* / Caulerpaceae / Caulerpales / trabécules

1. Dedicated to Susan Loiseaux-de Goër, beloved friend and esteemed colleague, on the occasion of her retirement.

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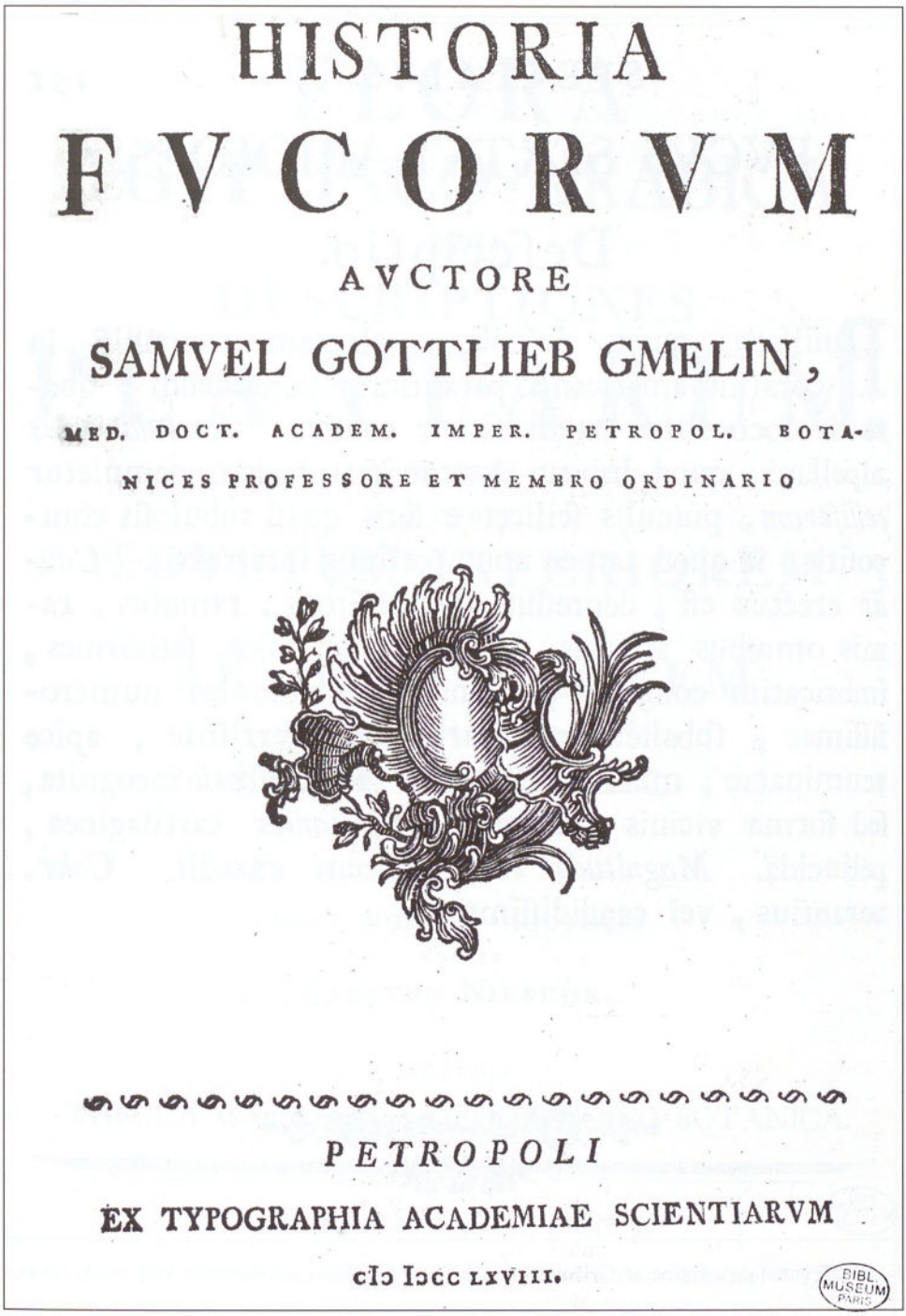
Caulerpa is one of the most widespread, conspicuous, and abundant seaweeds in tropical and subtropical waters everywhere, as well as in certain temperate waters. The discovery in 1984 that an aquarium strain of *Caulerpa taxifolia* had begun to colonize the area around Monaco (Meinesz & Hesse, 1991), followed by reports on its invasion of many other areas of the Mediterranean, including the Adriatic Sea (Žuljević & Antolić, 2000), and more recently California (Dalton, 2000; Jousson *et al.*, 2000; Kaiser, 2000; Raloff, 2000; Woodbridge, 2000) and Australia (Schaffelke *et al.*, 2002), has served as an enormous stimulus to research on *Caulerpa*. Since 1984, several hundred papers have been published on the genus, most of which deal with some aspect of *C. taxifolia*, such as its mode and rate of spreading, possible means of control, genetic diversity, and biochemistry, especially the neurotoxin caulerpenyne (an acetylenic sesquiterpene) and the hormone caulerpin (a dimer of indole-3-acrylic acid).

