



## Blitzkrieg in a marine invasion: *Caulerpa racemosa* var. *cylindracea* (Bryopsidales, Chlorophyta) reaches the Canary Islands (north-east Atlantic)

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### Abstract

On the basis of morphological and genetic studies (rDNA ITS1, 5.8S, ITS2, and a 18S rDNA intron), we confirm here that *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman et Boudouresque, a southwestern Australian taxon recently introduced into the Mediterranean Sea also occurs in the Canary Islands. This is the first report of *C. racemosa* var. *cylindracea* in the Atlantic. It was observed for the first time in the Canary Archipelago in 1997–1998. The speed and regional scale of expansion (north Atlantic Ocean and the Mediterranean Sea) of this invasive species appear to be among the most dramatic ever recorded. The possible outcome of this introduction in the Atlantic is discussed.

### Introduction

The *Caulerpa racemosa* (Forsskål) J. Agardh complex *sensu lato* is well represented in the Canary Islands. At least four taxa have been reported: *C. peltata* J.V. Lamouroux [= *C. racemosa* var. *peltata* (J.V. Lamouroux) Eubank] and *C. racemosa* var. *turbinata* (J. Agardh) Eubank [= var. *chemnitzia* (Esper) J.V. Lamouroux] in all the seven major islands (Lanzarote, Fuerteventura, Gran Canaria, Tenerife, La Gomera, El Hierro and La Palma), *C. racemosa* var. *racemosa* [= var. *clavifera* (Turner) Weber-van Bosse] in Lanzarote, Fuerteventura, Gran Canaria and Tenerife and *C. racemosa* var. *leatevirens* (Montagne) Weber-van Bosse in the two eastern islands, Lanzarote and Fuerteventura (Montagne 1839–1841; Piccone 1884; Vickers 1896; Weber-van Bosse 1898; Børgesen 1925; Gil-Rodríguez and Wildpret de la Torre 1978;

Afonso-Carrillo and Gil-Rodríguez 1980; Gil-Rodríguez and Afonso-Carrillo 1980; González Henríquez and Santos Guerra 1983; Haroun Tabraue et al. 1984; Haroun et al. 2002). These taxa are reported from lower mid-littoral pools and upper sub-littoral (a few meters deep) mostly on rocky substrates more or less exposed to swell (Afonso-Carrillo and Gil-Rodríguez 1980; González Henríquez and Santos Guerra 1983; Haroun Tabraue et al. 1984). Since the late 1990s, a variety of *C. racemosa*, previously unknown in the Canary Islands, has been spreading in several localities in Tenerife, Gran Canaria and Lanzarote. In Tenerife and Gran Canaria, dense populations have been observed between 21 and 30 m depth growing on sandy bottoms colonized by the pantropical seagrass *Halophila decipiens* Ostenfeld (Gil-Rodríguez et al. 2002; Rivas-Martínez et al. 2002).

Since the early 1990s, an invasive variety of *C. racemosa*, which occupies a wide range of habitats, has been spreading at a rapid rate throughout most of the Mediterranean Sea, generally resulting in the development of extensive populations (see Verlaque et al. 2000; Boudouresque and Verlaque 2002a). This variety has been successively regarded as a taxon closely related either to *C. racemosa* var. *occidentalis* J. Agardh ('aff. var. *occidentalis*', Verlaque et al. 2000) or *C. racemosa* var. *laetevirens* f. *cylindracea* (Sonder) Weber-van Bosse (Famà et al. 2000) or a hybrid (Durand et al. 2002). Finally, a morphological and genetic study (rDNA ITS1, 5.8S, ITS2, and a 18S rDNA intron) confirmed that the ongoing invasive Mediterranean episode is the result of a recent introduction and that the 'invasive variety' belongs to *C. racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman et Boudouresque, an endemic taxon described by Sonder (1845, as *C. cylindracea*) from the southwest coast of western Australia (Verlaque et al. 2003).

To determine the identity of the alga from the Canary Islands and the possible link between its recent appearance in the Archipelago and the invasive Mediterranean episode, we carried out a morphological and genetic comparative study between the Mediterranean varieties of *C. racemosa*, Australian and Mediterranean *C. racemosa* var. *cylindracea* and other *C. racemosa* from the Atlantic and Indo-Pacific. Finally, we carried out an update of the distribution of the Mediterranean invasive *C. racemosa* var. *cylindracea*.

## Materials and methods

### Specimen collection

Observations in the Canary Islands were performed from 1997 to 2003 and samples were collected in Gran Canaria and Lanzarote in 2002 and Tenerife in 2003:

- Specimens H6769, Gran Canaria, Castillo del Romeral, 27°48' N, 15°27' W, 5 May 2002, 1 m deep, sheltered rocks with fine sediment deposition, leg. José Carlos Pérez;
- Specimens H6770, Lanzarote, Bahía de Ávila, 28°53' N, 13°44' W, 5 November 2002, 35 m deep, leg. Alejandro Cruz Reyes;
- Specimens H7052, Tenerife, San Andrés, 28°30' N, 16°10' W, 25 April 2003, 24 m deep, leg. O. Monterroso.

Tissues of specimens H6769 were fixed in 80% ethanol and preserved at  $-20^{\circ}\text{C}$ . Genetic data from these specimens were analyzed with data from the *C. racemosa* isolates nos 1–9, 11–18 used in previous phylogenetic works on the origin of the Mediterranean invasive *C. racemosa* (Durand et al. 2002; Verlaque et al. 2003). *Caulerpa* isolates and collecting sites are listed in Table 1.

