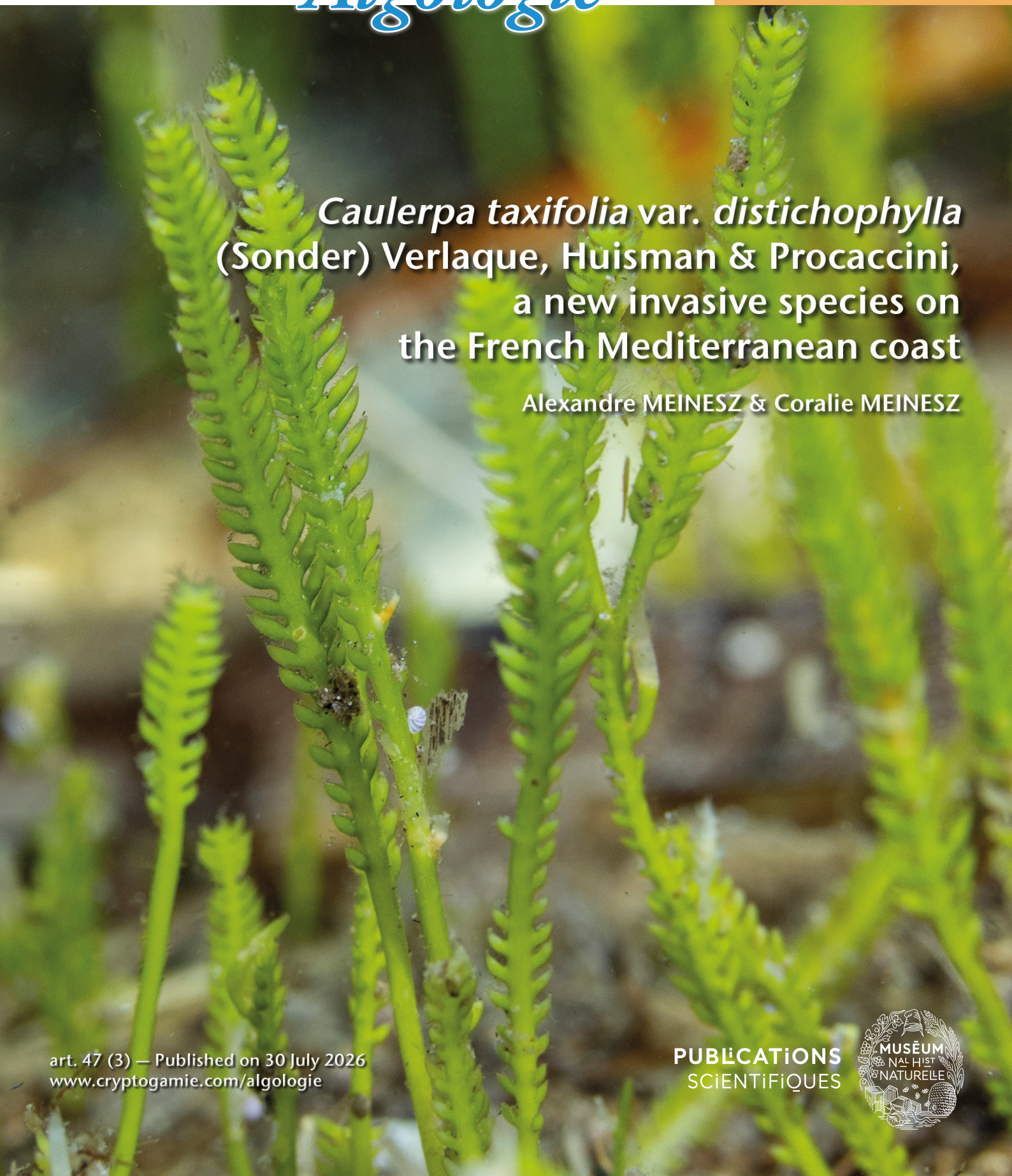
cryptogamie
Algologie
2026 • 47 • 3



Caulerpa taxifolia var. *distichophylla* (Sonder) Verlaque, Huisman & Procaccini, a new invasive species on the French Mediterranean coast

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art. 47 (3) — Published on 30 July 2026
www.cryptogamie.com/algologie

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Cryptogamie, Algologie est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Cryptogamie, Algologie *is a fast track journal published by the Museum Science Press, Paris*

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diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (électronique / *electronic*) : 1776-0984

Caulerpa taxifolia var. *distichophylla* (Sonder) Verlaque, Huisman & Procaccini, a new invasive species on the French Mediterranean coast

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Submitted 26 March 2026 | Accepted on 3 July 2026 | Published on 30 July 2026

Meinesz A. & Meinesz C. 2026. — *Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman & Procaccini, a new invasive species on the French Mediterranean coast. *Cryptogamie, Algologie* 47 (3): 33-46. https://doi.org/10.5252/cryptogamie-algologie2026v47a3. http://cryptogamie.com/algologie/47/3

ABSTRACT
In June 2025, we discovered the invasive and non-indigenous alga *Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman & Procaccini in the Bay of Villefranche (Alpes-Maritimes, France). This alga is native to Western Australia where it was originally described under the name of *Caulerpa distichophylla* Sonder. In the Mediterranean Sea, the alga was first recorded from Syria in 2003, and since spread to southern Turkey, Greece (Rhodes), Cyprus, Malta, Italy (Sicily, Calabria, and southern Sardinia), Libya and Tunisia and most recently to southern Spain (Andalusia). The previous closest record is located over 500 km from Villefranche-sur-Mer Bay, where we found over one hundred small colonies, each covering less than 0.1 m², at depths between 1.5 and 5 m, less than 60 m from the shoreline and spanning approximately 600 m of coastline. *Caulerpa taxifolia* var. *distichophylla* began to colonise the bay in which two other invasive species of *Caulerpa* J.V.Lamouroux had previously become established. We have been following their progress since they arrived in this bay as well as that of a native species of *Caulerpa*. Their spread has been characterised by phases of rapid expansion followed by abrupt and still-unexplained declines. This context enables us to formulate hypotheses regarding the potential for colonisation and invasive behaviour of *C. taxifolia* var. *distichophylla*.

KEY WORDS
Macroalgae,
Mediterranean,
Caulerpa taxifolia var. *distichophylla*,
non-indigenous species,
French coast.