While attending a conference on *C. taxifolia* (San Diego, California, 31 January - 1 February 2002), I became aware that many participants, representing commercial companies and government agencies as well as academic institutions, were poorly informed with regard to the taxonomic and morphological relationship of the genus to other marine algae. This situation suggested that a historical account of the development of our basic knowledge of the genus would contribute to a better understanding of current research. The present paper provides such a historical overview. It is not a review of the results of recent research on the genus

Caulerpa has been used for food for many centuries by Japanese, Polynesians, Filipinos, and Indonesians. It was first brought within the realm of western science by Samuel Gottlieb Gmelin (1745-1774), a German naturalist, who described what was to be known as *Caulerpa sertularioides* from the West Indies in 1768 (Figs 1, 2). A few years later, four more species were described when a manuscript left at the death of the botanical collector Pehr Forsskål (1732-1763) was edited and published in 1775 (Figs 3, 4). Forsskål was a Danish naturalist who explored Lower Egypt and the eastern side of the Red Sea before dying in the field at the age of 31. Because his manuscript was not illustrated, many of his new species were of uncertain identity. As far as the algae are concerned, this uncertainty was not settled until 1932, when Frederick Børgesen, also a Dane, rediscovered specimens that Forsskål had sent to Copenhagen. Among them were *C. prolifera*, which Forsskål found at Alexandria and which has proved to be widespread throughout the Mediterranean as well as the Caribbean, and three species from the Red Sea (*C. racemosa, C. serrulata,* and *C. plumaris*, the latter now believed to be conspecific with *C. sertularioides* from the West Indies). Two well-known species were described exactly two centuries ago by still another Dane, Martin Vahl (1749-1804), on the basis of collections made at St Croix in the Danish West Indies (called Virgin Islands after being purchased by the United States in 1917). These species (Vahl, 1802) were *C. cupressoides* and *C. taxifolia*. All of these species were originally placed in the genus *Fucus* in accordance with the classification of Linnaeus (*Species Plantarum*, 1753), who applied this name to a genus that comprised all fleshy forms of algae.

The genus *Caulerpa* was described near the beginning of the 19th century by a French botanist of remarkable insight, Jean Vincent Félix Lamouroux (1779-1825). Two important contributions were made by Lamouroux. He was the first to recognize the importance of pigmentation in the classification of seaweeds, thus providing the basis for the currently accepted divisions or phyla of red algae (Rhodophyta), brown algae (Phaeophyta), and green algae (Chlorophyta). Equally important, he was one of the first to address the heterogeneity of the clas-



HISTORIA

FVCORVM

AVCTORE

SAMVEL GOTTLIEB GMELIN,

MED. DOCT. ACADEM. IMPER. PETROPOL. BOTA-

NICES PROFESSORE ET MEMBRO ORDINARIO

PETROPOLI

EX TYPOGRAPHIA ACADEMIAE SCIENTIARVM

cIↃ IↃCC LXVIII.

Fig. 1. Title page of "Historia Fucorum" (Gmelin, 1768), wherein the first species of *Caulerpa* was described (*C. sertularioides*, as *Fucus sertularioides*).