The above material was deposited in the Herbarium Verlaque, COM, Marseille, France and duplicates at TFC (Departamento de Biología Vegetal, Botánica, Universidad de La Laguna, Canary Islands). Voucher material were compared with the following exsiccata:

- *Caulerpa racemosa* var. *cylindracea*, western Australia, Carnac Island, ( $32^{\circ}12' \text{S}$ ,  $115^{\circ}38' \text{E}$ ), 12 December 2001, 2 m deep, limestone reef exposed to swell, specimens H5527–5530, Herbarium Verlaque, COM, Marseille;
- Mediterranean and extra-Mediterranean specimens of *C. racemosa* cited in Verlaque et al. (2000);
- Specimens of *C. racemosa* previously collected in the Canary Islands and deposited at TFC (Departamento de Biología Vegetal, Botánica, Universidad de La Laguna, Canary Islands).

### DNA extraction

Before genomic DNA extraction, tissue samples were dehydrated (silica gel) and frozen in liquid nitrogen. Total DNA was extracted using the Plant Tissue Promega genomic DNA purification kit (Promega France, Charbonnières, France). After O.D. measurement at 260/280 nm genomic DNA was resuspended in ddH<sub>2</sub>O at a final concentration of  $1 \mu\text{g} \mu\text{l}^{-1}$ .

### PCR amplification, RFLP and sequencing

Primers specific for *Caulerpa* were designed from an alignment of all sequences of the nuclear ribosomal genes cluster from *Caulerpa* species available in the GenBank database. We amplified by PCR a 1100-bp region spanning from the 3' end of the 18S rDNA to the 5' end of the 28S rDNA, including the 18S rDNA intron, and the ITS1 and ITS2 sequences.

PCR amplifications were performed using a forward primer hybridizing in the 3' region of the 18S rDNA sequence (5'-GCAATAACAGGTCTGTGATGC-3') and a reverse primer located near the 5' extremity of the 28S rDNA (5'-TCCTCCGCTTATTGATATGCT-3'). The amplified region contains the 3' end of the

Table 1. Isolates of *Caulerpa racemosa* and *Caulerpa mexicana*: taxon, geographical origin, collectors and accession numbers.

No.	Taxon	Origin	Collector	Accession no.
1	<i>C. racemosa</i> var. <i>turbinata-uvifera</i>	Bizerte, Tunisia	A. Djellouli	AJ297632
2	<i>C. racemosa</i> var. <i>turbinata-uvifera</i>	Salakta, Tunisia	N. Ben Maiz	AJ297633
3	<i>C. racemosa</i> var. <i>lamourouxii</i>	Famagusta, Cyprus	M. Verlaque	AJ297634
4	<i>C. racemosa</i> var. <i>lamourouxii</i>	Selaata, Lebanon	J.G. Harmelin and H. Zibrowius	AJ297635
5	<i>C. racemosa</i> var. <i>lamourouxii</i>	Ishigaki, Japan	C.F. Boudouresque and A. Meinesz	AJ297636
6	<i>C. racemosa</i> var. <i>cylindracea</i>	Samos, Greece	J. Laborel	AJ297637 clone a AL297638 clone b
7	<i>C. racemosa</i> var. <i>cylindracea</i>	Saronikos, Greece	P. Panayotidis	AJ297639 clone a AJ297640 clone b
8	<i>C. racemosa</i> var. <i>cylindracea</i>	Famagusta, Cyprus	M. Verlaque	AJ297641 clone a AJ297642 clone b AJ297643 clone c
9	<i>C. racemosa</i> var. <i>cylindracea</i>	Marseilles, France	T. Pérez	AJ297644 clone a AJ297645 clone b
11	<i>C. racemosa</i> var. <i>clavifera</i>	Red Sea	A. Meinesz	AJ297646
12	<i>C. racemosa</i> var. <i>clavifera</i>	Mayotte Island, Indian Ocean	C. Marschall	AJ297647
13	<i>C. racemosa</i> var. <i>peltata</i>	Ishigaki, Japan	C.F. Boudouresque and A. Meinesz	AJ297648
14	<i>C. racemosa</i> var. <i>macrophysa</i>	Ishigaki, Japan	C.F. Boudouresque and A. Meinesz	AJ297649 clone a AJ297650 clone b
15	<i>C. racemosa</i> var. <i>racemosa</i>	Heron Island, Australia	M. Manuel	AJ297651
16	<i>C. racemosa</i> var. <i>racemosa</i>	Balicasag Island, Philippines	A. Gómez and M.A. Ribera	AJ297652 clone a AJ297653 clone b
17	<i>C. racemosa</i>	Panama, Atlantic	W.H.C.F. Kooistra	AF479702 (Kooistra 2002)
18	<i>C. racemosa</i> var. <i>cylindracea</i>	Carnac Island, Western Australia	J.M. Huisman	AY173116 clone a AY173117 clone b AY173118 clone c (Verlaque et al. 2003)
19	<i>C. racemosa</i> var. <i>cylindracea</i>	Canary Islands, Spain	José Carlos Pérez	<b>AY173119 clone a</b> <b>AY173120 clone b</b>
	<i>C. mexicana</i>	Canary Islands, Spain	Y.S.D.M. De Jong and W.F. Prud'homme van Reine	AJ007816 (Olsen et al. 1998)

Mediterranean specimens of *C. racemosa* (nos 1–4 and 6–9) are named according to Verlaque et al. (2000, 2003). Specimen Nos 11–16 are named from their morphological characters, according to the literature. The 18S intron, ITS1 and ITS2 of rDNA sequences corresponding to the isolates were deposited in the GenBank database. Accession numbers without reference are from Durand et al. (2002). New accession numbers associated with this study are given in bold.

