

Rediscovery of a forgotten Mediterranean *Chaetomorpha* species in the Venice Lagoon (North Adriatic Sea): *Chaetomorpha stricta* Schiffner (Cladophorales, Chlorophyta)

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Abstract – On the basis of bibliographical, morphological and molecular studies (SSU rDNA), the reinstatement of species rank for *Chaetomorpha stricta* Schiffner, a poorly known Mediterranean endemic species described in the early 20th century, is proposed. Previously reduced to a posterior heterotypic synonym of *C. linum* (O.F. Müller) Kützing, *C. stricta* clearly differs from the latter by its small, light green, free-living filaments entangled in dense masses, the cells 0.5 to 1.6 (rarely 2) times as long as broad, with cell walls lamellate and broad up to 75-90 µm thick, and by molecular data. *Chaetomorpha stricta* was rediscovered, in May 2011, in oligotrophic clear waters of a closed fishing pond in the Valle Cavallino (northern basin of the Venice Lagoon). A critical review of *Chaetomorpha* taxa reported in the Mediterranean Sea and a taxonomic key to the Mediterranean taxa currently accepted are presented.

***Chaetomorpha stricta* / Taxonomy / Identification key / Venice Lagoon / Italy / Mediterranean Sea**

Résumé – Sur la base d'une analyse bibliographique, morphologique et génétique (SSU rDNA), le rétablissement dans son rang d'espèce de *Chaetomorpha stricta* Schiffner, une espèce endémique méditerranéenne peu connue décrite au début du XX^e siècle est proposé. Précédemment réduite au rang de synonyme hétérotypique de *C. linum* (O.F. Müller) Kützing, *C. stricta* diffère nettement de cette dernière par ses filaments non-fixés et enchevêtrés en masses denses, constitués de cellules 0,5 à 1,6 (rarement 2) fois plus longues que larges à

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parois cellulaires lamelleuses et très épaisses (jusqu'à 75-90 μm), et par ses caractéristiques génétiques. *Chaetomorpha stricta* a été redécouverte, en mai 2011, dans les eaux claires et oligotrophes d'un étang de pêche de la Valle Cavallino (Bassin nord de la Lagune de Venise). Un inventaire critique des taxons de *Chaetomorpha* signalés en Méditerranée et une clé de détermination des espèces méditerranéennes actuellement acceptées sont présentées.

***Chaetomorpha stricta* / Taxonomie / Clé d'identification / Lagune de Venise / Italie / Méditerranée**

INTRODUCTION

Chaetomorpha Kützing (Cladophorales, Chlorophyta) is a cosmopolitan green algal genus characterized by attached or unattached, unbranched and polynucleate filaments without lateral rhizoids. Members of this taxon occur intertidally in marine and brackish waters (Leliaert & Boedeker, 2007). Most *Chaetomorpha* species have relatively robust macroscopic thalli, and several species frequently form extensive mats of intertwining filaments that often cause green tides in different regions of the world (Flindt *et al.*, 1997; Deng *et al.*, 2013; Zhang *et al.*, 2014). For example, in North China and Western Australia the massive growth of *C. linum* (O.F. Müller) Kützing mats has replaced other species in some lagoon areas, with a negative impact on seagrass ecosystems and benthic bivalves (Zhang *et al.*, 2014).

The morphology of this genus is very simple, and only few characters are available to discriminate species, e.g.: attached or unattached growth, filament diameter, shape and size of the basal cells, length/diameter ratio of cells, presence of constrictions between cells (Leliaert & Boedeker, 2007). For this reason, the taxonomy of *Chaetomorpha* is very problematic and so far 99 taxa have been reported, of which 70 are currently accepted taxonomically (Guiry & Guiry, 2017). An example of the taxonomic complexity of the genus is illustrated by the species complex containing *C. aerea* (Dillwyn) Kützing and *C. linum*, two common algae widespread in warm and temperate waters and treated, according to the authors, as only one taxon or two different taxa. In addition to the morphological simplicity and the low number of diagnostic features, phenotypic plasticity, influenced by different environmental factors, can lead to overlapping morphological characters. These considerations highlight the need for molecular data to discriminate among species in the genus *Chaetomorpha* (Leliaert *et al.*, 2009, 2011). Several molecular studies, based on gene sequence data of the ribosomal small subunit (SSU) or/and partial large subunit (LSU), were conducted to understand the relationships within Cladophorales (Bakker *et al.*, 1994; Hanyuda *et al.*, 2002; Leliaert *et al.*, 2003, 2007; Boedeker *et al.*, 2016).

In this study, we used morphological data coupled with phylogenetic analyses, based on the partial nuclear small subunit (SSU) rDNA, to discriminate a species of *Chaetomorpha* described from the Venice Lagoon (Italy) in the early 20th century and since forgotten: *Chaetomorpha stricta* Schiffner.

MATERIAL AND METHODS

Sampling and morphological study

The species (hereafter: Valle Cavallino *Chaetomorpha*) was sampled, in May 2011, in Valle Cavallino during the assessment of the ecological status of the Venice Lagoon according to the 2000/60/EC requirements (Fig. 1). The Valle Cavallino *Chaetomorpha* was collected both from a boat with a rake and manually by SCUBA diving and the associated vegetation was identified. A subsample was dried in silica gel for genetic analyses and the rest was preserved in 4% formalin/seawater for the morphological study. A voucher dried specimen was deposited at the Herbarium Patavinum (PAD) of the University of Padova, Italy, with the reference:

– A000622 – *Chaetomorpha stricta* Schiffner in Schiffner & Vatova, collection Adriano Sfriso, Valle Cavallino (sexagesimal coordinates 45°29'30" N, 12°33'57" E), Venice Lagoon, Italy.

The material was compared with two syntypes of *C. stricta* Schiffner deposited at the Natural History Museum, London (BM), Department of Botany, with the following references:

– 000515933 (BM), labeled as Schiffner, Algae marinae n° 232, *Chaetomorpha stricta* Schiffn. n. sp., Val Perini, 12.12.1930, Commissione Internazionale del Mediterraneo, Ricerche nella LAGUNA VENETA, leg. A. Vatova, 25 May 1937.

– BM001044761, labeled as Schiffner, Algae marinae n° 1233, *Chaetomorpha stricta* Schiffn. n. sp., Val Avertò, 6.6.1932, Commissione Internazionale del Mediterraneo, Ricerche nella LAGUNA VENETA, leg. A. Vatova, 25 May 1937.