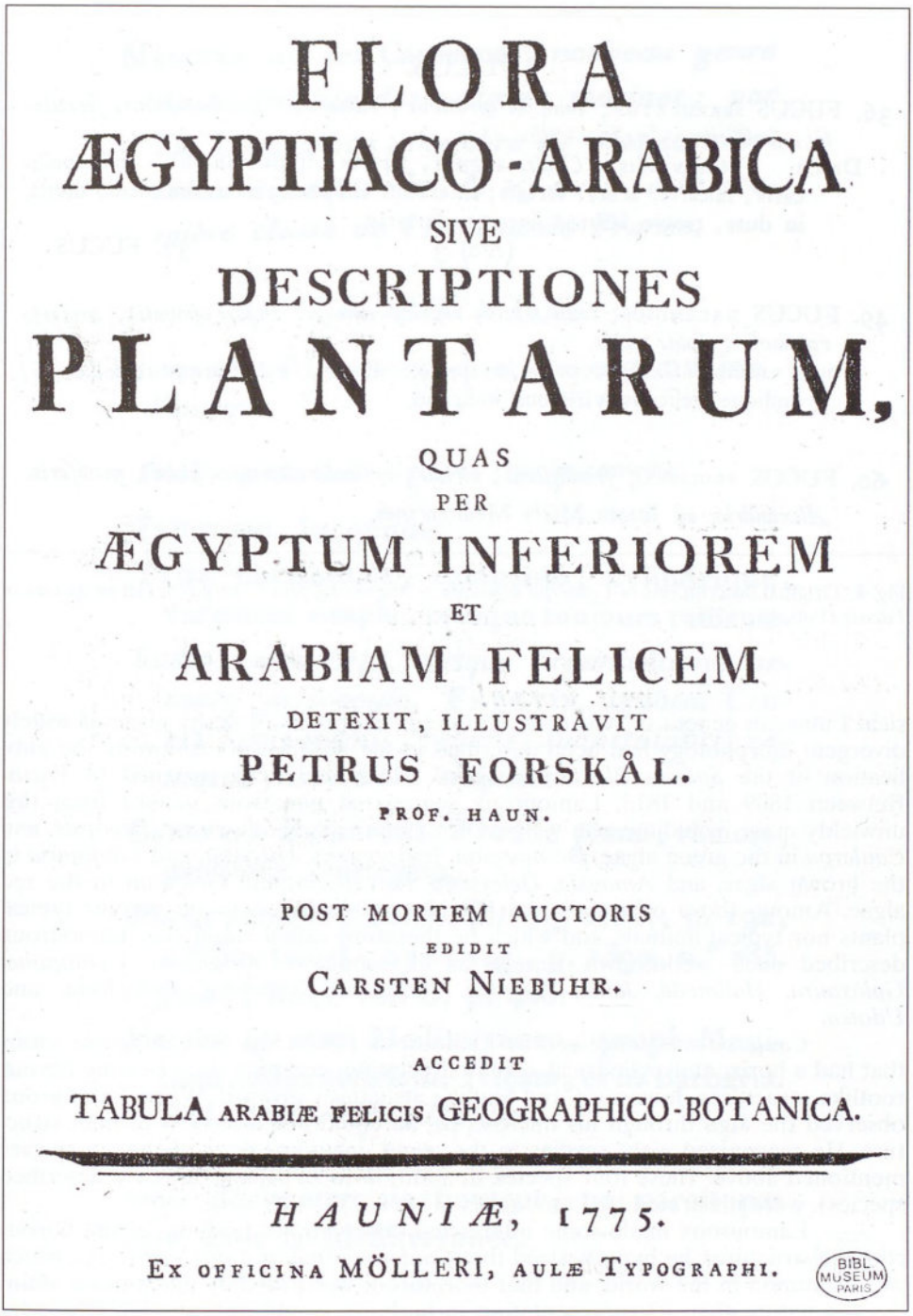
SPECIALIS. 151

FVCVS SERTVLARIOIDES.

Deſcriptio.

Puſillam, quam deſcribo, plantam, nonniſi in coralliis americanis paraſiticam deprehendi, quare de loco illius natali ſatis, conſtat. *Sertularioides* adpellaui, quod habitu externo ſertulariam aemuletur *celliferam*, pinnulis ſcilicet e ſetis quaſi tubuloſis compoſitis, id quod tamen non, cellulis intertextis. *Caulis* erectus eſt, depreſſus, tenuiſſimus, ramoſus, ramis omnibus alternis. *Frondes* ad illos ſetiformes, imbricatim congeſtae, pinnatae; pinnulae numeroſiſſimae, ſubalternae incuruae integerrimae, apice acuminatae, mucrone adunco. *Fructificatio* incognita, ſed forma vicinis iungitur. *Subſtantia* cartilaginea, pellucida. *Magnitudo* vix pollicem excedit. *Color.* aurantius, vel candidiſſimus.

Fig. 2. Original description of *Caulerpa sertularioides* (as *Fucus sertularioides*) (Gmelin, 1768).



FLORA
ÆGYPTIACO-ARABICA
SIVE
DESCRIPTIONES
PLANTARUM,
QUAS
PER
ÆGYPTUM INFERIOREM
ET
ARABIAM FELICEM
DETEXIT, ILLUSTRAVIT
PETRUS FORSKÅL.
PROF. HAUN.

POST MORTEM AUCTORIS
EDIDIT
CARSTEN NIEBUHR.

ACCEDIT
TABULA ARABIÆ FELICIS GEOGRAPHICO-BOTANICA.

HAUNIÆ, 1775.
EX OFFICINA MÖLLERI, AULÆ TYPOGRAPHI.

Fig. 3. Title page of "Flora Aegyptiaco-Arabica" (Forsskål, 1775), wherein *Caulerpa serrulata*, *C. racemosa*, and *C. prolifera* were originally described (all as species of *Fucus*).

FUCUS.

36. FUCUS SERRULATUS; *caulibus teretibus, ramoſis; foliis linearibus, ſerrulatis, ſimplicibus, veſicis nullis.*

DESCR. Totus viridis. *Caules* anguſti, teretes, ſpith. ramoſi. *Folia* pollicaria, linearia, acuta, ſerrata; interdum ſimplicia, interdum medio diviſa, in duas, tresve lacinias lineares, ſerratas.

(A a) 3 37. FUCUS

49. FUCUS RACEMOSUS; *caule tereti, repente-ramoſo; veſicis obovatis, conferte racemoſis; foliis nullis.*

Totus viridis. Caulis repens in fundo. Racemi veſicularum tripollicares, undique veſiculis viridibus imbricati.

60. FUCUS PROLIFER; *frondeſcens, viridis; articulis obovatis, planis, proliferis.*

Alexandriæ ad littora Maris Mediterranei.

Fig. 4. Original descriptions of *Caulerpa serrulata, C. racemosa,* and *C. prolifera* (all as species of *Fucus*) (Forsskål, 1775).

sical Linnaean genera of seaweeds. Hundreds of species of fleshy algae of widely divergent morphology had been described in the half-century following the publication of the *Species Plantarum*, all of which had been assigned to *Fucus*. Between 1809 and 1813, Lamouroux segregated numerous genera from this unwieldy mass, including such well-known genera as *Anadyomene, Bryopsis*, and *Caulerpa* in the green algae, *Desmarestia, Dictyopteris, Dictyota*, and *Laminaria* in the brown algae, and *Amansia, Delesseria, Furcellaria*, and *Gelidium* in the red algae. Among those organisms that Linnaeus considered to be neither typical plants nor typical animals, and which he therefore called zoophytes, Lamouroux described such well-known genera as *Acetabularia, Amphiroa, Cymopolia, Galaxaura, Halimeda, Jania, Liagora, Melobesia, Neomeris, Polyphysa,* and *Udotea*.