18S rDNA, including the intron (100–108 bases), the ITS1 (112–136 bases), 5.8S rDNA, ITS2 (281–315 bases), and the 5' end of the 28S rDNA. Genomic DNA was amplified by a DNA thermal cycler (Perkin Elmer Cetus). The 25 µl PCR mix contained 10 ng of genomic DNA, 5 µl of 10X taq DNA polymerase buffer, 8 µl of 1.25 mM dNTP mix (Pharmacia), 2.5 µl of each primer (20 µM) and 1.25 U of Taq DNA polymerase (Promega). Samples were amplified by 35 cycles of amplification. The procedure was as follows: denaturation at 94 °C for 1 min, primer annealing for 1 min at 57 °C, and extension for 2 min at 72 °C. Fragments were checked on 1.5% agarose gels and cleaned with a Qiaquick kit (Wesburg). PCR products were then cloned into pGem-T Easy vector (Promega).

To evaluate the sequence polymorphism, DNA inserts were amplified from 10 to 16 positive clones for each sample, using the primer set described above, and digested with a series of restriction enzymes (TaqI, HaeIII, Sau3A and AluI). AluI was found to be the most informative and was chosen for the final RFLP analysis. Digestions were performed using 5 µl of PCR product in a total volume of 10 µl. Electrophoresis was performed using 2% agarose gels. For each distinct restriction pattern, one to three clones were selected and sequenced using the dideoxy-nucleotide chain termination method (Sanger et al. 1977).

In the present study, we used combined ITS1, 5.8S, ITS2 sequences, and also a *Caulerpa*-specific fast-evolving intron of the 18S rDNA.

### Sequence alignment and phylogenetic analysis

Nucleotidic sequences were aligned automatically using the Mac Vector program. The alignments were then optimized manually using the program ClustalW (Thompson et al. 1994). The alignment is available from the authors upon request.

Trees were computed using the distance matrix Neighbor-Joining (NJ) method (Saitou and Nei 1987). Gaps are distributed proportionally. In distance analyses we used the option 'pairwise gap removal', which does not exclude *a priori* positions with gaps in distance computation. Distances were corrected for multiple hits, and for unequal transition and transversion rates using Kimura's two-parameter model (Kimura 1980). We performed heuristic searches with the branch swapping option, using the TBR algorithm. The statistical robustness of nodes was ascertained by bootstrapping (Felsenstein 1992) with 500 iterations. One published sequence (AJ007816) of *C. mexicana* Sonder ex Kützinger (Olsen et al. 1998) was used as outgroup taxa. A set of already published sequences of *C. racemosa* was used for the tree computation (Table 1).

### Update of the distribution of the Mediterranean invasive *Caulerpa racemosa* var. *cylindracea*

On the basis of the review of Verlaque et al. (2000), the Mediterranean distribution of *C. racemosa* var. *cylindracea* was updated to take into account recent works and unpublished data.

## Results

### Morphological data

A comparison of the variety of *C. racemosa* that recently appeared in the Canary Islands and *C. racemosa* var. *cylindracea* from western Australia and the Mediterranean Sea showed no morphological differences. The slender thallus is fixed to the substratum by means of thin rhizoids, 1.0–10.0 (–20.0) mm long and 0.3–0.8 (–1.0) mm in diameter that are closely arranged along the stolon (Figures 1 and 2). The stolon is 0.7–2.0 mm in diameter and bears simple upright axes, 1.0–10.0 cm high and 3.0–10.0 mm across. The basal part of upright axes is slightly inflated immediately above the attachment to the stolon (Figure 3: arrows). Upright axes bear uncrowded

vesiculate branchlets that are radially or distichously arranged (sometimes both on the same thallus) on a cylindrical rachis (Figures 1–2, 4–6). The branchlets are clavate, (1.5–) 2.0–5.0 (–7.0) mm long and 1.0–2.0 (–3.0) mm in greatest diameter shortly below the rounded apices, and upwardly directed.