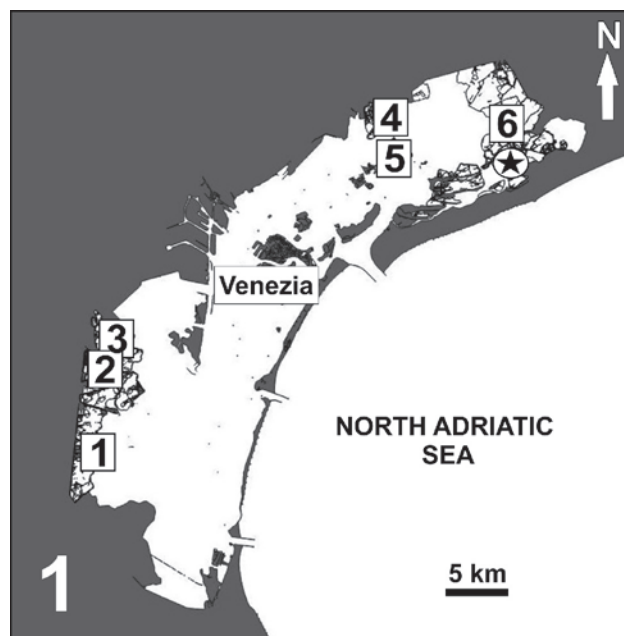


Fig. 1. The Venice Lagoon with the sampling site of Valle Cavallino (STAR) and the six syntype localities of *Chaetomorpha stricta* Schiffner (Schiffner & Vatova, 1937): 1. Valle Morosina; 2. Val Avertò; 3. Val Serraglia; 4. Val Perini; 5. Isola La Cura; 6. Val Grassabò.

The study was completed by comparisons with species of *Chaetomorpha* deposited at the Herbarium HCOM of the Mediterranean Institute of Oceanography (MIO), Aix-Marseille University, in particular with the species possessing upper cells with thick and lamellate cell walls:

– *C. ligustica* (Kützing) Kützing – H8324, coll. Marc Verlaque, Sausset-les Pins, France, 23.09.2017, sea level.

– *C. pachynema* (Montagne) Kützing – H5634, coll. Marc Verlaque, Cala Petraghja, Corsica, 22.08.1992, 3 m depth.

Specimens were studied by means of Leica MZ16® and M80® stereo zoom microscopes and Leica 5000® and Optiphot-2 Nikon® light microscopes equipped with a digital image acquisition system. A subsample of the Valle Cavallino specimen A000622 was treated according to Moro *et al.* (2010) and studied with a scanning electron microscope FEI Quanta 200® (Oregon, USA). Herbarium abbreviations follow Thiers (2015).

Molecular analyses

Genomic DNA extractions using the Genomic DNA purification kit (Thermo Scientific™) were performed on the Valle Cavallino *Chaetomorpha*. The partial SSU gene was amplified using the primer pair SR-4 and 18S-6M (Hanyuda *et al.*, 2002) under the following PCR conditions: initial denaturation step of 94°C for 3 min, followed by 35 cycles of 94°C for 50 sec, 50°C for 50 sec, 72°C for 1 min, followed by a final extension of 3 min at 72°C. PCR products were cleaned by using the HT ExoSAP-IT (Applied Biosystems™). Sequencing of the amplified fragments was accomplished with the same primer pair at the BMR Genomics Sequencing Service (University of Padova, Italy). The SeqMan II program from the Lasergene software package (DNASTar©, Madison, WI, USA) was used to assemble the final consensus sequence. Since the partial SSU sequences obtained for 9 samples of the Valle Cavallino *Chaetomorpha* were all identical, only one was deposited in the International Nucleotide Sequence Database (INSD) through the European Nucleotide Archive (ENA) platform with the following accession number: LT898516.

To infer the phylogenetic position of the Valle Cavallino *Chaetomorpha*, a dataset of 16 sequences belonging to different *Chaetomorpha* species was constructed (Table 1). The genus *Siphonocladus* F. Schmitz was chosen as outgroup [*S. tropicus* (P.Crouan & H.Crouan) J.Agardh, accession number AM498761]. Sequences for comparison were downloaded from the USA National Center for Biotechnology Information (NCBI) web server (<http://www.ncbi.nlm.nih.gov>). Sequence alignment was obtained by the ClustalW computer program (Thompson *et al.*, 1994). Phylogenetic analyses were performed using the MEGA 5.1 (Molecular Evolutionary Genetics Analysis) program (Tamura *et al.*, 2011) according to Neighbour Joining (NJ), Maximum Likelihood (ML), applying the T92 + G + I evolutionary model (Tamura, 1992), and Maximum Parsimony (MP) methods. Non-parametric bootstrap re-sampling (Felsenstein, 1985) was performed to test the robustness of the tree topology (1000 replicates).

Bibliographical analysis

A critical analysis of the literature was conducted to establish the exhaustive list of *Chaetomorpha* taxa described or reported from the Mediterranean. The diagnostic characters have been researched and critically analysed to identify the current taxonomic status of each taxon.

Table 1. 18S rDNA sequences with accession numbers of *Chaetomorpha* species downloaded from GenBank for comparison with the Valle Cavallino *Chaetomorpha* (accession number: LT898516)

<i>Taxon</i>	<i>Country of the type locality</i>	<i>Sampling area or country</i>	<i>Accession No.</i>
<i>C. aerea</i> (Dillwyn) Kützing	England	North Sea, Germany	LT607325
<i>C. antennina</i> (Bory) Kützing	Réunion	KwaZulu Natal, South Africa	LT607328
<i>C. clavata</i> Kützing	West Indies	Panama	LT607334
<i>C. coliformis</i> (Montagne) Kützing	Probably Tasmania	Otago, New Zealand	LT607335
<i>C. firma</i> Levring	Juan Fernandez Isl.	Coquimbo, Chile	LT607336
<i>C. ligustica</i> (Kützing) Kützing	Italy	Zeeland, Netherlands	LT607340
<i>C. linum</i> (O.F.Müller) Kützing	Denmark	North Sea, Germany	LT607341
<i>C. linum</i> (O.F.Müller) Kützing	Denmark	Qingdao, China	JN540034
<i>C. linum</i> (O.F.Müller) Kützing	Denmark	Australia	KT593552
<i>C. melagonium</i> (F.Weber & D.Mohr) Kützing	Sweden	Iceland	LT607342
<i>C. moniligera</i> Kjellman	Japan	Japan	LT607343
<i>C. robusta</i> (Areschoug) Papenfuss	South Africa	Cape Town, South Africa	LT607344
<i>C. spiralis</i> Okamura	Japan	Eastern Cape, South Africa	LT607345
<i>C. valida</i> (J.D.Hooker & Harvey) Kützing	Tasmania	Rongcheng, China	JQ308276
<i>C. vieillardii</i> (Kützing) M.J.Wynne	New Caledonia	Kenya	LT607346

RESULTS

Morphological description of the Valle Cavallino *Chaetomorpha* (Figs 2-7). Filaments free-living (basal cell not observed), light green, 10-20 cm long, entangled to form masses twisted or wrapped around other macrophytes; cells, 250-350 µm broad and 1-2 times as long as broad, with colourless lamellar cell walls, 48-75 µm thick; filaments frequently covered by calcareous algae, especially *Pneophyllum fragile* Kützing, cyanobacteria and diatoms belonging to the genus *Cocconeis* Ehrenberg.