RÉSUMÉ
Caulerpa taxifolia *var.* distichophylla *(Sonder) Verlaque, Huisman & Procaccini, une nouvelle espèce envahissante des côtes françaises de la Méditerranée.*
En juin 2025, nous avons découvert dans la baie de Villefranche (Alpes-Maritimes, France) *Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman & Procaccini, une algue envahissante non indigène mais déjà présente en mer Méditerranée. Cette algue est originaire d'Australie occidentale, où elle a été initialement décrite sous le nom de *Caulerpa distichophylla* Sonder. En Méditerranée, elle a été signalée pour la première fois en 2003 en Syrie, puis s'est propagée vers le sud de la Turquie, la

Grèce (Rhodes), Chypre, Malte, l'Italie (Sicile, Calabre et sud de la Sardaigne), la Libye, la Tunisie et, plus récemment, le sud de l'Espagne (Andalousie). La présence la plus proche enregistrée auparavant se situe à plus de 500 km de la baie de Villefranche, où nous avons trouvé plus d'une centaine de petites colonies, chacune couvrant moins de 0,1 m², situées entre 1,5 et 5 m de profondeur, à moins de 50 m du rivage, sur environ 600 m de littoral. *Caulerpa taxifolia* var. *distichophylla* a commencé à coloniser la baie où deux autres espèces envahissantes de *Caulerpa* J.V.Lamouroux s'étaient précédemment établies successivement. Nous avons suivi leur progression depuis leur arrivée dans cette baie, ainsi que celle d'une espèce indigène de *Caulerpa*. Leur propagation s'est caractérisée par des phases d'expansion rapide suivies de déclins abrupts et encore inexpliqués. Ce contexte nous permet de proposer des hypothèses concernant les potentialités de colonisation et de comportement envahissant de *C. taxifolia* var. *distichophylla*.

MOTS CLÉS
Macro-algue, Méditerranée, *Caulerpa taxifolia* var. *distichophylla*, espèce introduite, côtes françaises.

INTRODUCTION

The invasive alga *Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman & Procaccini, was originally described from the west coast of Australia near Fremantle (Womersley 1984) under the name *Caulerpa distichophylla* Sonder. It has since spread rapidly across the Mediterranean Sea.

It was first recorded in Syria in 2003 at a depth of –32 m near Cape Ras El Bassit, Oum al-Toyour, 12 km south of the Turkish border (Bitar *et al.* 2003, 2017; Bitar 2010). It was misidentified as a dwarf form of *Caulerpa mexicana* Sonder ex Kützing.

In 2006 the alga was subsequently recorded from southern Turkey (Yumurtalık, Gulf of Iskenderun), 100 km north of the Syrian record, under the name *C. taxifolia* (Vahl) C.Agardh (Cevik *et al.* 2007). In 2007, it was recorded in Sicily – Italy (Cormaci & Furnari 2009) under the name *C. taxifolia*, and under the name *C. distichophylla* (Meinesz *et al.* 2010).

Following its reassignment to *C. taxifolia* var. *distichophylla* by Jongma *et al.* (2013), the alga was recorded under this name in 2010 from Greece (around the island of Rhodes: Aplikioti *et al.* 2016), in 2012 around Cyprus (Çiçek *et al.* 2013), in 2014 from Malta (Schembri *et al.* 2015), in 2016 in Lebanon (Bitar *et al.* 2017), in 2017 from Libya (Tripoli: Shakman *et al.* 2017), in 2015-2018 from mainland Italy (Scilla, Strait of Messina, Calabria, and southern Sardinia at Faro-Cagliari: Di Martino *et al.* 2018), in 2015-2018 from Tunisia (Di Martino *et al.* 2018; Chartosia *et al.* 2018), in 2022 from Turkey in the Sea of Marmara (Taşkın *et al.* 2023). Lastly, in 2023, it was found off the coast of Spain in Andalusia at Cabo de Gata-Nijar (Martinez-Garrido *et al.* 2025).

Subsequent studies have documented its expansion near previously reported sites in Mediterranean, particularly around Sicily (Jongma *et al.* 2013; Musco *et al.* 2014, Picciotto *et al.* 2016; Mannino & Balistreri 2017; Di Martino *et al.* 2018; Mannino *et al.* 2019) and in Turkey (Gulf of Iskenderun: Cevik *et al.* 2012; Jongma *et al.* 2013; Antalya Bay: Cevik *et al.* 2012; Mutlu *et al.* 2022, 2025a, b; Alanya Bay and Kaş Bay, Taşkın *et al.* 2023). It has also been found in Cyprus (Aplikioti *et al.* 2016), Malta (Ellul *et al.* 2019a, b), and Libya (Mahklouf & Talha 2018), under the name *C. taxifolia*. These records, which span from 2003 to 2025, illustrate the macroalga's rapid expansion in the eastern and central Mediterranean, as well as its incursion into the western basin since 2024 (Fig. 1).

Since the seaweed first appeared in Sicily, we have been asked divers in France to help us report any sightings of the seaweed in France (Meinesz *et al.* 2010; Meinesz & Verlaque 2016-2019).

In June 2025 we recorded *C. taxifolia* var. *distichophylla* on the French coast. Here, we provide a description of the sites observed in the Bay of Villefranche along with a description of the thallus characteristics.

We discuss the likely consequences of the arrival of this *Caulerpa* J.V.Lamouroux taxon in France are discussed in relation to invasion patterns observed in other affected Mediterranean regions, the colonisation dynamics of three other invasive *Caulerpa* species in the Bay of Villefranche as well as other introduced and invasive *Caulerpa* species worldwide.

MATERIAL AND METHODS

The present record was obtained during a snorkelling survey on the distribution of marine phanerogams in the Bay of Villefranche (Alpes-Maritimes, France), covering the areas of Nice, Villefranche-sur-Mer, and Saint-Jean-Cap-Ferrat).

Following the discovery of an isolated thallus, we mapped the limits of *C. taxifolia* var. *distichophylla* colonisation in the bay. A total of six snorkelling surveys (each covering approximately 600 m of coastline) were conducted between 21 June and 4 July 2025, along a 4 km stretch of coastline (between 43°42'23.91"N, 07°18'52.15"W and 43°41'38.31"N, 7°19'29.86"W). The surveys extended from the shoreline to the upper limit of dense *Posidonia oceanica* (Linnaeus) Delile meadows, which occurred at depths of 1-5 m and at distances of 0 to 10-50 m from the shoreline. (Fig. 2).

The positions of the isolated colonies were localised on aerial photographs. Samples of isolated thalli were collected, and 20 herbarium voucher specimens were deposited at the CNRS ECOMAIR laboratory, University Côte d'Azur. In addition colonies were photographed *in situ*.