### Sequence data

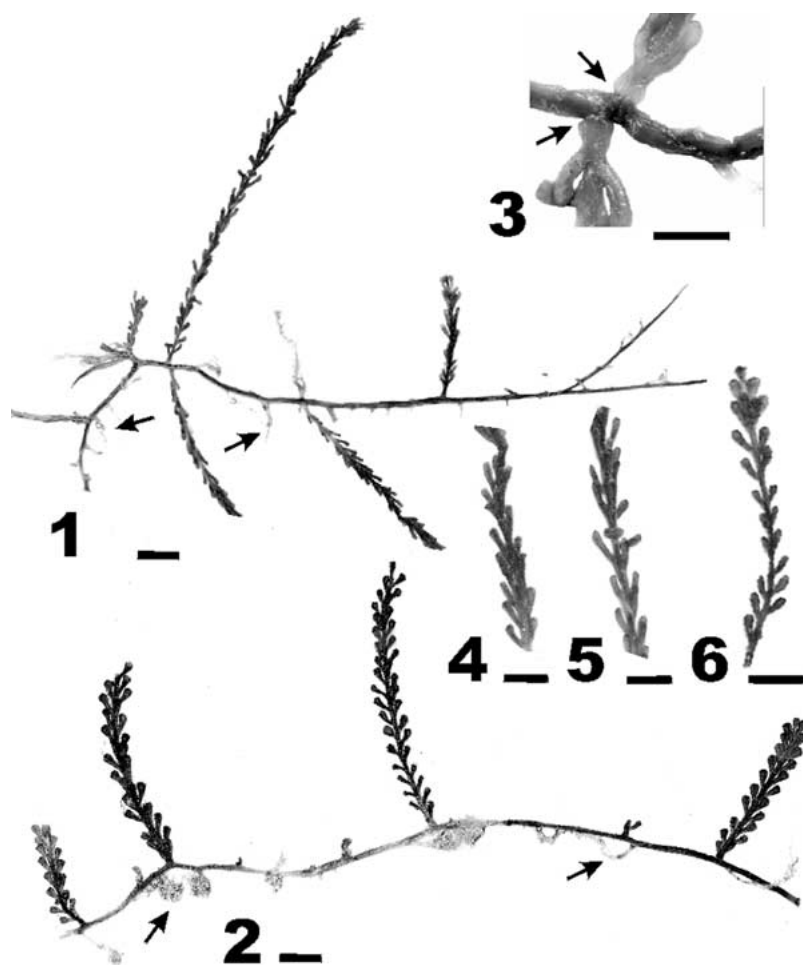
As for all specimens belonging to the *C. racemosa* var. *cylindracea*, we found an intra-individual polymorphism in the Canary Islands isolate. RFLP analysis showed two distinct restriction patterns. The sequence representing the majority of the clones was named 'a' and the other sequence 'b'. Sequence data are consistent with the results of RFLP analysis. Polymorphic individuals are polymorphic for both ITS sequences and for the 18S intron.

The result of a combined NJ analysis of ITS1, 5.8S, ITS2 sequences is shown in Figure 7. In the tree, the sequences referring to the Canary Islands variety of *C. racemosa* (nos 19a–b) fall within the var. *cylindracea* clade (clade 1), which is supported by 100% of bootstraps (Figure 7). The two *C. racemosa* varieties from the Mediterranean Sea, var. *turbinata-uvifera* and var. *lamourouxii*, constitute two distinct clades (clades 2 and 4, respectively), each one being supported by 100% of bootstraps, and extra-Mediterranean isolates of *C. racemosa* fall into two distinct robust clades (clades 3 and 5) (Figure 7).

Figure 8 shows the NJ tree computed from an alignment of sequences of the 18S intron. As in previous studies (Durand et al. 2002; Verlaque et al. 2003), the intron tree shows a major inconsistency with the tree derived from ITS sequences, in that clade 1 (*C. racemosa* var. *cylindracea*) is split into two distinct unrelated clades, named here 1A and 1B. For the Canary Islands sequences of *C. racemosa* var. *cylindracea*, sequence no. 19a falls within clade 1B, whereas sequence 19b falls within clade 1A. Clade 1A is the sister-group of Mediterranean *C. racemosa* var. *turbinata-uvifera* (clade 2) with high bootstrap support (99%). In contrast, clade 1B is the sister-group of clade 3 of extra-Mediterranean isolates (90% of bootstraps) (Figure 8).

### First observations in the Canary Islands

The presence of *C. racemosa* var. *cylindracea* began to be regularly detected only at the end of the 1990s (1997



Figures 1–6. Canary Islands specimens of *Caulerpa racemosa* (Forsskål) J. Agardh var. *cylindracea* (Sonder) Verlaque, Huisman et Boudouresque. Figures 1 and 2. Habit of plants (Herbarium specimens H6769, Gran Canaria and H6770, Lanzarote, respectively; arrow: rhizoids). Figure 3. Detail of attachment of upright axes to the stolon (arrow) (H6769, Gran Canaria, alcohol-preserved specimen). Figures 4–6. Detail of radial to distichous arrangement of branchlets (Herbarium specimen H6769, Gran Canaria). (Scale bars: Figures 1 and 2 = 1 cm; Figures 3–6 = 5 mm).

and 1998) (unpubl. data). The study of the collections of TFC (Universidad de La Laguna, Canary Islands) showed that there was no *C. racemosa* deposited prior to 1991 belonging to this variety. Unfortunately, no new specimens were deposited between 1991 and 2000 and the populations of *C. racemosa* were not considered in recent works on the distribution of the main marine communities in the Canary Islands (Reyes et al. 1995; Lorenzo Nespereira and Brito Hernández 1997). Finally, the first herbarium specimen of this variety present in TFC (TFC Phyc 10977) was collected in 2000 at La Caleta – El Veril, Tenerife, 18 February 2000, 18 m deep, leg. Jesús Manuel Falcón.

#### *Distribution and ecology in the Canary Islands*

Currently, *C. racemosa* var. *cylindracea* is present in several localities of Tenerife, Gran Canaria and Lanzarote (Figure 9, localities: 1–6).