Distribution: The Valle Cavallino *Chaetomorpha* was never found in the open lagoon or in other fishing ponds.

Habitat: The Valle Cavallino *Chaetomorpha* grew in oligotrophic clear waters of a closed fishing pond of the northern basin of the Venice Lagoon where it formed small entangled masses of filaments within the angiosperm shoots and other macroalgae. The species coexisted with the larger species *C. linum*, the only other species of *Chaetomorpha* recorded in Valle Cavallino. The environment of the fishing pond was characterized by high water quality and was prevalently populated by the angiosperms *Ruppia cirrhosa* (Petagna) Grande and *Cymodocea nodosa* (Ucria) Ascherson. The macroalgal vegetation of the Valle Cavallino is mainly composed of *Lamprothamnium papulosum* (K.Wallroth) J.Groves, a species never recorded in the open lagoon, *Chaetomorpha linum* (O.F.Müller) Kützing, *Pneophyllum fragile*, *Polysiphonia spinosa* (C Agardh) J. Agardh, and *Valonia aegagropila* C. Agardh. No Ulvaceae were recorded in the area.

DNA sequence available: LT898516 nuclear SSU rDNA.

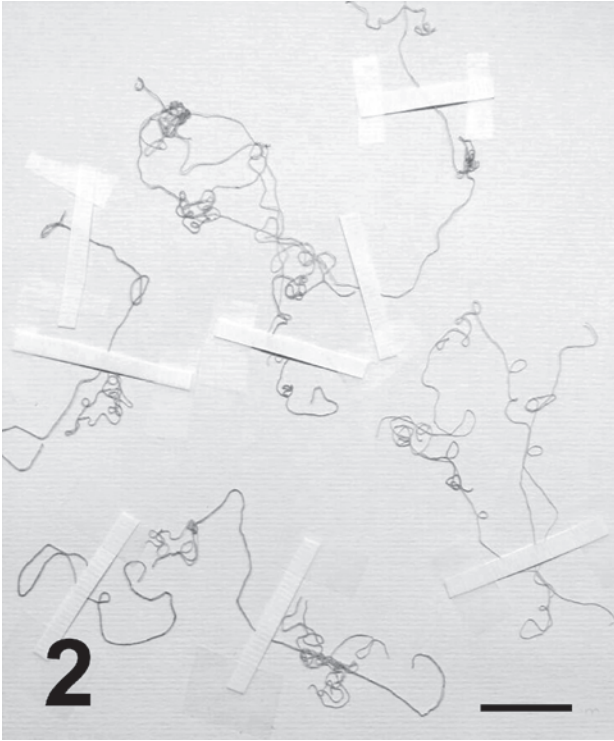


Fig. 2. Dried specimens (Ref. A000622) of *Chaetomorpha stricta* Schiffner collected in May 2011 in Valle Cavallino (45.493611°N, 12.566667°E), Venice Lagoon. Scale bar = 2 cm.

Molecular analyses

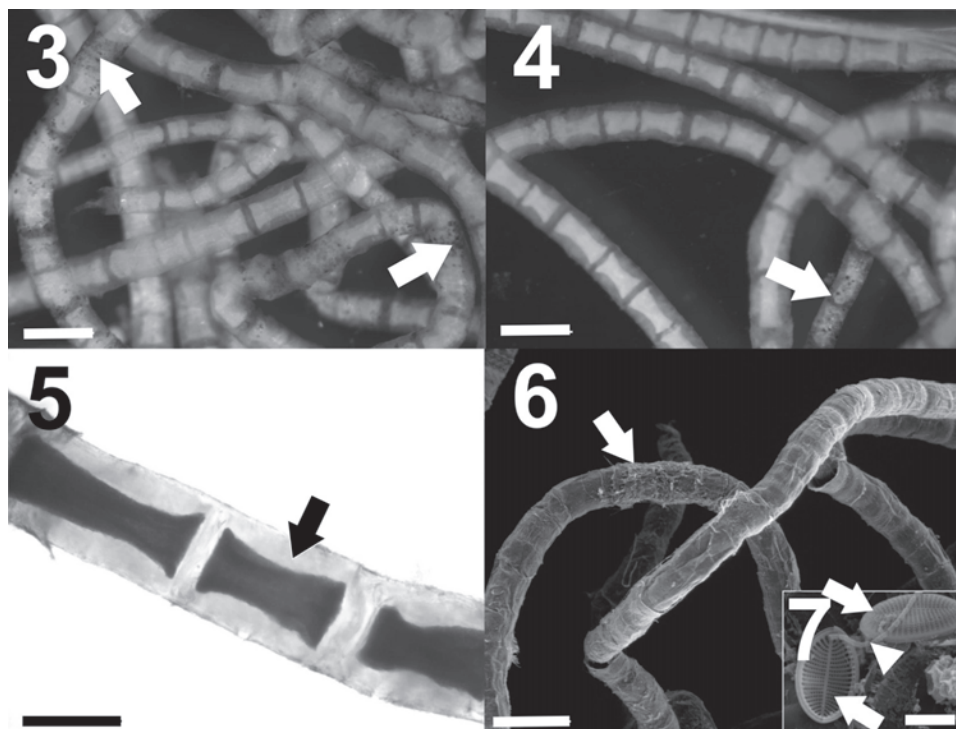
In the phylogenetic reconstruction, the SSU sequence of the Valle Cavallino *Chaetomorpha* was placed in a well-supported clade (NJ 100%, ML 99%, MP 99% of bootstrap support) with samples belonging to *C. linum* and *C. aerea* from different regions of the world (Fig. 8). The nucleotide divergences of the Valle Cavallino *Chaetomorpha* and the sequences of the other specimens are: 0.30% with *C. linum* (Australia), 0.44% with *C. linum* (Germany and China) and 0.44% with *C. aerea* (Germany).