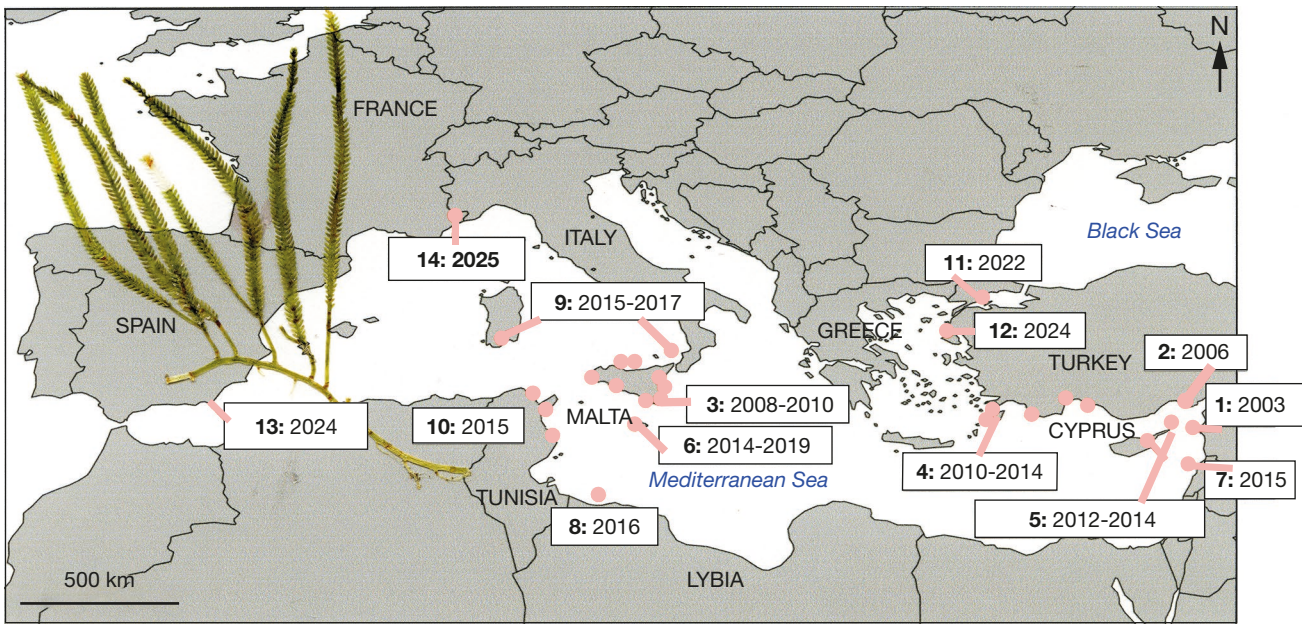

FIG. 1. — Map of the Mediterranean Sea showing the dates of the first main recorded observations (not the date of the reference) of *Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman & Procaccini in various locations (in chronological order): **1**, Syria: Cape Ras El Bassit (Bitar *et al.* 2003); **2**, Turkey: Iskenderun Gulf, Yumurtalik (Cevik *et al.* 2007); **3**, Italy: Sicily, Punta Braccetto (Cormaci & Furnari 2009), with an 85 km invaded area between Isole delle Correnti and Capo Passero (Meinesz *et al.* 2010); **4**, Greece: Island of Rhodes (Aplikioti *et al.* 2016); **5**, Cyprus: northern coast (Çiçek *et al.* 2013); **6**, Malta: northern coast (Schembri *et al.* 2015), Gozo, Comino, and northern Malta (Ellul *et al.* 2019a); **7**, Lebanon (Bitar *et al.* 2017); **8**, Lybia: Tripoli (Shakman *et al.* 2017; Mahklouf & Talha 2018); **9**, Italy : Calabria-Scilla, Sardinia-Faro Cagliari (Di Martino *et al.* 2018); **10**, Tunisia: Tabarka, Alataya, Djerba (Di Martino *et al.* 2018); **11**, Turkey: Sea of Marmara, Paşalimanı Island (Taşkin *et al.* 2023); **12**, Turkey: Tatlısu Gulf, Altınova Bay (Mutlu *et al.* 2025b); **13**, Spain: Andalousia, Cabo de Gata-Nijar (Martinez-Garrido *et al.* 2025); **14**, France: Bay of Villefranche (this study). Source: Eurogeographics 2024.

RESULTS

Our thallus samples exhibited a physiognomy characterised by distal, ramified stolon portions that supported a dense arrangement of fronds (6-10 branches per cm) and long, unbranched apical stolons (10-27 cm) that bore sparse fronds (1-3 per cm).

Along the surveyed coastline, approximately one hundred small and scattered colonies were observed, each represented by a single thallus covering less than 0.1 m². Overall colonisation extended over more than 600 m of coastline, at distances of 20 to 60 m from the shoreline. This was always in shallow waters (1-5 m depth) and exclusively on dead *P. oceanica* mats. Only one site exhibited denser colonisation with numerous isolated thalli spread over an area approximately 100 m² (43°42'01.99"N, 7°19'26.39"W) (Fig. 2).

In some areas, delicate fronds extended to the edges of, and between, scattered *P. oceanica* patches, however, at this early stage of colonisation, the alga did not overgrow the seagrass leaves (Fig. 3).

Within the colonised area, the alga was never observed on sandy or rocky substrates and water temperature during sampling was 24°C.

DISCUSSION

THE ARRIVAL OF THIS TAXON IN THE MEDITERRANEAN SEA

In the absence of precise information on the initial establishment site in the Mediterranean, any discussion of the introduction pathway remains speculative.

The first recorded observation in Syria is more than 600 km away from the Suez Canal, the main corridor for Red Sea species entering the Mediterranean Sea. This effectively excludes introduction via Red Sea, particularly since this alga has never been reported from the Red Sea.

However, the region of first observation is a major commercial shipping hub, including the Syrian port of Latakia (prior to the 2011 sanctions) and multiple Turkish ports in the Gulf of Iskenderun. Nevertheless, the journey from Western Australia to the Eastern Mediterranean requires at least 48 days at sea, which raises doubts as to whether a thallus could survive for such a long time in the darkness of ballast water.

The aquarium trade is a more plausible introduction pathway, as demonstrated in investigations into the introduction of *Caulerpa taxifolia* into the Mediterranean (Meinesz & Hesse 1991; Jousson *et al.* 1998, 2000; Meyer & Meinesz 2001). Jongma *et al.* (2013) therefore hypothesised that *C. taxifolia var. distichophylla* originates from Eastern Australia (the Fremantle region near Perth), as do two other species endemic to the Perth region that have invaded the Mediterranean: *Asparagopsis sandfordiana,* (Delile) Trevisan de Saint-Léon and *Caulerpa cylindracea* Sonder. Jongma *et al.* (2013) therefore hypothesised that these Australian species were introduced via the aquarium trade.

The long-distance dispersal of the invasive *Caulerpa taxifolia* strain from the Mediterranean to California (San Diego and San Francisco) has also been attributed to aquarists (Meinesz 2000, 2001: 303-310). Another distant introduction to Notojima in Japan, has been conclusively linked to the release of the

species from a public aquarium located on the coast (Komatsu *et al.* 2003). A similar explanation has been proposed for the recent arrival of *C. prolifera* in California. It was first observed in China Cove (Newport Bay) in 2021 and at Coronado Cays in San Diego Bay in 2023 (Waters *et al.* 2024).