#### *Localities in Tenerife:*

- (1) Caleta de Adeje – Playa del Veril. *C. racemosa* var. *cylindracea* forms populations with low density with *Caulerpa prolifera* (Forsskål) J.V. Lamouroux, at 18 m depth on sandy bottoms. The locality is located at 1.5 km to the north of Port Colón harbour.
- (2) Los Cristianos – El Palm-Mar. *C. racemosa* var. *cylindracea* is present as small populations

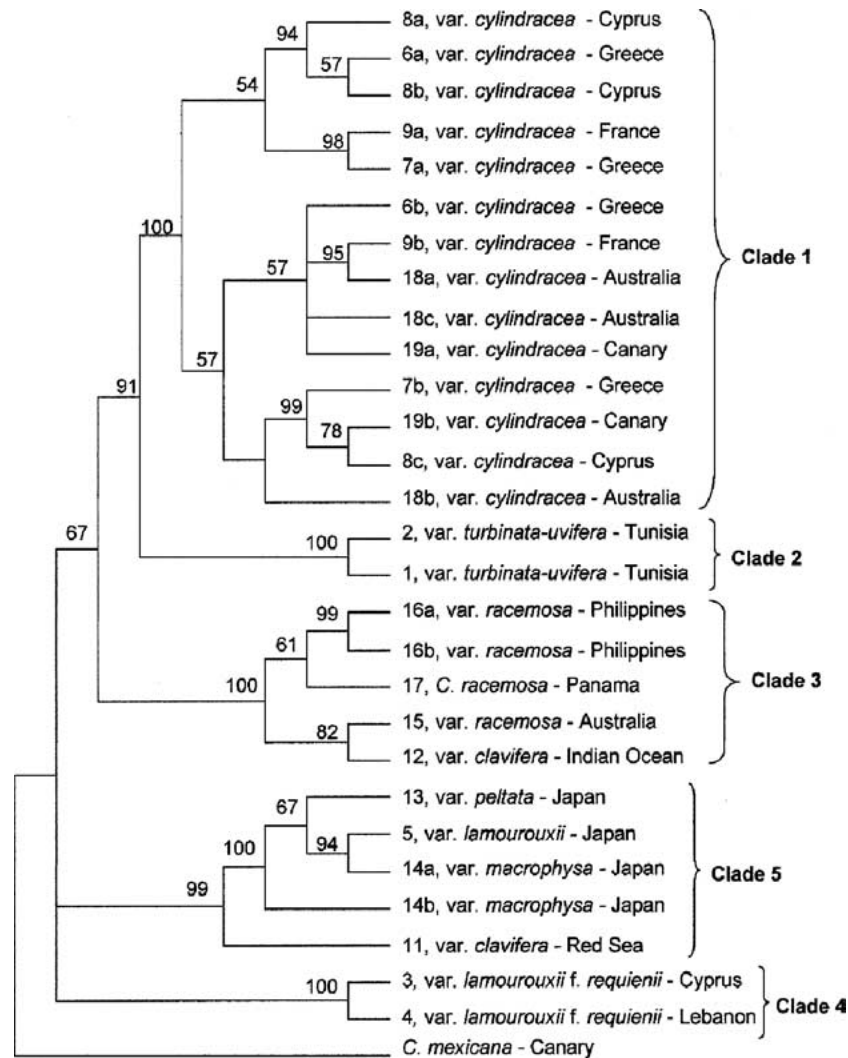


Figure 7. Molecular phylogenetic tree based on a comparison of ITS1, 5.8S, ITS2 sequences from a range of *Caulerpa racemosa* isolates. This tree was obtained using the NJ method with the *Caulerpa mexicana* lineage as the outgroup. Results of 500 NJ bootstrap replicates are shown above the branches.

between 25 and 30 m depth on sandy bottoms colonized by *Halophila decipiens*, close to the harbour area of Los Cristianos.

- (3) La Tejita – Los Abrigos. An extensive population of near 3 km in length has been detected in this locality. *Caulerpa racemosa* var. *cylindracea* is present between 25 and 50 m depth, mainly on sandy bottoms, although some specimens growing on gravels and maerl [*Lithothamnion corallioides* (P.L. Crouan et H.M. Crouan) P.L. Crouan et H.M. Crouan] were also observed. At the lower limit of the *Cymodocea nodosa* (Ucria) Ascherson meadows (around 25 m depth), *C. racemosa* var. *cylindracea* grows when the

*C. nodosa* shoot density is low. It intermingles with *C. nodosa* and *C. prolifera*, and forms a dense population with tubicolous polychaeta worms *Chone* spp. (Sabellidae). Large oil product tankers that supply the Tenerife Sur Airport frequent this area, which also includes the small Amarilla-Golf Marina.

- (4) San Andrés. An extensive population of *C. racemosa* var. *cylindracea* has been detected in this locality, around 24 m depth, mainly on sandy bottoms. The area colonized is located 5 km to the north-east of Santa Cruz de Tenerife, the major commercial and fishing harbour of the island.