Caulerpa was conceived by Lamouroux (1809; Fig. 5) to comprise forms that had a horizontal, cylindrical, essentially hollow, creeping stem bearing fibrous rootlike structures downward and leaflike structures upward. When Lamouroux observed the alga through his microscope, he could not discern a distinct structure. He recognized eight species in the genus, including four of the six species mentioned above. These four species, in addition to *C. peltata* (a newly described species), were illustrated by Lamouroux (Figs 6, 7).

Lamouroux made some interesting observations. Looking at the fibrous rootlike structures, he hypothesized that *Caulerpa* inhabited soft substrates, which were common in the world, and that therefore it was probably much more abundant in nature than its representation in herbaria would indicate. He gave as a probable explanation the fact that collectors routinely head for rocky outcrops or rummage through the drift, avoiding muddy shores. Perceiving *Caulerpa* to have animal-like characters as well as plant-like characters, Lamouroux sought

Mémoire *sur les* **Caulerpes**, *nouveau genre de la famille des Algues marines ; par* **M. Lamouroux**, *membre de plusieurs Sociétés savantes : lu, le* 19 *avril, à la première classe de l'Institut de France.*

CAULERPA (1).

Substance. Presque opaque, sans organisation distincte.

(1) Du grec *caulos* tige, et *erpo* je rampe.

Fructific. Inconnue.

Tige horizontale, rampante, cylindrique, rarement simple, presque toujours rameuse.

Subst. *subopaca, absque organisatione armato etsi oculo.* **Fructif.** *ignota.* **Caulis** *horizontalis, repens, subfistulosus, ramosus, interdùm simplex.*

Caulerpa Prolifera. Fronde plana, ramosa, prolifera, variegata.

Fucus prolifer, Forsk. Fl. æg. arab., p. 192, n.° 60. Gmel., Syst. vég., p. 1390, n.° 135. Poir., Enc. vol. 8, p. 406.

Habitat *in* mari Mediterraneo, propè Massiliam, Alexandriam, Iviçam, et *in* Barbariâ. Ded. *Delaroche, Delille.*

Cette belle espèce, qui s'élève souvent à trois décimètres de hauteur, ne paroît pas rare dans la Méditerranée.

Fig. 5. Original description of the genus *Caulerpa* (Lamouroux, 1809).

Fig. 6. Lamouroux's illustrations of *Caulerpa* (Lamouroux, 1809, pl. II): (fig. 1. *C. prolifera*; fig. 2. *C. taxifolia*; fig. 3. *C. racemosa*).