The distribution of observations of *C. taxifolia var. distichophylla* in the Mediterranean in 2025 reveals three distinct spreading clusters (Fig. 1): 1) eastern Mediterranean (from Lebanon to the Sea of Marmara), where the species was first reported in 2003. Transport of fragments by boat anchoring systems, and prevailing currents has facilitated spread from Syria to Turkey, Cyprus, and the Greek island of Rhodes, with a single establishment in the Sea of Marmara; 2) central Mediterranean, where the alga arrived before 2009 and subsequently spread around Sicily, Malta, Libya, Tunisia, and northwards to southern Sardinia; and 3) western Mediterranean, with recent observations in 2024 along the Andalusian coast of Spain (Martinez-Garrido *et al.* 2025) and the arrival of *C. taxifolia* var. *distichophylla* in the northern part of the western Mediterranean basin indicates its high potential for further geographical expansion along the Italian, French, and Spanish coasts, following prevailing currents and boat mooring routes.

The arrival of the alga in France

Caulerpa taxifolia var. *distichophylla* is the fifth *Caulerpa* taxon recorded along the French Mediterranean coast, in addition to the native species *Caulerpa prolifera* and *Caulerpa ollivieri* Dostál, and the introduced species *C. taxifolia* and *C. cylindracea*.

The Bay of Villefranche, located between Nice and Monaco, is a popular anchorage for pleasure boats due to its favourable mooring conditions and strong tourist appeal (over 400 pleasure boats anchor in the bay on some summer days). It is therefore highly likely that *C. taxifolia* var. *distichophylla* was introduced via fragments transported on boat anchors from other Mediterranean locations where the species is established or remains undetected.

The spread of the invasive *C. taxifolia* strain across distant regions of the Mediterranean between 1984 and 2001, including Tunisia, Croatia, Spain (the Balearic Islands), Sardinia, Sicily, and multiple mainland French and Italian sites, has been attributed to dispersal through vegetative fragments (Meinesz 1992, 2001; Meinesz *et al.* 2001). Similarly, the Mediterranean expansion of *C. cylindracea* primarily occurs through fragment transport, followed by sexual reproduction once established (Piazzi *et al.* 2005; Klein & Verlaque 2008; Pierucci *et al.* 2019).

Colonisation processes and biology

Thalli of *Caulerpa* species, first described by Lamouroux (1809), are characterised by a creeping stolon (the main axis) that bears rhizoidal pillars for attachment, as well as erect chlorophyllous fronds. As documented for *C. prolifera*, the distal portion of the stolon represents the oldest part and gradually undergoes necrosis, whereas the apical (proximal) stolon drives colony expansion (Meinesz 1979a).

The wide distribution of small colonies along a 600 m stretch of coastline makes it difficult to identify the precise point at which the alga was first introduced to the Bay of Villefranche. The presence of numerous small and scattered colonies suggests that they originate from a larger, yet undiscovered, source population within the area.

Sexual reproduction has not yet been observed in Mediterranean populations of *C. taxifolia* var. *distichophylla* nor in native Australian thalli (originally named *C. distichophylla*) (Phillips 2009). However, Martinez-Garrido *et al.* (2025) observed thalli that had been emptied of their contents in a population of *C. taxifolia* var. *distichophylla* from Andalusia, Spain, during the summer. This suggests that sexual reproduction had ceased, although it is unclear whether the reproductive papillae that protrude from the thallus were visible. In Mediterranean *Caulerpa* species, reproductive events may occur several times during the summer as observed in *C. prolifera* along the French Riviera: Dostál 1928a, 1928b; Meinesz 1979b, 1980b) an in the Mediterranean strain of *C. taxifolia* (Zuljevic & Antolić 2000; Panayotidis & Zuljevic 2001). This process involves all nuclei within the thallus transforming into gametes which are released early in the morning. This results in the death of the emptied thallus (holocarpic reproduction). The male and female gametes released into the water column fuse to form zygotes approximately 5 µm in diameter.

Caulerpa's life history (Miyake & Kunieda 1937; Price 1972; Ishiwara *et al.* 1981; Ohba *et al.* 1992) begins with the zygote increasing in volume and transforming into the classic *Caulerpa* morphology, which can be haploid, diploid, or polyploid (Varela-Álvarez *et al.* 2012, 2015). However, Liddle *et al.* 1998 recognise only three chromosomes in the small nuclei (2 µm). In related siphoneaceous and holocarpic Bryopsidales such as *Halimeda tuna* (Ellis & Solander) Lamouroux, and *Flabellia* (ex *Udotea*) *petiolata* (Turra) Nizamuddin, the initial stage is called the 'protosphaera' (Meinesz 1972a, b, 1980a, b), and can measure up to 150 µm in diameter, with a single large (10 µm) polyploid nucleus. After five-seven months, the first filament emerges, initiating the formation of stolons and rhizoids and giving rise to the characteristic thallus containing small nuclei (2 µm). However, the protosphaera stage of *Caulerpa brachypus* Harvey, was cultivated for four months without the formation of the first filament (Miyake & Kunieda 1937). The protosphaera stage of *C. racemosa* var. *peltata* (reinstated as *Caulerpa chemnitzia* (Esper) Lamouroux (Belton *et al.* 2014) lasts 35 days, and reaches a diameter of 100 µm before developing the first germling filament (Ohba *et al.* 1992). These data suggest that the protosphaera stage can be transported by currents, and can move around for more than one month before settling down with the development of the first filament. This characteristic of *Caulerpa* biology enables a widespread colonisation from a single origin.

The colonisation pattern of *C. taxifolia* var. *distichophylla* in the shallow waters of the Bay of Villefranche characterised by more than one hundred small colonies (isolated thalli <0.1 m² each) distributed over 600 m of coastline, appears to be more consistent with dispersal via sexual reproduction of the protosphaera stage than with the simultaneous introduction of numerous identical vegetative fragments.

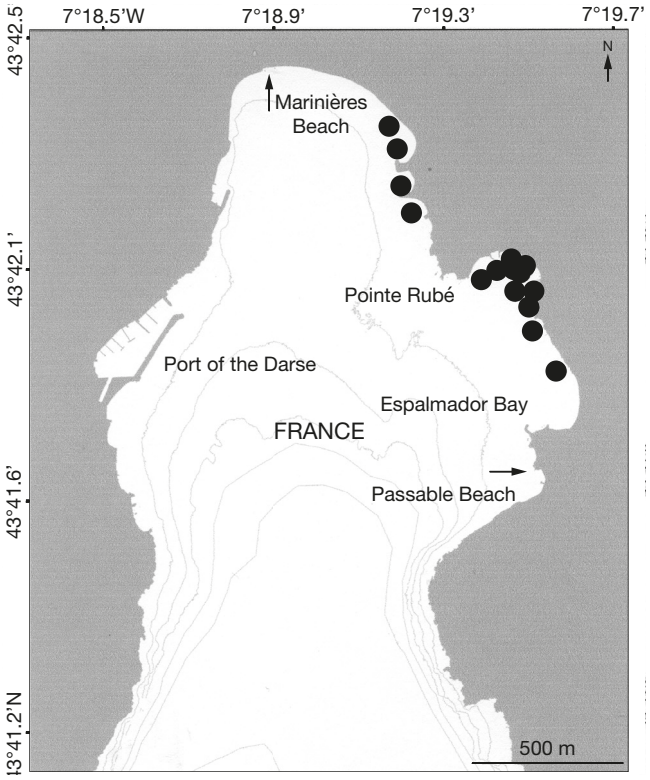

Fig. 2. — Map of Villefranche Bay showing the colonization points of *Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman & Procaccini (21 June 2025). **Arrows** indicate the explored coastal area. Coordinate system: WGS 84. Sources: BD_ORTHO 2023, Litto3D_PACA 2015, SHOM MNT_GdL-CA 2015.