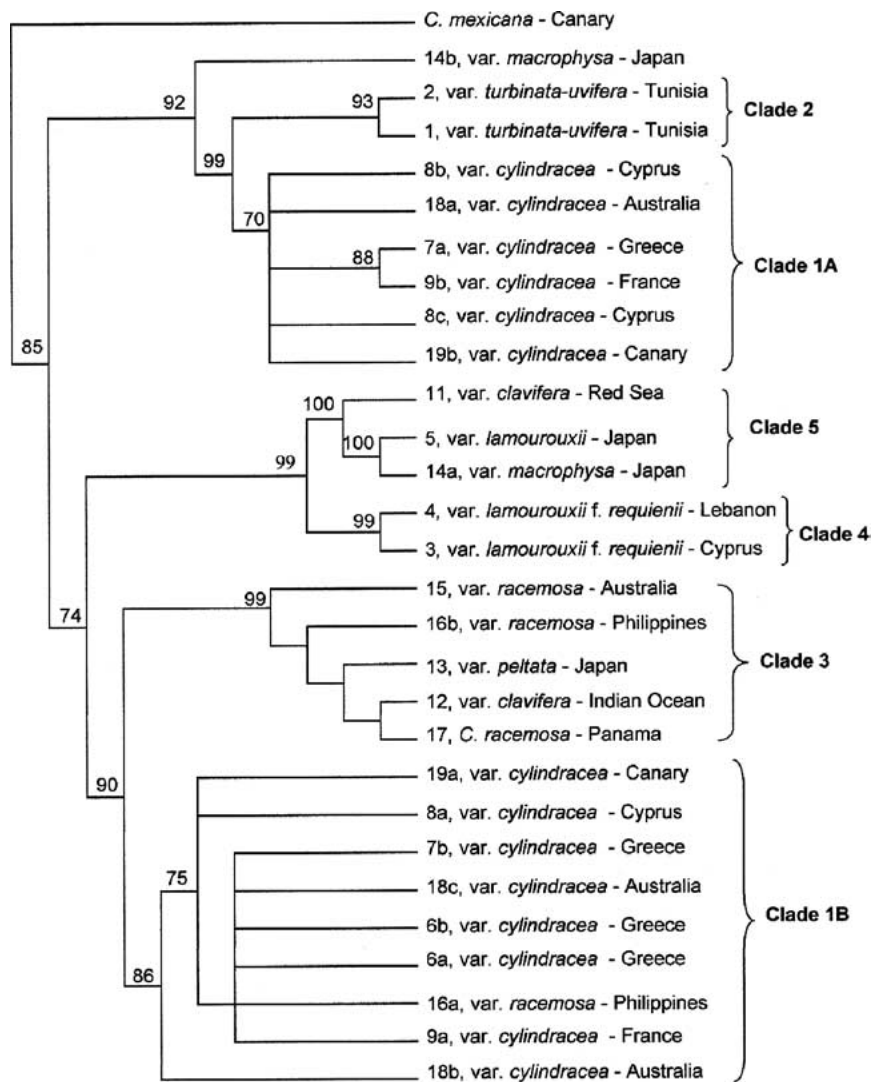


Figure 8. Molecular phylogenetic tree based on a comparison of 18S intron sequences from a range of *Caulerpa racemosa* isolates. This tree was obtained using NJ method with the *Caulerpa mexicana* lineage as the outgroup. Results of 500 NJ bootstrap replicates are shown above the branches.

#### Localities in Gran Canaria:

- (5) Agaete. *C. racemosa* var. *cylindracea* grows between 25 and 40 m depth on sandy bottoms, where it forms mixed populations of low density with *C. prolifera*, co-occurs with the benthic fish *Heteroconger longissimus* Günher, and grows in association with the polychaete worms *Chone* spp. The area colonized by *C. racemosa* is located 1 km to the north of Puerto de las Nieves, a commercial and fishing harbour that has daily exchanges with Tenerife.
- (6) Castillo del Romeral. Two different populations of *C. racemosa* var. *cylindracea* were located close

to Castillo del Romeral, one on sheltered shallow rocks (1 m depth) and another, between 10 and 15 m depth, on sandy bottoms, the former growing on rocks with fine sediment deposition, *Corallina elongata* Ellis et Solander and *Jania adhaerens* J.V. Lamouroux and the latter forming an extensive (up to 1000 m × 700 m) but discontinuous meadow with *C. prolifera*. Castillo del Romeral is a yacht harbour.

#### Locality in Lanzarote:

- (7) Bahía de Ávila. *C. racemosa* var. *cylindracea*, which grows at 35 m depth, has been known in this locality since February 2001. Bahía de Ávila

is located to the south-west of Arrecife commercial harbour, and 5 km from the small Puerto del Carmen harbour.

Except for a shallow locality where the variety grows on sheltered rocks, all the others colonize the sandy bottoms ranging from 18 to 50 m in depth. No observations including an annual cycle are available, but apparently the plant seems to persist throughout the year.

*Update of the distribution of Caulerpa racemosa var. cylindracea*

To update the review by Verlaque et al. (2000), we analyzed recent works and some unpublished data. Numerous new localities of the invasive Mediterranean

*C. racemosa* were found in the following countries:

- Albania (Di Martino and Giaccone 1995);
- France (Renoncourt and Meinesz 2002, see also <http://www.caulerpa.org>);
- Italy (Cecere et al. 2000; Cantasano 2001; Costantino et al. 2001; Dappiano et al. 2001; Gambi et al. 2001; Marino et al. 2001);
- Malta (Mifsud 2000);
- Tunisia (Djellouli 2000; Djellouli et al. 2000);
- Turkey (Tolay et al. 2001a, b; Okudan et al. 2002).