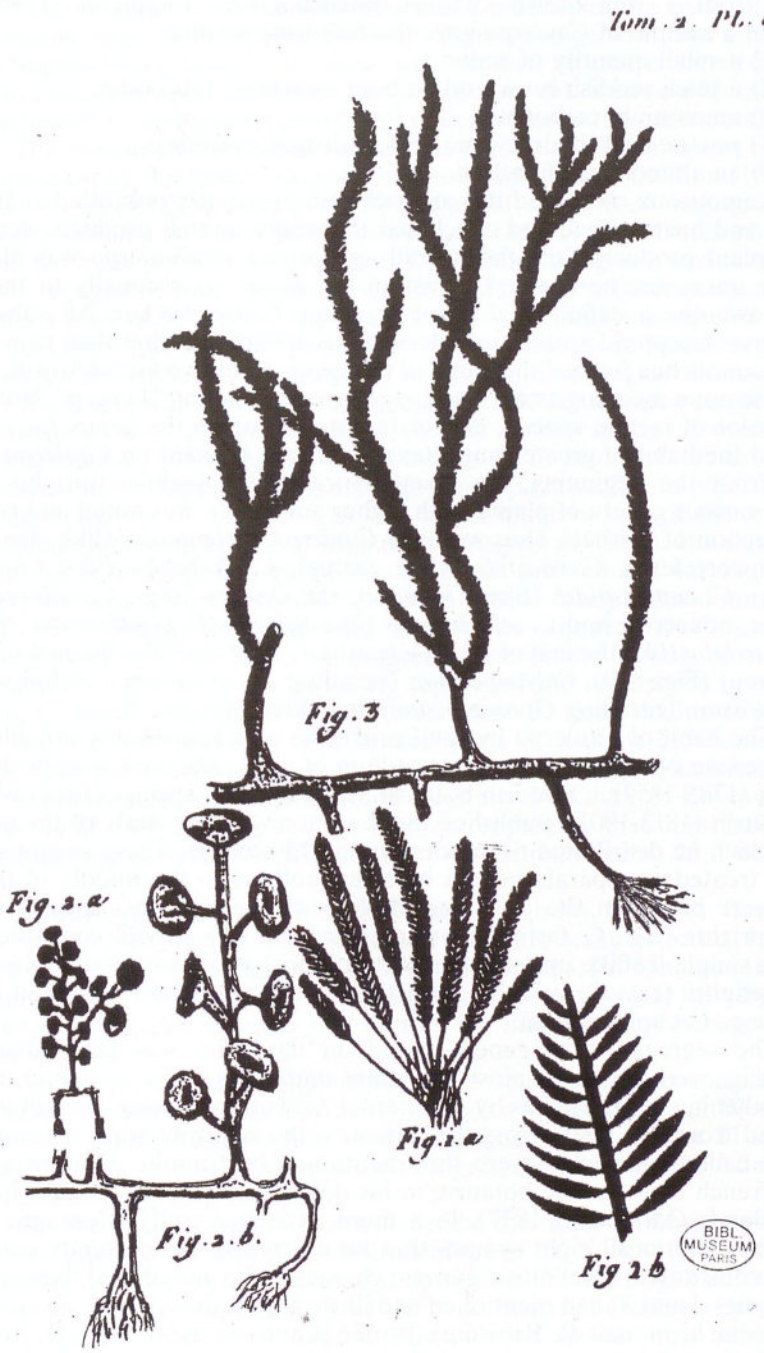


Fig. 7. Lamouroux's illustrations of *Caulerpa* (Lamouroux, 1809, pl. III): (fig. 2. *C. peltata*; fig. 3. *C. cupressoides*).

guidance from a well-known chemist, Nicolas-Louis Vauquelin (1763-1829). Analysis of a sample of *Caulerpa* gave the following results:

1) a small quantity of water
2) a thick reddish brown oil with an extremely fetid odor
3) ammonium carbonate
4) prussic acid [hydrocyanic acid, hydrogen cyanide]
5) an abundance of carbon

Lamouroux compared this analysis with previously published analyses of red algae and brown algae and concluded that more animal products were present than plant products. Still, the overall appearance of *Caulerpa* was plantlike. Obviously uncertain, he decided to assign the genus provisionally to the plant kingdom awaiting a definitive decision by some future worker. All subsequent authors have accepted Lamouroux's decision as definitive rather than provisional.

Lamouroux formed the name of the genus from two Greek words, *caulos*, a masculine noun meaning "stem", and *erpo*, a verb meaning "I creep". Noting the brilliant color of certain species, he was tempted to name the genus *Lucidia*, but considered the habit of greater importance and thus decided on *Caulerpa*.

From the beginning, the resemblance of the leaflike uprights to the foliage of various genera of plants, both higher and lower, was noted and reflected in the selection of epithets. Thus we have *Caulerpa asplenioides* (like *Asplenium*, the spleenwort fern), *C. cactoides* (like cactus), *C. charoides* (like *Chara*, the stonewort), *C. cupressoides* (like *Cupressus*, the cypress tree), *C. sedoides* (like *Sedum*, the stonecrop, and *C. selaginoides* (like *Selaginella*, a clubmoss). Also, we have *C. ericifolia* (like the leaf of *Erica*, a heath), *C. taxifolia* (like the leaf of *Taxus*, the yew tree) (Figs 8, 9), *C. lycopodium* (recalling *Lycopodium*, a clubmoss), and *C. ophioglossum* (recalling *Ophioglossum*, the adder's tongue fern).

The habit of Caulerpa by itself proved to be a remarkably reliable guide for a succession of authors. In a compendium of seaweeds on a worldwide basis, C. Agardh (1785-1859), a Swedish botanist, recognized 19 species (1822) while his son, J. Agardh (1813-1901), published the first monographic study of the genus in 1873, in which he distributed 64 species among 13 sections. These sections, which had been treated as separate genera by a few authors in the middle of the 19th century, were based on the gross morphology of the uprights. Species without leaflike uprights (e.g., C. fastigiata) were placed in one group, contrasted with those with simple leaflike uprights (e.g., C. prolifera), those with pinnately divided leaflike uprights (e.g., C. taxifolia), and those with compoundly divided leaflike uprights (e.g., C. cupressoides).

The segregation of genera based on the habit was soon abandoned because it ignored the single most important unifying generic character, namely, the strengthening of the thallus by an internal network of strands of wall material that extend from one wall across the lumen to the opposite wall. These strands, which are called trabeculae, were first mentioned by Camille Montagne (1784-1866), a French cryptogamic botanist, in his description of *C. webbiana* from the Canary Islands (Montagne, 1837). In a more extensive study, Montagne (1838) found trabeculae in all eight species that he examined. He correctly concluded that they constituted a definitive generic character. He noted that Turner (1811: 93, pl. 173, figs d and 3) had mentioned and illustrated trabeculae for an Australian species, *Fucus hypnoides* R. Brown ex Turner [*Caulerpa hypnoides* (R. Brown ex Turner) C. Agardh], but considered their presence to be a specific character. Montagne was mildly critical of Turner for failing to determine the extent of this character among the many other species of *Caulerpa* that Turner treated (all as species of *Fucus*). The structure of these trabeculae was first studied by Nägeli

(1817-1781), the great Swiss botanist who was a pioneer in the study of developmental morphology, anatomy, and cytology of plants in general, and algae in particular (Nägeli, 1844). Later, trabeculae were studied in greater detail by Dippel (1876). In essence, an initial fibrillar core, which may anastomose with other cores, is strengthened by multiple layers of wall material deposited centripetally.