Dynamics of colonisation

To evaluate the invasion potential of this *Caulerpa*, reference should be made to previous studies monitoring its spread at various Mediterranean sites.

All published reports on *C. taxifolia* var. *distichophylla* colonisation (cited in the introduction) describe rapid geographic expansion through both local and long-distance dispersal. The thallus, appears fragile and is easily detached by hydrodynamic forces allowing it to float. Shorelines may become covered by stranded thalli, as was observed in Sicily (Cormaci & Furnari 2009; Meinesz *et al.* 2010; Jongma *et al.* 2013).

Mannino *et al.* (2019) summarised the bathymetric distribution recorded at other Mediterranean sites. The species shows a marked preference for shallow waters (0 to –5 m) but has been reported at depths of up to –32 m in Syria (Bitar *et al.* 2003) and –100 m off Rhodes (Aplikioti *et al.* 2016). However, the latter record requires confirmation, as it is remains unclear whether the thalli were attached or detached.

The alga most frequently colonises dead *Posidonia oceanica* mats, but it also grows on rocky substrates, shipwrecks, and sandy-muddy bottoms (Mannino *et al.* 2019). It may also occur in *Cymodocea nodosa* (Ucria) Ascherson, (Martinez-Garrido *et al.* 2025) or *Halophila stipulacea* (Forsskål) Ascherson, meadows (Picciotto *et al.* 2016).

Its presence in the Sea of Marmara (Taşkın *et al.* 2023) suggests tolerance to low salinity (23‰); however, the authors only collected a few specimens in June, when the temperature of the seawater was 22°C. Near Paşalimanı Island in the Sea of Marmara, where the alga was collected, winter temperatures can drop to 8°C (Meinesz *et al.* 2005). Further information on its spread would be valuable to better understand the colonisation capacity of this alga in low-salinity conditions and cold winter temperatures.

Caulerpa taxifolia var. *distichophylla* can form dense stands that cover up to 100% of the substrate (Mannino *et al.* 2019), thereby competing with other macroalgae and having a negative impact on small benthic fauna that inhabit the substrate or sediments (Musco *et al.* 2015).

These ecological traits must now be reassessed in the newly colonised region, where winter seawater temperatures (12 to 13°C) in shallow waters are lower than in all previously colonised sites (so far restricted to regions above the 15°C winter isotherm), except for the Sea of Marmara, where winter temperatures may fall below 8°C.

The potential persistence of this species in relation to the population dynamics of the other *Caulerpa* species recorded in the Bay of Villefranche

The Bay of Villefranche has hosted all recorded *Caulerpa* species along the French Mediterranean coast, and their establishment histories are well documented. This accumulated knowledge of *Caulerpa* behaviour in the region provides a valuable framework for predicting the persistence and potential ecological impact of *C. taxifolia* var. *distichophylla*.

Caulerpa prolifera is a subtropical alga that is common in the Mediterranean Sea and the tropical/subtropical Atlantic Ocean. Historical records from the French Mediterranean continental coast (Meinesz 1973) indicate that this species has been present in the Bay of Villefranche since 1912, particularly in three areas: between Passable Beach and Pointe du Rubé, and in the Port of La Darse (Fig. 2) (Ollivier 1929, Dostál 1929). Episodes of very strong proliferation (as suggested by the species name) were observed in the bay during 1925-1927 (Ollivier 1929; Dostál 1929) and again in 1954 (Gilet 1954) and 1959 (Gessner & Hammer 1960). In 1967, the algae declined considerably; with only a few rare thalli found north of Passable Beach (Meinesz 1973). However, in 1994, several dense colonies were observed again within *C. taxifolia* vegetation in Espalmador Bay at a depth of –5 m. But since 2004, *C. prolifera* has no longer been observed in the Bay of Villefranche.

In the Bay of Naples, Funk (1927), also described a significant invasion of *C. prolifera* between 1914 and 1924.

These observations reveal cycles of proliferation followed by marked declines.

In 1929, Dostál described the species *Caulerpa ollivieri*, based primarily on specimens collected near the surface (0 to –2 m) in the Bay of Villefranche. Initially identified by Ollivier (Ollivier 1929) as *Caulerpa parvifolia* Harvey, this species was distinguished from *C. prolifera* only by its smaller fronds and stolon diameter. As these thallus characteristics are likely related to high light intensity and given that transitional forms between *C. ollivieri* and *C. prolifera* can be observed, *C. ollivieri* is probably not a valid taxon (conspecific with

C. prolifera) (Meinesz & Hesse 1991). This form of *Caulerpa* has disappeared from the sites on the French Riviera coast described by Ollivier & Dostál. Genetic studies on other reported occurrences of this taxon in the Mediterranean Sea and in the Atlantic Ocean could be valuable.

The introduced species *C. taxifolia* first appeared in the Bay of Villefranche in 1992 (Meinesz *et al.* 1993) proliferating spectacularly until 2004, when it covered nearly 176 hectares of the bay. It then underwent a sharp decline (Cottalorda *et al.* 2008, Meinesz *et al.* 2010). Today, only a few scattered thalli persist sporadically in the bay (Fig. 5A).

C. cylindracea was introduced to the bay in 1999 (Cottalorda *et al.* 2008), where it spread to cover certain muddy seabeds with up to 1 km of stolons per m² (Capiomont *et al.* 2005). However, since then, it has become much rarer. During snorkelling surveys conducted in June and July 2025 for this study, only a single thallus was observed along 6 km of seabed.

Similar declines or disappearances of *C. cylindracea* from previously dense populations have been reported in Andalusia (Martinez-Garido *et al.* 2025).