The speed of the range expansion of *C. racemosa* var. *cylindracea* is dramatic. Thirteen years after its first observation in the Mediterranean Sea (Libya) (Nizamuddin 1991), nearly the whole basin has been colonized (Figure 10). By late 2002, at least

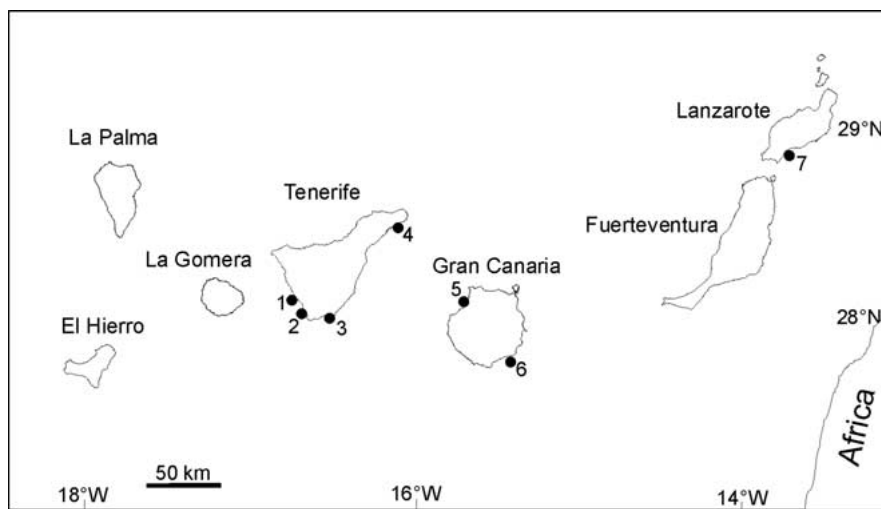


Figure 9. Distribution of *Caulerpa racemosa* var. *cylindracea* in the Canary Islands: (1) Caleta de Adeje – Playa del Veril; (2) Los Cristianos – El Palm-Mar; (3) La Tejita – Los Abrigos; (4) San Andrés; (5) Agaete; (6) Castillo del Romeral; (7) Bahía de Ávila.

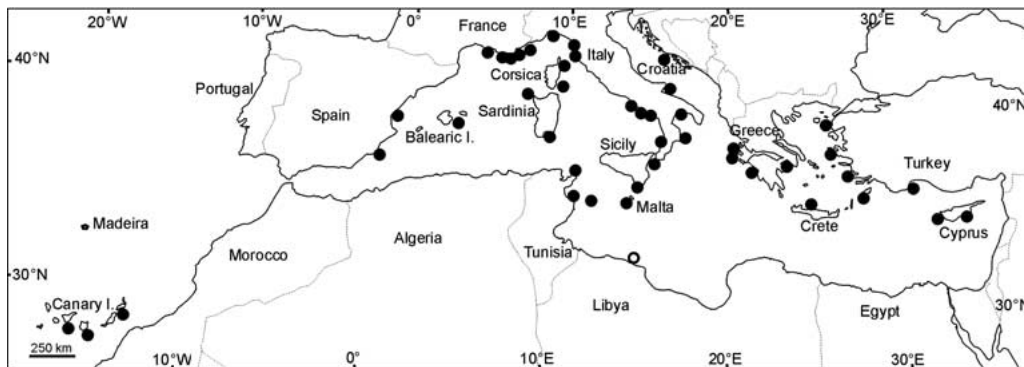


Figure 10. Distribution of *Caulerpa racemosa* var. *cylindracea* in the Mediterranean Sea and Atlantic (from Verlaque et al. 2000, amended). Open circle: first Mediterranean report (Libya, Nizamuddin 1991).



11 Mediterranean countries (Albania, Croatia, Cyprus, France, Greece, Italy, Libya, Malta, Spain, Tunisia and Turkey) and all the major islands (Balearic Islands, Corsica, Crete, Cyprus, Sardinia and Sicily) had been affected by the invasion. The rarity of *C. racemosa* var. *cylindracea* along southern Mediterranean shores might be just an artifact, due to the scarcity of observations there. Now, it has reached the Canary Islands, which represents a new breakthrough in its range area.

## Discussion

In the present work, comparisons between *C. racemosa* specimens from Gran Canaria and Lanzarote, *C. racemosa* var. *cylindracea* from Australia and Mediterranean Sea and other *C. racemosa* from Atlantic and Indo-Pacific demonstrated that the alga that has been spreading in the Canary Islands since the late 1990s belongs to *C. racemosa* var. *cylindracea*, an Australian taxon introduced into the Mediterranean Sea in the early 1990s.

The discovery of *C. racemosa* var. *cylindracea* in the Canary Islands constitutes the first report from the Atlantic. The lack of sightings and samples from the Canary Islands before the late 1990s strongly suggests that the alga has been recently introduced, probably from the Mediterranean Sea. In the first genetic study devoted to the invasive variety of *C. racemosa* (Famà et al. 2000), one specimen from Gran Canaria (leg. H.J. van de Strate) falls within an unresolved clade with a western Australian and six Mediterranean isolates [five attributed to the 'invasive variety' and another to var. *lamourouxii* (Rhodes Island, Greece)]. This specimen from Gran Canaria could be the first *C. racemosa* var. *cylindracea* sampled in the Canary Islands in 1998. This hypothesis is in good agreement with the start of our observations of the alga around Tenerife in 1997–1998.

The finding of all the *C. racemosa* var. *cylindracea* populations in proximity to commercial or yacht harbours supports the hypothesis already put forward for the Mediterranean Sea (Boudouresque and Verlaque 2002b) of possible dispersal by the ship traffic (anchor gears, fouling and ballast waters). Sansón and Reyes (1995) and Rojas-González and Afonso-Carrillo (2000) have already suggested the introduction of seaweeds into several harbours in the Canary Islands.