The maximum number of recognized species of *Caulerpa* was reached in the compilation by the Italian phycologist Giovanni-Battista De Toni (1864-1924), who listed 80 species (De Toni, 1889). Soon thereafter (1898), a monograph of the genus was published by Anna Weber-van Bosse (1852-1942), a Dutch phycologist, and none has been published subsequently. Retaining J. Agardh's sections, Weber-van Bosse recognized only 54 species, but in 23 of these she distinguished varieties and forms, a total of 36 and 58, respectively, excluding those infraspecific taxa that include the type of the specific name. Many of the varieties are based on previously published species, while the forms represent trivial morphological differences.

When establishing *Caulerpa*, Lamouroux had commented on the presence of intermediate forms, and he wondered whether his new species *C. ocellata* (from the Mediterranean) might be merely a variant of *C. prolifera*. Observations by subsequent workers support this synonymy. *Caulerpa* is similar to other large genera of algae, indeed of all plants, in that approximately half of the species are clearly defined, showing relatively little morphological variation. The remainder of the genus, as in all large genera, poses taxonomic problems of varying difficulty, ranging from morphologically variable species with a clearly defined range of variability to the unmanageable polymorphic complex centering on *C. racemosa*, *C. laetevirens*, and *C. peltata*. There are numerous anecdotal accounts of morphological variability in this complex, including reports of the occurrence of more than one nomenclaturally recognizable growth form on the same thallus. *In situ* observations confirm this situation, with shaded parts of a plant developing peltate uprights while parts exposed to high light intensity develop cylindrical uprights. This interrelationship was demonstrated elegantly by Ohba & Enomoto (1987) and Ohba *et al.* (1992), using a cross-gradient apparatus that combined five different temperatures with five different light intensities, yielding 25 different environments.

Knowing the cause of morphological variability, however, does little to help the taxonomist who is faced with a bewildering array of forms. In a recent paper on the marine green algae of Papua New Guinea, for example, the authors (Coppejans *et al.*, 2001) recognize 16 species and 13 non-typical infraspecific taxa of *Caulerpa*. They also provide five entries for intermediates between pairs of forms or varieties.

At the present time, approximately 75 species are recognized, with the richest area in number of species being the coast extending from Western Australia through South Australia and Victoria to Queensland. About 27 species are found in this area. About 22 species are recognized in the western Atlantic while 18 species are recognized in Japan.

On the Pacific coast of North America, the northernmost populations of indigenous *Caulerpa* are found at Isla Guadalupe at 29° N, out of range of the cold waters brought to the surface by coastal upwelling. On the Baja California mainland, however, the northern limit is 24° 30'N. In contrast, *Caulerpa* occurs on the Atlantic coast as far north as Onslow Bay, North Carolina, at a latitude of 34° 30'N. At this northern limit, however, the habitat is restricted to the subtidal (15-48 m), where the algae are bathed by warm waters of the Gulf Stream. The Pacific coast of South America is truly deficient in *Caulerpa*, which occurs only as far south as Islas de Lobos in Peru at a latitude of 6° 30' S.