The occurrence of spectacular *Caulerpa* species invasions in the Bay of Villefranche, followed by sudden declines, may indicate a life-history characteristic of this genus that remains to be explained. These algae appear to undergo cyclical phases favourable to their development, followed by unfavourable periods leading to regression. Such abrupt fluctuations do not appear to be linked to local temperature variations, as the regression of *C. taxifolia* between 2004 and 2010 occurred simultaneously across all invaded regions during the same period (2004-2010), including areas with milder winter conditions such as Tunisia and Sicily in the southern Western Mediterranean basin (Meinesz *et al.* 2010). Nevertheless, *C. taxifolia* still persists in several Mediterranean regions and continues to spread in Turkey, including the Gulf of Izmir (Turan *et al.* 2011) and Dikili Bay in the Aegean Sea (Mutlu *et al.* 2025a). Therefore, although *C. taxifolia* var. *distichophylla* is expanding in the Bay of Villefranche, it may undergo cycles of rapid expansion followed by sudden decline, as seen with other *Caulerpa* species.

The reappearance of *C. prolifera* in the Bay of Villefranche between 1990 and 2004 occurred at exactly the same locations previously occupied by this species (metric surfaces observed accurately on the seabeds of La Darse Harbour and Espalmador Bay). A similar pattern was observed at other specific sites where *C. prolifera* had been described historically (Meinesz 1973), followed by decades-long absences after which it reappeared in the same highly localised areas.

For *C. cylindracea*, the formation of propagules has been documented (Renoncourt & Meinesz 2002), indicating a high potential for vegetative reproduction from very small thallus fragments. Therefore, it is likely that *Caulerpa* species can persist perennially, even in the absence of visible thalli, through the survival of microscopic thallus fragments or dormant coenocytic rhizoid fragments within the substrate.

Thallus characteristics

The morphology of the different thallus components of *C. taxifolia* var. *distichophylla* (fronds, stolons, and rhizoid pillars) from the Bay of Villefranche matched the 27 previous descriptions of the alga reported from other Mediterranean sites (references in the introduction), including the biometric study of Mutlu *et al.* 2025b, as well as and material from eastern Australia (Womersley 1984). The newly recorded alga in France is therefore confirmed as *C. taxifolia* var. *distichophylla*. As noted by other authors, the morphology of different parts of the thallus varies considerably according to irradiance levels and sea temperature.

Differences in frond length have been observed in relation to light exposure. Fronds are significantly longer at greater depths (Di Martino *et al.* 2018; Mannino *et al.* 2019) and in shaded areas beneath *Posidonia oceanica* leaves. In such shaded environments, fronds of *C. distichophylla* can reach an average length of 20 cm, with a maximum of 35 cm (Musco *et al.* 2014). Similar patterns were observed in the present study (Fig. 5B, C). Descriptions of the morphological characteristics of the thallus of *C. taxifolia* var. *distichophylla* are therefore highly dependent on irradiance as well as seasonal temperature variations. Such variation is common among *Caulerpa* species. In the Mediterranean, Meinesz *et al.* (1995) recorded *C. taxifolia* fronds along the French Riviera with an average length of 5 cm in shallow waters (–2 to –5 m) and up to 60 cm at greater depths (–10 to –30 m). A precise correlation between in situ irradiance and morphological changes has been described for *Caulerpa urvilliana* Montagne (Jaubert & Meinesz 1981).

Caulerpa species growing on muddy substrates rich in organic matter or nutrient-enriched sediments (e.g. urban waste) may also display frond gigantism (Chisholm *et al.* 1996, 1997; Ceccherelli & Cinelli 1997, 1998, 1999; Ceccherelli & Sechi 2002; Chisholm & Moulin 2003; Gennaro *et al.* 2015). On the French Riviera, *C. prolifera* fronds typically measure around 4 cm in shallow waters (–2 to –5 m), but can reach up to 50 cm at –5 m depth in muddy substrate areas near urban wastewater outfalls (Meinesz 1979a).

In late June, the thallus physionomy of *C. taxifolia* var. *distichophylla* at each colonised site is characterised by short, distal ramified stolon portions bearing dense frond arrangements (6-10 branches per cm and 20-40 fronds on intricately interwoven stolons, as shown in Fig. 4) and long apical stolons (10-27 cm) with sparse fronds (1-3 per cm) (Fig. 4 and 5C). This physionomy is closely comparable to that of *C. prolifera* observed at the beginning of summer on the French Riviera. Seasonal morphogenesis has been described for the latter species: at the end of spring, new stolons develop from old stolons that have overwintered. These new stolons bear scattered fronds and rise above the substrate in order to colonise the periphery of the initial colony (Meinesz 1979a; Fig. 2). The seasonal morphogenesis of *C. taxifolia* thalli observed in the bay of Villefranche is identical: with rapid stolon development occurring at the end of spring (Komatsu *et al.* 1994; Meinesz *et al.* 1995).

Thus the physionomy of the reduced thallus (spreading over >0,1m² in late June) of *C. taxifolia* var. *distichophylla* with long stolons bearing few fronds, indicates that the colonisation has survived the cold winter temperatures (13°C)