In its native region (southwestern Australia), *C. racemosa* var. *cylindracea* is found in areas where

the seawater surface temperature and salinity range from about 14.0 °C in winter to 22.5 °C in summer and from 35.27 to 37.00 PSU, respectively, and in the Mediterranean Sea, it grows in the subtidal zone from 1 m down to 60 m in depth, on all types of hard and soft substrates and communities, with the sole exception of unstable sandy substrates (Verlaque et al. 2003). In the Canary Islands, sea surface temperatures range from about 17.5–19.5 °C in winter to 22.0–23.5 °C in summer (Mascareño 1972; Afonso-Carrillo and Gil-Rodríguez 1982; unpublished data from Instituto Nacional de Meteorología). Our data indicate a distribution of *C. racemosa* var. *cylindracea* primarily on deep, soft substrates from 18 to 50 m deep, very similar to that observed in the Mediterranean Sea. Only one population was found on sheltered rocks, i.e., at Castillo del Romeral, Gran Canaria. According to Reyes et al. (1995), in the Canary Islands, the sandy bottoms down to 35 m in depth are colonized by *C. nodosa*. At its lower limit, *C. nodosa* is less abundant, being progressively replaced by *C. prolifera* that can go down to 50 m in depth. Apparently, *C. racemosa* var. *cylindracea* preferentially spreads over sandy bottoms with *C. prolifera*.

If we consider the other marine and brackish water macrophytes introduced into western Europe and the Mediterranean Sea (nearly 120 species; see Ribera-Siguan 2002; Wallentinus 2002), and more especially the invasive ones (Boudouresque and Verlaque 2002a) (Table 2), only two species have achieved a similar blitzkrieg: *Asparagopsis armata* in the 1920s and 1930s and *Womersleyella setacea*, the range expansion of the latter more or less paralleling, in space and time, that of *C. racemosa* var. *cylindracea*.

Taking into consideration the seawater temperature and salinity of areas where *C. racemosa* var. *cylindracea* is native or already established, one can anticipate its further spread along the European and North African Atlantic shores. Following the example of *C. taxifolia* (Vahl) C. Agardh (Jousson et al. 2000), if nothing is done to control the possible vectors of the spread of *C. racemosa* var. *cylindracea* (i.e.: aquarium trade and ships; see Boudouresque and Verlaque 2002a), other parts of the world could soon become infested by this highly invasive algal species. In countries where national legislation includes a 'blacklist' of banned species, *C. racemosa* var. *cylindracea* should urgently be added to this list.

Table 2. Range extension of invasive marine macrophytes, over 15 years after being first observed in Europe and/or the Mediterranean Sea (n.s.: no spread recorded over the considered period).

Taxon	Date of earliest discovery	N, S, E and/or W extreme sites, 15 years after the date of first observation	Latitudinal range (15 years after)	Longitudinal range (15 years after)	References
<b>Rhodobionta</b>					
<i>Acrothamnion preissii</i> (Boergesen) Wollaston	1969	French Riviera, Tuscany	0°47'	3°40'	Cinelli and Sartoni (1969), Cinelli et al. (1984), Thélin (1984), Ribera and Boudouresque (1995)
<i>Asparagopsis armata</i> Harvey <sup>a</sup>	1923	Normandy, western Sahara, French Riviera, Flores (Azores I.)	27°26'	38°31'	Sauvageau (1925), Feldmann and Feldmann (1942)
<i>Grateloupia turuturu</i> Yamada <sup>b</sup>	1969	Wales, Calabria	13°36'	20°41'	Farnham and Irvine (1973), Maggs and Stegenga (1999)
<i>Womersleyella setacea</i> (Hollenberg) R.E. Norris	1987	Croatia, Canary I., Greece	17°15'	42°27'	Verlaque (1989), Athanasiadis (1997), Sartoni and Rossi (1998), Rojas-González and Afonso-Carrillo (2000)
<b>Stramenopiles</b>					
<i>Sargassum muticum</i> (Yendo) Fensholt	1966 <sup>c</sup>	Germany, Brittany, Cornwall	10°46'	14°27'	Critchley et al. (1983), Boudouresque et al. (1985), Ribera and Boudouresque (1995)
<i>Styopodium schimperi</i> (Kützting) Verlaque et Boudouresque	1973	Syria, Egypt, Israel, Libya	4°49'	15°53'	Verlaque and Boudouresque (1991), Ribera and Boudouresque (1995)
<i>Undaria pinnatifida</i> (Harvey) Suringar	1971	Brittany <sup>d</sup> , French Catalonia, Thau lagoon	5°39'	8°39'	Anonymous (1980), Pérez et al. (1981), Floc'h et al. (1996)
<b>Plantae</b>					
<i>Caulerpa racemosa</i> var. <i>cylindracea</i> (Sonder) Verlaque, Huisman et Boudouresque	1990	Liguria, Canary I., Cyprus	16°39' <sup>e</sup>	50°47' <sup>e</sup>	Nizamuddin (1991), this work
<i>Caulerpa taxifolia</i> (Vahl) C. Agardh	1984	Croatia, Sicily, Balearic I.	6°50'	13°36'	Meinesz and Hesse (1991), Meinesz et al. (2001)
<i>Codium fragile</i> var. <i>tomentosoides</i> (Van Goor) P.C. Silva	1900	The Netherlands	n.s.	n.s.	Van Goor (1923), Silva (1955), Coppejans (1982)

<sup>a</sup>Including the *Falkenbergia rufolanosa* life-history phase.

<sup>b</sup>Often misidentified as *Grateloupia doryphora* (Montagne) Howe (see Verlaque 2001; Gavio and Fredericq 2002).

<sup>c</sup>See Verlaque (1994).

<sup>d</sup>Deliberately introduced for aquaculture purpose.

<sup>e</sup>Less than 15 years after the first observation.

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