Taxonomic analyses

According to the literature analysed, a total of 43, 31 and 15 taxa of *Chaetomorpha* were reported from the Mediterranean Sea, the Adriatic Sea and the Venice Lagoon, respectively. Among them, 8 taxa were described from the Venice Lagoon (Table 2). Cormaci *et al.* (2014) reduced this list to only 4 accepted taxa:

- *C. gracilis* Kützing
- *C. ligustica* (Kützing) Kützing
- *C. linum* (O.F. Müller) Kützing
- *C. pachynema* (Montagne) Kützing

We agree with this treatment, except for two taxa: *C. aerea* and *C. stricta*. With regard to the taxonomic status of *C. aerea*, there are two different viewpoints. Some authors considered the taxon as a growth form of *C. linum* (Burrows, 1991; John *et al.*, 2003; Leliaert & Boedeker, 2007; Mystikou *et al.*, 2016), in disagreement



Figs 3-7. *Chaetomorpha stricta* Schiffner, (Specimen A000622) Valle Cavallino, May 2011. 3-4. Filaments with epiphytic calcareous taxa (arrows). 5. Details of cells showing the thick and lamellate cell walls (arrow). 6. Scanning electron microscope image of filaments showing epiphytes (arrows). 7. Detail of epiphytes; arrows: *Cocconeis* sp.; arrow head: Cyanobacteria. Scale bars: 3 & 4 = 400 μm ; 5 = 200 μm ; 6 = 500 μm ; 7 = 10 μm .

with others who reported *C. aerea* and *C. linum* as two separate entities (Stegenga & Mol, 1983; Silva *et al.*, 1996; Sfriso, 2010; Brodie *et al.*, 2016; Huang *et al.*, 2016). The relationship between these species is still uncertain (John *et al.*, 2003). On this point, Sfriso (2010) highlighted that these taxa should also be considered as distinct entities on the basis of the different habitats they colonize: *C. linum* grows free-floating in environments covered by seagrasses whereas *C. aerea* is mostly present in eutrophic environments attached to hard substrata. On the basis of morphological data and ecological requirements, we chose to treat the two taxa separately in the critical review of *Chaetomorpha* reported in the Mediterranean Sea (Table 2).

Since its description from different parts of the Venice Lagoon (Schiffner & Vatova, 1937) (Fig. 1), the status of *C. stricta* has changed over time. The species was successively reported, always without any description, in the Adriatic Sea: Venice Lagoon (Vatova, 1940), Trieste (Italy) (Pignatti & Giaccone, 1967; Giaccone, 1969), Pianosa Island and Tremiti Islands (Italy) (Rizzi *et al.*, 1967b; Giaccone, 1969; Rizzi Longo, 1972), Testa del Gargano (Italy) (Rizzi *et al.*, 1967a; Giaccone, 1969), and Supetarska-Druga (Croatia) (Rizzi Longo, 1972a), and in the Tyrrhenian Sea: Costa dell'Argentario (Italy) (Rizzi Longo, 1972b, as "*Chaetomorpha-stadio stricta* Schiffn."). Subsequently, *C. stricta* was treated as taxon inquirendum (Gallardo *et al.*, 1993), before being downgraded to a heterotypic synonym of

Table 2. *Chaetomorpha* species reported from the Venice Lagoon, the Adriatic and the Mediterranean Sea according to De Toni & Levi (1888), De Toni (1889), Gallardo *et al.* (1993), Furnari *et al.* (1999), Leliaert & Boedeker (2007), Sfriso & Curiel (2007), Sfriso & Boedeker (2007), Sfriso & Curiel (2007), Cormaci *et al.* (2014), Guiry & Guiry (2017) and references in the Table. Diagnostic characters are: (i) plant: free-living or fixed, (ii) cells: cylindrical, slightly constricted at septa, locally swollen or barrel-shaped; (iii) diameter and L/D ratio of cells (iv) cell walls: thin, relatively thick or thick and lamellate. Missing data: m.d. Taxa accepted are in boldface

Taxon	Basionym	References	Type locality	Venice Lagoon	Adriatic Sea	Mediterranean Sea	Diagnostic characters of Mediterranean populations	Accepted name or status
<i>C. aerea</i> (Dillwyn) Kützting	<i>Conferva aerea</i>	Dillwyn, 1806: pl. 80; Kützting, 1849: 1853, pl. 59 figs 1a,b	Norfolk, England	X	X	X	Fixed, cylindrical to slightly constricted at septa, 150-700 µm, L/D: 0.5 to 2, cell walls lamellate to thin	<i>C. aerea</i> (Dillwyn) Kützting
<i>C. brachyarthra</i> (Kützting) Kützting	<i>Conferva brachyarthra</i>	Kützting, 1843: 260; 1845; 1849; 1853, tab; 53 fig. IV	Venice, Italy	X	X	X	m.d., cylindrical, 161 µm, L/D 0.5 to 1, cell walls thin	<i>C. aerea</i> (Dillwyn) Kützting
<i>C. chlorotica</i> (Montagne) Kützting	<i>Conferva chlorotica</i>	Montagne, 1846: 165; Kützting, 1849; 1853, tab; 54 fig. II	Algers, Algeria	-	-	X	Fixed, slightly constricted at septa, 125-200µm, L/D: 1.5 to 2, cell walls thin	<i>C. aerea</i> (Dillwyn) Kützting
<i>C. crassa</i> (C. Agardh) Kützting	<i>Conferva crassa</i>	C. Agardh, 1824: 99; Kützting, 1845; 1849; 1853, pl. 59, fig. II	Trieste, Venice, Italy and England	X	X	X	m.d., constricted at septa, 300-700 µm, L/D: 1 to 2, cell walls thin	<i>C. aerea</i> (Dillwyn) Kützting
<i>C. crassa</i> f. <i>genuina</i> Schiffner in Schiffner & Vatova nom. inval.	-	Schiffner & Vatova, 1938: 185, pl. XXXII: fig. 3	Venice, Italy	X	X	X	m.d., constricted at septa, 600-700 µm, L/D: 1, cell walls thin	<i>C. aerea</i> (Dillwyn) Kützting
<i>C. dubyana</i> Kützting	-	Kützting, 1853: 8, pl. 56: figs 1a,b	Mediterranean Sea	-	-	X	Fixed, slightly constricted at septa, 226-282 µm, L/D: 1 to 1.5, cell walls thin	<i>C. aerea</i> (Dillwyn) Kützting
<i>C. herbacea</i> Kützting	-	Kützting 1847: 167; 1849; 1853, pl. 57, fig. I	Marseille, France	-	-	X	Fixed, slightly constricted at septa, 150-282 µm, L/D: 1 to 1.5, cell walls thin	<i>C. aerea</i> (Dillwyn) Kützting
<i>C. monilina</i> (Zanardini) Zanardini	<i>Conferva monilina</i>	Zanardini, 1847: 255; 1858	Venice, Italy	X	X	X	m.d., barrel-shaped, 732 µm, L/D: 2, m.d.	<i>C. aerea</i> (Dillwyn) Kützting ?
<i>C. princeps</i> (Kützting) Kützting	<i>Conferva princeps</i>	Kützting, 1843: 261; 1845; 1849; 1853, pl.61, figs IIIa-d	Trieste, Italy	-	X	X	Fixed, slightly constricted at septa, 280-750 µm, L/D: 1, cell walls thin	<i>C. aerea</i> (Dillwyn) Kützting