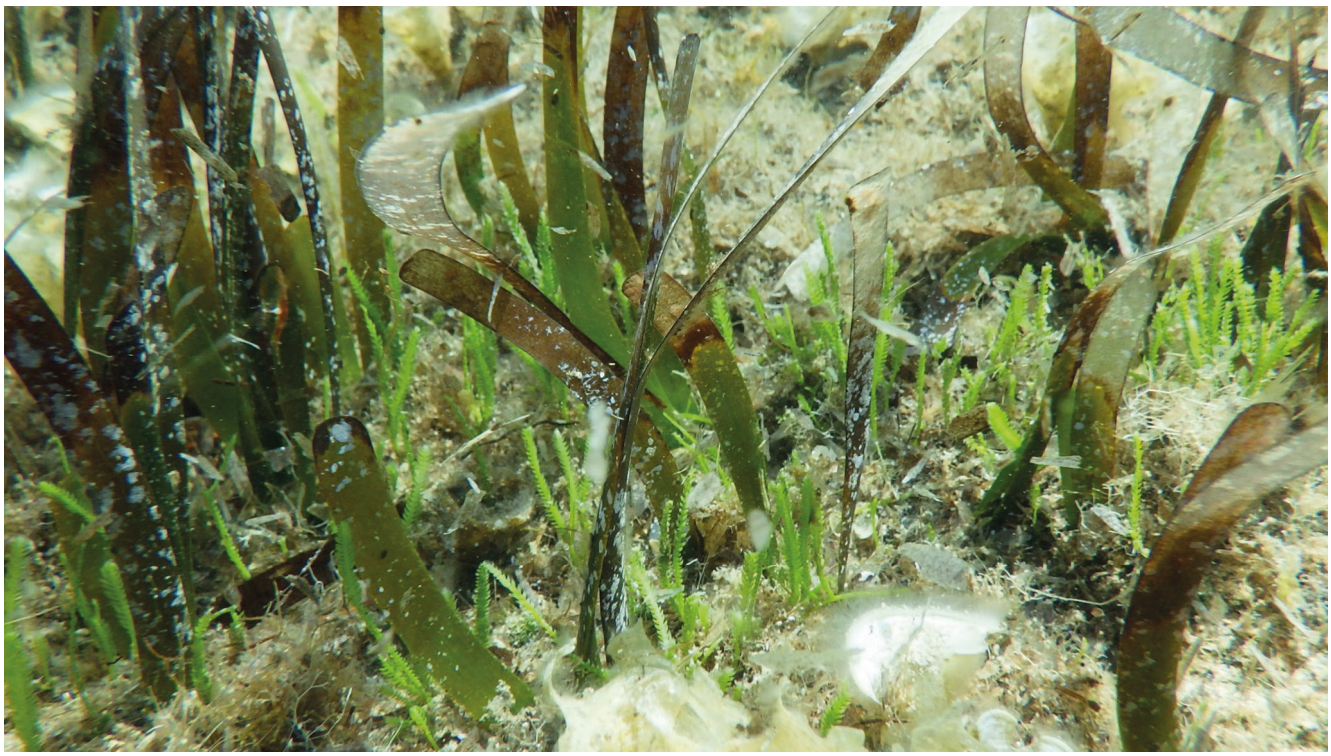

FIG. 3. — Underwater photograph of *Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman & Procaccini growing among rhizomes and leaves of *Posidonia oceanica* (Linnaeus) Delile, Bay of Villefranche, 27 july 2025, –3m. Photo credits: Alexandre Meinesz.

of the north-western Mediterranean and began before the winter of 2024-2025, possibly following sexual reproduction in summer.

THE NAME *CAULERPA TAXIFOLIA* VAR. *DISTICHOPHYLLA*

Caulerpa taxifolia var. *distichophylla* can be distinguished from *C. taxifolia* by the consistent fragility, shorter length and narrower width of all parts of the thallus (fronds, stolons and pinnules) under all conditions of settlement. Another diagnostic feature is the density of rhizoid pillars per unit length of stolon (Jongma *et al.* 2013). *Caulerpa taxifolia* var. *distichophylla* exhibits a high density and thin diameter of rhizoid pillars, whereas *C. taxifolia* var. *distichophylla* shows much thicker pillars at a lower density in *C. taxifolia* (one each 15 to 20 mm of stolon, Meinesz *et al.* 1995).

In the Bay of Villefranche, the ecological characteristics of the sites where the two introduced taxa are found in the Mediterranean are identical. On 30 June 2025, thalli of *C. taxifolia* and *C. distichophylla* were observed at the same depths and on the same substrate, separated by only 50 m. This excludes morphological variation induced by local conditions (Fig. 5).

These two taxa originate from geographically distant regions of Australia: the invasive strain of *C. taxifolia* is found near Brisbane on the east coast, while *C. distichophylla* is found near Fremantle on the west coast. Additional records include the Torres Strait, northern Australia (Jongma *et al.* 2013), and another from Ningaloo Reef south to Cape Naturaliste, approximately 1000 km north of Perth (Belton *et al.* 2019). Despite now occurring side by side in the Mediterranean, the two taxa remain clearly and consistently distinct morphologically (Fig. 4).

The morphological and biogeographical distinctions are robust and reflect stable, heritable differences from *C. taxifolia* (Jongma *et al.* 2013).

Since 1990, the large-scale invasion of parts of the Mediterranean by *C. taxifolia* and *C. cylindracea* has resulted in several hundred papers being published on the genus *Caulerpa* (Silva 2003).

Genetic analyses have been widely used to distinguish or group taxa of this highly polymorphic genus, which currently includes nearly 106 specific names and approximately 300 infraspecific epithets, and incorporates the concept of 'ecads' (i.e., morphological forms shaped by environmental conditions) (Guiry & Guiry 2025). The invasion of the Mediterranean between 1984 and 2004 by *C. taxifolia* initially confused with a form of *C. mexicana* from the Red Sea (Chisholm *et al.* 1995; Meinesz & Boudouresque 1996) prompted numerous genetic studies, some of which were contradictory. The conclusions of these studies did not always align with prevailing taxonomic interpretations.

The case of the invasive species *C. cylindracea* in the Mediterranean Sea illustrates these taxonomic shifts. Initially reported as *Caulerpa racemosa* (Forsskål) J. Agardh, when first recorded in Libya (Nizamuddin 1991), later referred to as *Caulerpa racemosa* var. *occidentalis* (J. Agardh) Børgesen, (Verlaque *et al.* 2000), then as *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman & Boudouresque, (Verlaque *et al.* 2003),