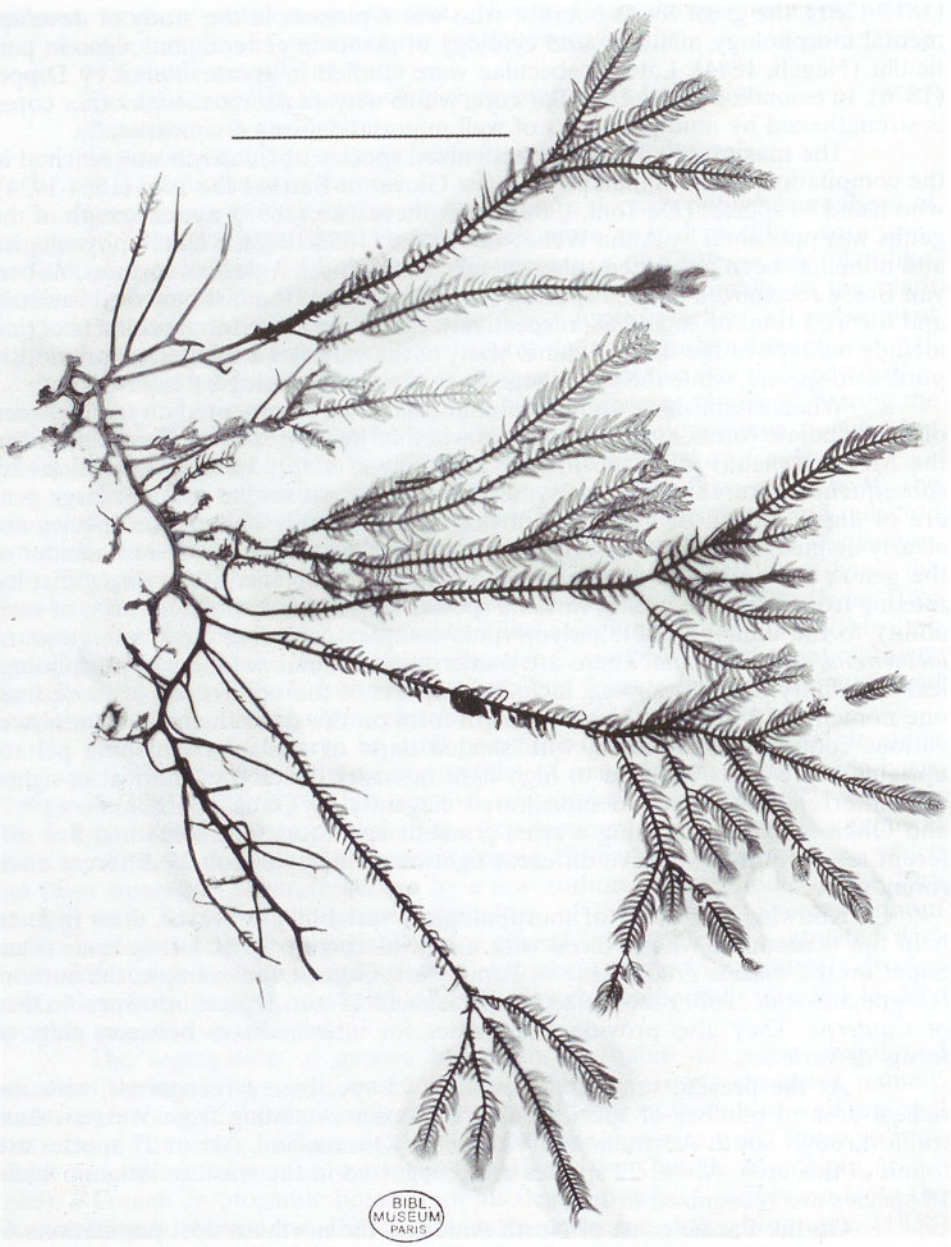


Fig. 8. *Caulerpa taxifolia* from Kingston, Jamaica (*leg. G.F. Papenfuss*, 27.vii.1932, UC). Scale bar = 5 cm.

Fig. 9. *Caulerpa taxifolia* introduced into Agua Hedionda, San Diego County, California (*leg. Rachel Woodfield*, x. 2000, UC). Scale bar = 5 cm.

The unique structure of *Caulerpa* was considered worthy of taxonomic recognition at a level higher than genus as early as 1830, when Greville (1830: lxiii) proposed the monotypic family Caulerpaceae («Caulerpeae»), but without giving a description to validate the name. Validation was provided by Kützing (1843: 302), to whom we are indebted for many currently recognized algal families. The Caulerpaceae has always been associated with other families of siphonous green algae, to which the name Siphonales has been applied. This name, however, may not be used because an ordinal name must be based on the legitimate name of an included genus. When the order to which the Caulerpaceae is assigned excludes the Bryopsidaceae, the correct name is Caulerpales J. Feldmann (1946: 753), but when it includes the Bryopsidaceae the correct name is Bryopsidales Schaffner (1922: 133). In an early example of hierarchical inflation, Bessey (1907) recognized two classes of siphonous algae. The Vaucheriophyceae ("Vaucherioideae") included several families of fungi together with the Cladophoraceae and genera now placed in the Codiaceae, Halimedaceae, and Udoteaceae. The Bryopsidophyceae ("Bryopsidoideae") included the Chytridiaceae together with the Botrydiaceae, Valoniaceae, Derbesiaceae, Bryopsidaceae, Dasycladaceae, and Caulerpaceae. Bessey placed these two classes in their own phylum, the Siphonophyceae.

Considering the size, abundance, and unique structure of *Caulerpa* plants, one might expect them to engage the imagination of those biologists who were trying to determine how marine algae met their daily challenges. Because many of the better-known marine laboratories, such as Plymouth, Woods Hole, and Helgoland, were in *Caulerpa*-free areas, research was initially restricted to the Mediterranean, where *Caulerpa prolifera* was readily available at such laboratories as Villefranche-sur-Mer (near Nice) and Naples.

Early investigators (e.g., Janse, 1889) were fascinated by protoplasmic streaming, which heretofore had been observed almost exclusively in the giant internodal cells of *Chara* and *Nitella*. Morphogenesis proved to be a source of amusement for several workers (e.g., Janse, 1904, 1905, 1906, 1910); whose experiments showed that the frond of *Caulerpa prolifera* was both polar and medusoid. A piece of the blade would produce rhizoids basally and proliferous blades somewhat below the apex. Polarity could be overruled by geotropism, so that a blade positioned upside down would produce rhizoids from the tip. In the words of Fritsch (1935, p. 383), "[Vegetative reproduction] takes place abundantly by a gradual dying away of the older parts of the rhizomes, whereby the branches become independent plants; by this means rapid local multiplication is effected. Dispersal is attained by detached fragments which are able rapidly to heal any exposed surface and possess a remarkable power of regenerating new plants when lodged in a suitable position." These observations foretold of impending invasive strains.

An important physiological character of *Caulerpa*, namely, the division of labor among plastids between photosynthetic chloroplasts and starch-storing amyloplasts, was first studied by Nägeli (1844) and later, in greater detail, by such workers as Czurda (1928). *Caulerpa* shares this character (heteroplastidy) with three other families of siphonous green algae, namely, Dichotomosiphonaceae, Halimedaceae, and Udoteaceae.

The composition of the pigments in the chloroplasts of *Caulerpa*, which are characteristic of siphonous green algae but not unique to that group, was first determined by Strain (1949), who named the distinctive xanthophyll "siphonaxanthin" and the distinctive carotene "siphonein".