<i>C. urbica</i> (Zanardini) Kützing	<i>Conferva urbica</i>	Zanardini, 1840: 135; Kützing, 1847: 1849; 1853, pl. 54, fig. IV	Venice, Italy	X	X	X	Fixed, slightly constricted at septa, 188 µm, L/D: 0.5 to 1, cell walls thin	<i>C. aerea</i> (Dillwyn) Kützing
<i>C. variabilis</i> (Kützing) Kützing	<i>Conferva variabilis</i>	Kützing, 1843: 260; 1845; 1849; 1853, pl. 55, figs IIa,b	Trieste, Italy	–	X	X	Fixed, slightly constricted at septa, 140-226 µm, L/D: 1 to 2, cell walls relatively thick and lamellate	<i>C. aerea</i> (Dillwyn) Kützing
<i>C. vasta</i> (Kützing) Kützing	<i>Conferva vasta</i>	Kützing, 1843: 260; 1849; 1853, pl. 56, figs a,b	Trieste, Italy	–	X	X	Fixed, slightly constricted at septa, 188-250 µm, L/D: 1 to 1.5 (-2), cell walls thin	<i>C. aerea</i> (Dillwyn) Kützing
<i>C. vasta</i> var. <i>inflata</i> Kützing	–	Kützing, 1849: 378	Adriatic Sea	–	X	X	Fixed, barrel-shaped, 188-250 µm, L/D: 1 to 1.5 (-2), cell walls thin	<i>C. aerea</i> (Dillwyn) Kützing
<i>C. gracilis</i> Kützing	–	Kützing, 1845: 203; 1849; 1853, pl. 52, fig. I	Trieste, Italy	X ¹	X	X	Free-living, cylindrical, 24-75 µm, L/D: 0.5 to 7, cell walls thin	<i>C. gracilis</i> Kützing
<i>C. gracilis</i> var.? <i>longitarticalata</i> Hauck	–	Hauck, 1884: 440	Adriatic sea	–	X	X	Free-living, cylindrical, 24-32 µm, L/D: 1.5 to 7, m.d.	<i>C. gracilis</i> Kützing
<i>C. ligustica</i> (Kützing) Kützing	<i>Conferva ligustica</i>	Kützing, 1843: 259; 1849; 1853, pl. 52, fig. II; Verlaque, unpubl. data	Genova, Italy	X	X	X	Free-living, cylindrical, 40-120 µm, L/D: 1 to 2, cell walls thin	<i>C. ligustica</i> (Kützing) Kützing
<i>C. breviaritcalata</i> Hauck, nom illeg.	–	Hauck, 1884: 440; Schiffner & Vatova, 1938: 107-108, pl. XXXII, fig. 5	Adriatic Sea	X	X	X	m.d., cylindrical, 40-60 µm, L/D: 0.5 to 1 (-2), cell walls thin	<i>C. ligustica</i> (Kützing) Kützing?
<i>C. callithrix</i> Kützing	–	Kützing, 1849: 376; 1853, pl. 51, figs a-c	Dalmatia	–	X	X	m.d., cylindrical to slightly constricted, 56 µm, L/D: 1 to 2, cell walls thin	<i>C. ligustica</i> (Kützing) Kützing?
<i>C. capillaris</i> (Kützing) Borgesen, nom. illeg.	<i>Rhizoclonium capillare</i>	Kützing, 1847: 166; Borgesen, 1925	Nice, France	–	–	X	Free-living, cylindrical, 60-70 (-150) µm, L/D: 1 to 2, cell walls thin	<i>C. ligustica</i> (Kützing) Kützing
<i>C. capillaris</i> var. <i>crispata</i> schousboe ex Feldmann	–	Feldmann, 1937: 209, figs. 17a-f	Banyuls, France	–	X	X	Free-living, cylindrical, 90-120 µm, L/D: 1 to 2, cell walls relatively thick	<i>C. ligustica</i> (Kützing) Kützing

Taxon	Basionym	References	Type locality	Venice Lagoon	Adriatic Sea	Mediterranean Sea	Diagnostic characters of Mediterranean populations	Accepted name or status
<i>C. mediterranea</i> (Kützing) Kützing	<i>Spongopsis mediterranea</i>	Kützing, 1843: 261; 1849; 1853, pl. 50, figs IIa,b	Livorno, Italy	X	X	X	Free-living, cylindrical, 50-60 µm, L/D: 1 to 2, cell walls thin	<i>C. ligustica</i> (Kützing) Kützing
<i>C. mediterranea</i> var. <i>crispa</i> (Feldmann) Gallardo <i>et al.</i>	<i>C. capillaris</i> var. <i>crispa</i> schousboe ex Feldmann	Gallardo <i>et al.</i> , 1993	Banyuls, France	–	X	X	Free-living, cylindrical, 90-120 µm, L/D: 1 to 2, cell walls relatively thick	<i>C. ligustica</i> (Kützing) Kützing
<i>C. tortuosa</i> Kützing, nom. illeg.	–	Kützing, 1849: 376; 1853, pl. 51, figs IIa,b; Schiffner & Vatova, 1938: 107, pl. XXXII, fig. 4	Cette (Sète), Nice, France and Genova, Livorno, Italy	X	X	X	Free-living, cylindrical, 40-100 µm, L/D: 1 to 2, cell walls thin	<i>C. ligustica</i> (Kützing) Kützing
<i>C. linum</i> (O.F. Müller) Kützing	<i>Conferva linum</i>	Müller, 1778; Kützing, 1845; 1849; 1853, pl. 55, figs IIIa,b	Nakskov Fjord, Lolland, Denmark	X	X	X	Free-living, cylindrical, 120-350, L/D: 1 to 2 (-5), cell walls thin	<i>C. linum</i> (O.F. Müller) Kützing
<i>C. linum</i> var. <i>brachyarthra</i> Schiffner	–	Schiffner, 1916: 177	Rovinj, Croatia	–	X	X	Free-living, 150-250 µm, L/D: 0.5 to 1 (-1.5), m.d.	<i>C. linum</i> (O.F. Müller) Kützing
<i>C. crassa</i> f. <i>tenior</i> Schiffner in Schiffner & Vatova	–	Schiffner & Vatova, 1938: 109, pl. XXXII, fig. 3	Venice, Italy	X	X	X	Free-living, cylindrical, 300-450 µm, L/D: 2 to 3 (-5), cell walls thin	<i>C. linum</i> (O.F. Müller) Kützing
<i>C. crassiuscula</i> (Zanardini) Zanardini	<i>Conferva crassiuscula</i> Zanardini	Frauentfeld, 1854: 328; 1855	Dalmatia	–	X	X	Close to <i>C. fibrosa</i> and <i>C. dalmatica</i> (Frauentfeld, 1855)	<i>C. linum</i> (O.F. Müller) Kützing?
<i>C. dalmatica</i> (Kützing) Kützing	<i>Conferva dalmatica</i>	Kützing, 1843: 260; 1845; 1849; 1853, pl. 55, figs Ia,b	Adriatic Sea	–	X	X	Free-living, cylindrical to slightly constricted, 188-226 µm, L/D: 1.5 to 2, cell walls thin	<i>C. linum</i> (O.F. Müller) Kützing
<i>C. reticulata</i> Kützing	–	Kützing 1853: 18, pl. 56: fig. IIIb; Schiffner & Vatova, 1938: 109-110, pl. XXXII, fig. 7	Adriatic Sea	–	X	X	Free-living, cylindrical, 150-220 µm, L/D: 1 to 3, cell walls thin	<i>C. linum</i> (O.F. Müller) Kützing

<i>C. setacea</i> (Agardh) Kützing	<i>Conferva setacea</i> nom. illeg.	C. Agardh (1824): 98; Kützing, 1843, pl. 11, fig. II; 1845; 1849; 1853, pl. 54, figs III	Venice, Italy	X	X	Free-living, cylindrical, 188 µm, L/D: 1 to 1.5, cell walls thin	<i>C. linum</i> (O.F. Müller) Kützing
<i>C. torulosa</i> (Zanardini) Kützing	<i>Conferva torulosa</i> nom. illeg.	Zanardini 1843: 61; Kützing, 1845; 1849; 1853, pl. 61, figs IIa,b	Brevilacqua (Privlaka), Croatia	-	X	Free-living, cylindrical, 640-752 µm, L/D: 2 to 3, cell walls thin	<i>C. linum</i> (O.F. Müller) Kützing
<i>C. pachynema</i> (Montagne) Kützing	<i>Conferva pachynema</i>	Montagne 1841: 184; Kützing, 1847; 1849; 1853, pl. 60, figs Ia,b; Cremades, 1989; M. Verlaque, unpubl. data	Canary Islands, Spain	-	X	Fixed, barrel-shaped, 500-1000 µm, L/D: < 1 to 3, cell walls thick	<i>C. pachynema</i> (Montagne) Kützing
<i>C. stricta</i> Schiffler in Schiffler & Vatova	-	Schiffler & Vatova 1938: 184, pl. XXXII: fig. 2	Venice, Italy	X	X	Free-living, cylindrical, 200-250 (-350) µm, L/D: 0.5 to 1 (rarely 2), cell walls thick and lamellate (30 µm)	<i>C. stricta</i> Schiffler in Schiffler & Vatova
<i>C. adriani</i> Feldmann	-	Feldmann, 1935: 363	Banyuls, France	-	X	Fixed, slightly constricted at septa, 60-90 to 100-120 µm, L/D: 3 to 4, cell walls relatively thick	<i>Taxon inquirendum</i> (Gallardo et al., 1993; Cormaci et al., 2014)
<i>C. breviaritculata</i> (Zanardini) ex Frauenfeld nom. illeg.	<i>Conferva breviaritculata</i>	Frauenfeld, 1854: 327; 1855	Dalmatia	-	X	m.d., cylindrical, 146-182 µm, m.d.	<i>Taxon inquirendum</i> (Cormaci et al., 2014)
<i>C. fibrosa</i> (Kützing) Kützing	<i>Conferva fibrosa</i>	Kützing 1843: 259; 1845; 1849; 1853, pl. 52, fig. V	Baltic Sea	-	(Kützing, 1853; De Toni, 1889)	m.d., cylindrical slightly constricted at septa, 80-100 µm, L/D: (1-) 1.5 to 2, cell walls thin (Kützing, 1853)	<i>Taxon inquirendum</i> (Gallardo et al., 1993; Cormaci et al., 2014)
<i>C. pallida</i> Zanardini ex Frauenfeld	<i>Conferva pallida</i>	Frauenfeld (1855): 9	Lesna, Adriatic Sea	-	X	m.d., very delicate, m.d., m.d., L/D: 2, m.d. (Frauenfeld, 1855)	<i>Taxon inquirendum</i>
<i>C. antennina</i> (Bory) Kützing	<i>Conferva antennina</i>	Bory 1804: 381; Kützing 1847; 1849; 1853, pl. 60, fig. IIa,b	Réunion, Indian Ocean	-	-	Free-living, m.d., 660 µm, L/D: 0.5, m.d. (Montagne, 1846)	<i>Taxon excludendum</i> (Gallardo et al., 1993; Cormaci et al., 2014), probable misidentification of <i>C. aerea</i>

Taxon	Basionym	References	Type locality	Venice Lagoon	Adriatic Sea	Mediterranean Sea	Diagnostic characters of Mediterranean populations	Accepted name or status
<i>C. herhipolensis</i> Lagerheim	–	Lagerheim 1887: 195, pl. IX: figs 1-10	Warm aquarium water, botanical garden, Germany	–	–	Spain (Margalef, 1950)	Freshwater species	<i>Taxon excludendum</i> (Cormaci <i>et al.</i> , 2014)
<i>C. implicata</i> Kützing	–	Kützing 1847: 167; 1849, as <i>C. implexa</i> Kützing nom. illeg. var. <i>montagneana</i> Kützing	Cuba, Atlantic Ocean	–	–	Balearic Islands (Colmeiro, 1868, as <i>C. implexa</i> Kützing nom. illeg.)	m.d.	<i>Taxon excludendum</i> (Cormaci <i>et al.</i> , 2014), misidentification
<i>C. indica</i> (Kützing) Kützing	<i>Conferva indica</i> Kützing 1843: 259	Kützing 1843: 259; 1849; 1853, pl. 52, fig. III	Tranquebar, Tamil Nadu, India	–	–	Libya (Nizamuddin, 1991)	Fixed or free-living, cylindrical, (70-) 85-145 (-200) µm, L/D: (0.6) 1 to 2 (3), cell walls up to 16 µm thick (Nizamuddin, 1991)	<i>Taxon excludendum</i> , probable misidentification of <i>C. linum</i> (Cormaci <i>et al.</i> , 2014)
<i>C. litorea</i> Harvey	–	Harvey 1858: 87	Scotland	–	–	Balearic Islands, (Rodríguez y Femenias, 1889), Naples, Italy (Funk, 1955)	m.d., cylindrical to locally swollen, 48-72 µm, L/D: 1 to 2, m.d. (Funk, 1955)	<i>Taxon excludendum</i> , probable misidentification of <i>C. ligustica</i> (Cormaci <i>et al.</i> , 2014)
<i>C. melagonium</i> (F. Weber & D. Mohr) Kützing	<i>Conferva melagonium</i>	F. Weber & D. Mohr 1804: 194, pl. 3: fig. 2; Kützing 1845: 1849; 1853, pl. 61, fig. 1a-d	Varberg, Sweden	–	–	Algeria (Debray, 1897), Libya (Nizamuddin, 1991)	Fixed, cylindrical, 325-640 µm, L/D: 0.6 to 1.6, cell walls thin (Nizamuddin, 1991)	<i>Taxon excludendum</i> , probable misidentification of <i>C. linum</i> (Cormaci <i>et al.</i> , 2014)

¹ Specimens from the Lagoon of Venice with filaments very narrow and cells very long included by Sfriso (2010) in the treatment of *C. ligustica* should be referred to *C. gracilis* (Cormaci *et al.*, 2014).