The first comprehensive study of the biology of *Caulerpa* was published in 1844 by Nägeli. The standard histochemical test for cellulose at that time (and even now) is hydrolysis with sulfuric acid followed or accompanied by staining of

the hydrolysate with IKI (iodine potassium iodide) solution. The hydrolysate from cellulose stains blue. When Nägeli tried this test on the wall of *C. prolifera*, the hydrolysate stained yellowish or brown. Nägeli concluded that the wall of *Caulerpa* was not like that of higher plants or other green algae, but he did not pursue the matter. Doubts as to Nägeli's results were expressed by two subsequent investigators but were firmly put to rest by Correns (1895). Like Nägeli, however, Correns did not attempt to determine the chemical composition of the wall. Many years later, this question was assigned to a French graduate student, Robert Mirande. Mirande (1913) concluded that the chief components of the wall were callose and pectic compounds. Callose is a complex carbohydrate found in sieve elements of higher plants. It remained for Mackie & Percival in 1959 to show that the so-called callose in *Caulerpa* was a β-1,3 linked D-xylose or xylan. Further work in Percival's laboratory and elsewhere showed that xylan replaces cellulose in members of the Bryopsidaceae, Dichotomosiphonaceae, Halimedaceae, and Udoteaceae as well as in *Caulerpa*, while a β-1,4 linked D-mannose or mannan replaces cellulose in *Codium* and in the Dasycladales.

For nearly a century after Lamouroux described *Caulerpa*, it was assumed that sexual reproduction in the genus was lacking. Some observers reported seeing papillae on the thallus and a reticulate pattern of the protoplast, suggesting some sort of reproductive activity. The problem was not addressed specifically, however, until the summer of 1927, when Rudolf Dostál, a Czech botanist, was working at Villefranche-sur-Mer. He saw papillae on the blade of *C. prolifera*, from some of which a glob of mucilaginous material was being exuded. Buried in the mucilage were several small green cells, which Dostál thought most likely were macrogametes. He also thought that the papilla was probably a macrogametangium. These results were published in May of 1928 (Dostál, 1928a). In the summer of 1928, however, Dostál corrected his misimpressions of the previous summer. He observed holocarpic reproduction, with most of the protoplast forming swarmers, which he called spores because he did not observe copulation. These results were published in October of 1928, within a month of Dostál's return to Brno (Dostál, 1928b).

In February of that same year (1928), Bruno Schussnig, a professor in Vienna, took up residence at the Zoological Station in Naples, having received a fellowship in support of his morphological studies of marine green algae. Upon seeing Dostál's first paper, Schussnig turned his attention to *C. prolifera* and soon observed the release of anisogametes through the papillae on the blade. These observations were published in January of 1929 (Schussnig, 1929a). The overlapping investigations led to the publication of two polemics in successive issues of the same journal, Dostál (1929) claiming priority of discovery and accusing Schussnig of taking unwarranted credit, Schussnig (1929b) claiming independence while conceding priority.

In 1972, Ian Price found that in *C. verticillata* the quadriflagellate zygote that resulted from copulation of anisogametes settled on the substrate, lost its flagella, and enlarged to form a spherical body before germinating in a bipolar fashion. The germling developed into a protonema of stout green axes and pale slender rhizoids. The green axes produced uprights, thus showing that the life history of *Caulerpa* is haplobiontic with the somatic phase being diploid. A more detailed account of sexual reproduction in *Caulerpa* was published by Enomoto & Ohba (1987), based on culture studies of *C. racemosa*.

Clifton (1997) recorded the mass release of gametes by siphonous green algae (the order Bryopsidales) on a Panamanian coral reef in intermittent predawn episodes that show no lunar or tidal cycling. Several genera, including

Table 1. Summary of *Caulerpa* characters with date of recognition

Habit (non-septate thallus composed of a creeping rhizome, colorless rhizoids, and green uprights)	1809
Anatomy (anastomosing trabeculae formed from wall material)	1837
Cytology (chloroplasts + amyloplasts)	1844
Sexual reproduction (anisogamic holocarpy)	1929
Pigmentation (siphonaxanthin and siphonein)	1949
Wall composition (xylan as replacement for cellulose)	1959

Halimeda and members of the Udoteaceae, discharge gametes along with *Caulerpa*. The surrounding waters become cloudy. The remaining colorless thalli soon disappear from the reef.

A chronological listing of the discovery of the most important diagnostic characters of *Caulerpa* is given in Tab. 1.

A fascinating account of the Mediterranean invasion has been published by Meinesz (1999), who chronicles the devastation of indigenous ecosystems resulting from failure by government agencies to recognize the seriousness of the situation. Whether agencies and organizations seeking to control invasions beyond the Mediterranean (e.g., California and Australia) can avoid crippling political entanglements remains to be seen. Meanwhile, the spread in the Mediterranean of another weedy strain of *Caulerpa*, this one referable to the *C. racemosa* complex, is being monitored (Piazzi *et al.*, 1994, 1997, 2001b; Piazzi & Cinelli, 1999; Verlaque *et al.*, 2000). The co-occurrence of both invasive strains in the Ligurian Sea provides an unusual context for the study of competitive interspecific interactions. The results of a preliminary study (Piazzi *et al.*, 2001a) showed that the weedy strain of *C. racemosa* has an even higher invasive potential than the weedy strain of *C. taxifolia*, suggesting that the number of sites where both strains occur may increase rapidly in the future.

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