C. linum (Furnari *et al.*, 1999, 2003; Cormaci *et al.*, 2014). The comparison of diagnostic characters of the Valle Cavallino *Chaetomorpha* with the protologue of *C. stricta* and the two *C. stricta* syntypes deposited at the Natural History Museum, London (Figs 9-14), showed that they belong to the same taxon and that

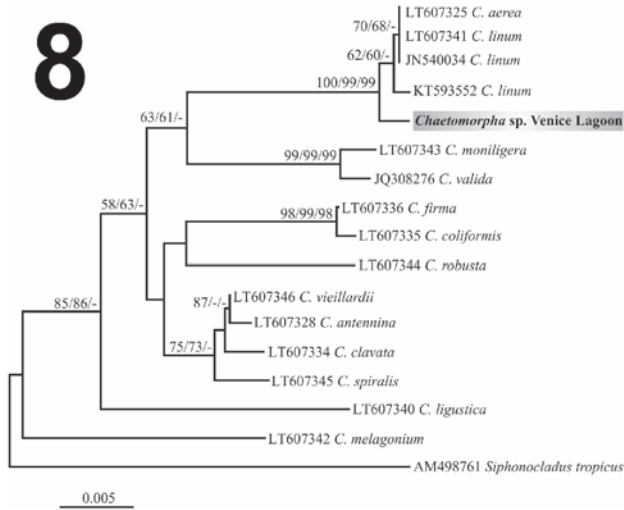
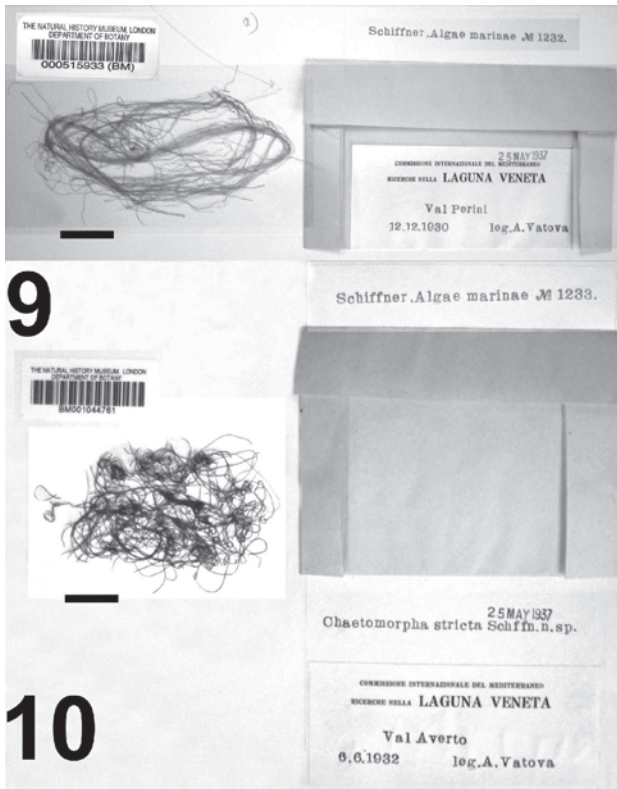
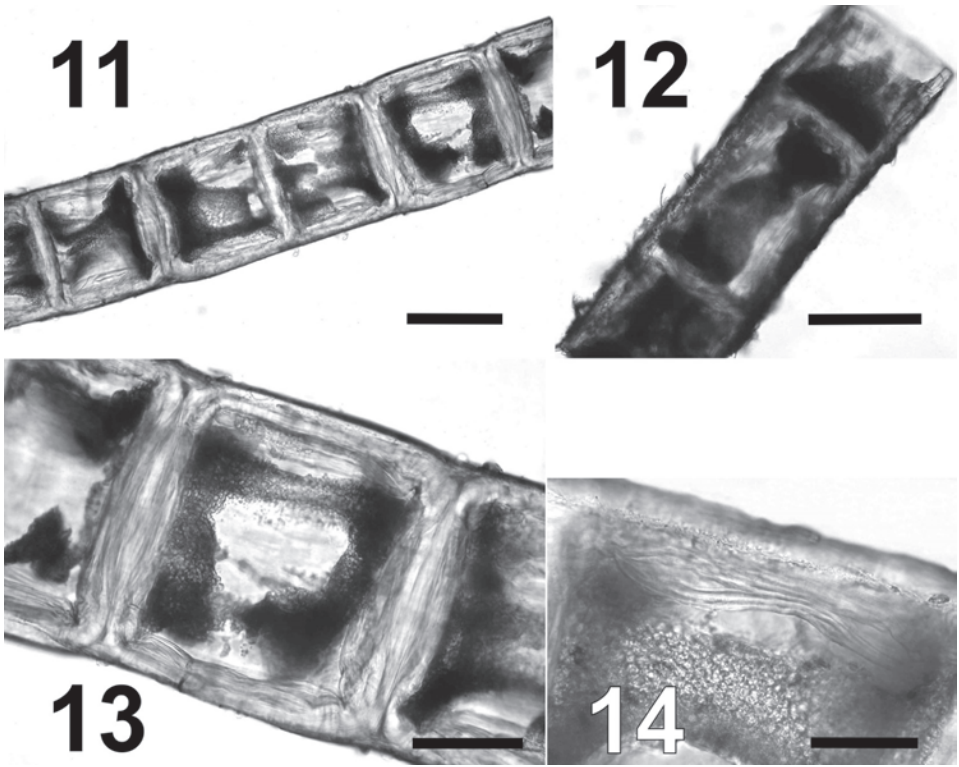


Fig. 8. ML tree inferred from partial SSU nrDNA sequences. New species sequence is in bold. NJ/ML/MP bootstrap values (> 50) are given at nodes.



Figs 9-10. Two syntypes of *Chaetomorpha stricta* Schiffner deposited at the Natural History Museum, London (BM). 9. Specimen BM 000515933, Val Perini, Laguna Veneta, 12 December 1930, leg. A. VatoVA. 10. Specimen BM001044761, Val Avertto, Laguna Veneta, 6 June 1932, leg. A. VatoVA. Scale bars: 9 & 10 = 2 cm.



Figs 11-14. Syntype BM 000515933 of *Chaetomorpha stricta* Schiffner. **11.** Part of a filament with isodiametric cells. **12.** Part of filament with rectangular cells. **13-14.** Details of cells showing the thick and lamellate cell walls. Scale bars: 11 & 12 = 200 μm ; 13 = 100 μm ; 14 = 50 μm .

the reduction of *C. stricta* to a posterior heterotypic synonym of *C. linum* was unjustifiable. *Chaetomorpha stricta* is a species that differs very clearly from all the other Mediterranean species in having free-living filaments, 189-370 μm in diameter, with cylindrical cells and lamellate and thick cell walls up to 90 μm thick (Table 3).

DISCUSSION

As highlighted by other authors, the morphological simplicity, the low number of diagnostic features and the phenotypic plasticity of species belonging to this genus makes necessary the use of molecular data to discriminate among different entities (Leliaert & Boedeker, 2007; Leliaert *et al.*, 2009, 2011). During the assessment of the ecological status of the Venice Lagoon according to the 2000/60/EC requirements, we collected *C. stricta* Schiffner, a species described from the Venice Lagoon in the early 20th century, and subsequently erroneously downgraded to a heterotypic synonym of *C. linum*. In the ML tree obtained in this work, the nuclear SSU rDNA sequence of the *C. stricta* clustered with sequences belonging to two other species present in the lagoon, *C. linum* and *C. aerea*, but its phylogenetic

Table 3. Diagnostic characters of Mediterranean *Chaetomorpha* species, with references and data sources

	<i>C. aerea</i> (Dillwyn) Kützing	<i>C. gracilis</i> Kützing	<i>C. ligustica</i> (Kützing) Kützing	<i>C. linum</i> (O.F. Müller) Kützing	<i>C. pachymema</i> (Montagne) Kützing	<i>C. stricta</i> Schiffner in Schiffner & Vatova			
Reference/ source	Cf. references Table II	Cf. references Table II	Present study, specimen H8324	Cf. references Table II	Present study, specimen H5634	Schiffner & Vatova, 1938	Syntype BM001044761	Syntype BM000515933	Present study, specimen A000622
Locality	Mediterranean Sea & Atlantic Ocean	Mediterranean Sea	Mediterranean Sea, Saussat-Ies- Pins, France (23.09.2017)	Mediterranean Sea & Atlantic Ocean	Mediterranean Sea, Cala Petraghja, Corsica (22.08.1992)	Venice Lagoon, see localities Fig. 1	Venice Lagoon, Val Averto, (6.6.1932)	Venice Lagoon, Val Permi (12.12.1930)	Venice Lagoon, Valle Cavallino, (05.2011)
Fully-grown plant	Fixed by a basal cell < 1.2 mm long with discoid holdfast	Free-living	Free-living	Free-living	Fixed by a basal cell > 1.5 mm long with highly digitate holdfast	Free-living	Free-living	Free-living	Free-living
Cells	Cylindrical to barrel-shaped	Cylindrical	Cylindrical	Cylindrical	Barrel-shaped	Cylindrical	Cylindrical	Cylindrical	Cylindrical
Diameter	(125-) 150-750 µm	24-75 µm	86-130 µm	120-450 (-752) µm	423-919 µm	200-350 µm, usually 250 µm	189-370 µm	255-288 µm	250-350 µm
Length/ Diameter ratio	0.5 to 2.0	0.5 to 7	0.8 to 2.8	(0.5-) 1.0 to 3.0 (-5.0)	0.6 to 2.4	0.5 to 1.0 (rarely 2.0)	0.6 to 1.5	0.6 to 1.6	1.0 to 2.0
Cell walls	Relatively thick and lamellate (basal cells) to thin (upper cells)	Thin	Thick and lamellate, 8-20 µm	Thin	Thick, 25-57 µm	Thick and lamellate, ca 30 µm	Thick and lamellate, 41-90 µm	Thick and lamellate, 30-57 µm	Thick and lamellate, 48-75 µm

position is clearly distinct from them. A third species reported from the lagoon, *C. ligustica*, is phylogenetically distant from this clade. The nucleotide divergences calculated between *C. stricta* and the other species of the lagoon are greater than or comparable with the divergences found between other species of the same genus, e.g. *C. viellardii* – *C. antennina* (0.15%), *C. firma* – *C. coliformis* (0.15%) and *C. viellardii* – *C. clavata* (0.44%). These results together with the morphological analyses support the species-level distinction of *C. stricta*.

Currently, six species of *Chaetomorpha* occur in the Mediterranean Sea (see below the Key to the Mediterranean *Chaetomorpha* species). All of them were reported from the Venice Lagoon, except for *C. pachynema*.

In the Venice Lagoon, the most abundant *Chaetomorpha* species are *C. linum*, *C. gracilis* and *C. ligustica* that can form blooms reaching many kilograms of biomass per square meter. The first is especially present in the southern lagoon in association with meadows of angiosperms, whereas *C. gracilis* and *C. ligustica* form a mixture that colonizes mostly eutrophic and turbid areas. All form long free-living filaments which can exceed one meter in length. *Chaetomorpha aerea* is also common in eutrophic and turbid environments, but forms shorter filaments (10–30 cm long) that usually grow attached to hard substrata by a long basal cell. Although the protologue of *C. stricta* was based on material collected all around the Venice Lagoon, we hitherto observed the species in only one closed fishing pond of the Valle Cavallino (northern basin); consequently, it would be worth searching for this species in the rest of the Venice Lagoon and in other Mediterranean coastal lagoons, especially in the Adriatic Sea.

Key to the Mediterranean *Chaetomorpha* species

1. Adult plants fixed; cells cylindrical to barrel-shaped 2
 Adult plants free-living; cells cylindrical 3
 2. Filaments, up to 3 cm long and 0.5 to 1 mm in diameter, fixed by a digitate holdfast; basal cell 1.5 to 3 mm long with cell walls 50–100 µm thick
 ***C. pachynema* (Montagne) Kützinger**
 Filaments, up to 40 cm long and 150–700 µm in diameter, fixed by a discoidal holdfast; basal cell up to 1.2 mm long with cell walls < 30 µm thick
 ***C. aerea* (Dillwyn) Kützinger**
3. Cell walls thin 4
 Cell walls thick and lamellate 5
 4. Cells < 100 µm (24–75 µm) in diameter and 0.5 to 7 times as long as broad ***C. gracilis* Kützinger**
 Cells > 100 µm (120–450 µm, rarely more) in diameter and 0.5 to 3 (rarely 5) times as long as broad ***C. linum* (O.F. Müller) Kützinger**
5. Cells < 150 µm (86–130 µm) in diameter and 0.8 to 2.8 times as long as broad; cell walls 8–20 µm thick ***C. ligustica* (Kützinger) Kützinger**
 Cells > 150 µm (189–370 µm) in diameter and 0.5 to 1.6 (rarely 2) times as long as broad; cell walls 30–75 (–90) µm thick ***C. stricta* Schiffner**

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