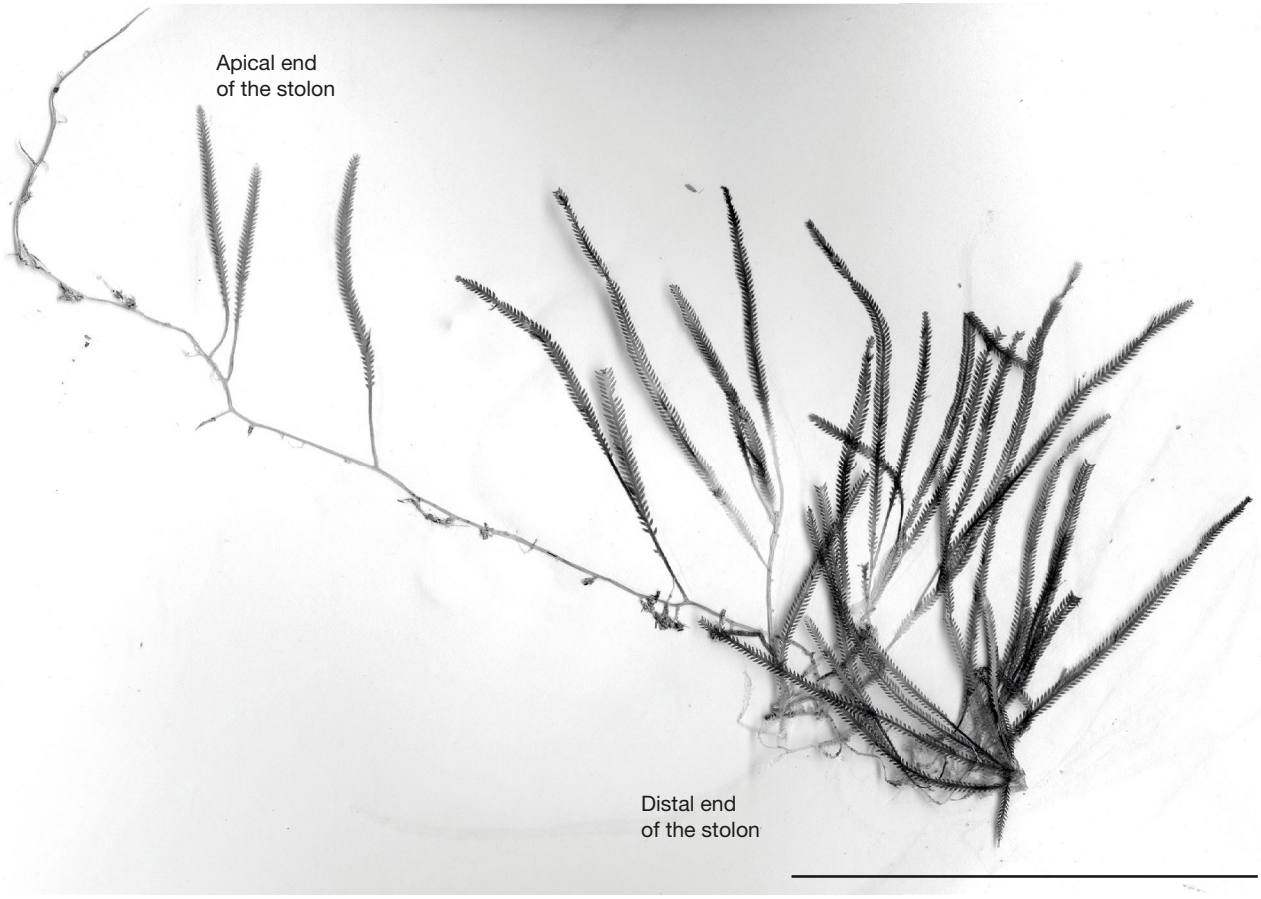

Fig. 4. — Herbarium plate of a *Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman & Procaccini thallus (Bay of Villefranche 27 June 2025, –4m) showing numerous fronds on the distal part of the stolon (**right**) and the stolon expansion with few fronds on the apical part (**left**). Scale bar: 10 cm. Photo credits: Alexandre Meinesz.

and ultimately reinstated at the species level as *C. cylindracea* Sonder (Belton *et al.* 2014).

Current genetic analyses suggest that *C. taxifolia* and *C. taxifolia* var. *distichophylla* are very closely related. Based on a single *C. distichophylla* specimen from the Perth region and chloroplast tufA sequence analysis, Famà *et al.* (2002a, b) identified *C. distichophylla* as the sister taxon of *C. taxifolia*, with a sequence divergence of only 0.24%, which is slightly higher than the intraspecific divergence observed within *C. taxifolia* (0.2%). The authors suggested that the two taxa might represent morphotypes of a single species but emphasised that unequivocal conspecific status would require molecular analyses of more variable genetic regions and additional specimens of *C. distichophylla* from the Indian Ocean where the taxon appears to be confined (Silva 2003). Subsequently, Jongma *et al.* (2013) found no statistically significant differences from *C. taxifolia* when using tufA, rDNA ITS and chloroplast 16S rDNA intron-2 sequences from two additional Australian specimens of *C. taxifolia* var. *distichophylla*. Belton *et al.* (2019) detected a single nucleotide difference between *C. taxifolia* and *C. taxifolia* var. *distichophylla*. This formed a distinct cluster within the *C. taxifolia* lineage in tufA alignments. However, this separation was not supported by the Generalized Mixed Yule Coalescent model.

According to Zubia *et al.* (2019), no complete *Caulerpa* nuclear genome has yet been published. Complete chloroplast genomes are available for only four species (none of which belong to the *C. taxifolia-C. distichophylla* complex), and a complete mitochondrial genome has been sequenced only for *C. lentillifera* J. Agardh, representing three subgenera.

Future genetic investigations on the genus *Caulerpa*, should take into account key morphological and structural characteristics: 1) the thallus is coenocytic, consisting of a single siphon, rather than a classic multicellular structure (thus its architecture - morphology is not composed of joined cells); 2) the distribution of organelles within the siphon and their role in morphogenesis are poorly understood; 3) siphons host endosymbiotic bacteria whose functions are unclear (Liddle *et al.* 1998; Meusnier *et al.* 2001; Aires *et al.* 2015; Zubia *et al.* 2019); and 4) the influence of ploidy level and genome size on *Caulerpa* morphology and invasive behaviour is largely unexplored (Varela-Álvarez *et al.* 2012; 2015).

The high invasive potential of *Caulerpa* species

The continued spread of introduced *Caulerpa* species into the Mediterranean once again highlights the remarkable invasive potential of the genus. Over the past fifty years, *Caulerpa* invasions far outside their native ranges have

FIG. 5. — **A**, *Caulerpa taxifolia* (Vahl) C.Agardh; **B**, *Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman & Procaccini collected on the same day (21 June 2025), a 50 meters apart and at the same depth (–3 m) on dead *Posidonia oceanica* (L.) Delile matte in Villefranche Bay, France; **C**, *Caulerpa taxifolia* var. *distichophylla* collected at shallow depth (–1 m) exhibiting small fronds. Scale bar: 5 cm. Photo credits: Alexandre Meinesz.

attracted considerable scientific attention and concern, sometimes leading to eradication or control measures. Several species are implicated: 1) in 1984, an invasive strain of *C. taxifolia*, native to Brisbane, Australia, was introduced to the Mediterranean Sea via aquarium discharge in Monaco. It continued to spread until 2004 (Meinesz *et al.* 2010). In 1992, the unsuccessful establishment of the Mediterranean strain was reported near the Notojima Public Aquarium in the Sea of Japan (Komatsu *et al.* 2003). The invasive strain was also recorded in California in 2000 (San Diego: Agua Hedionda lagoon and in Port Huntington near Los Angeles; Jousson *et al.* 2000; Meinesz 2000), attributed to aquarists (Meinesz 2001: 303-310). These colonisations were successfully eradicated (Muñoz 2016). This species has also spread along the south-eastern coast of Australia (New South Wales; Millar 2001; Schaffelke *et al.* 2002; Creese *et al.* 2004; Glasby *et al.* 2005) and two other native species of *Caulerpa* from Australia : *Caulerpa scalpelliformis* (R. Brown ex Turner) C. Agardh and *Caulerpa filiformis* (Suhr) Hering, have similarly expanded into southeastern Australia (Davis *et al.* 2005); 2) in 1991, *C. cylindracea*, native to western Australia, was first recorded in the Mediterranean (Nizamuddin 1991).Within two decades, it colonised almost the entire Mediterranean coastline (Piazzi *et al.* 2005; Pierucci *et al.* 2019) and subsequently spread into the Atlantic Ocean near the Canary Islands (Verlaque *et al.* 2004). This species is also expanding near Adelaide (Collins *et al.* 2004). Since the early 2000s, *Caulerpa webbiana* Montagne, has colonised several islands of Azores (North Atlantic) (Amat *et al.* 2008); 3) in 2001, *Caulerpa brachypus* f. *parvifolia* (Harvey) Cribb, native to the Pacific, was reported as invasive on coral reefs in southeastern Florida, (Lapointe & Bedford 2010); 4) in 2003, *Caulerpa ollivieri*, native from French Mediterranean coasts, invaded coastal waters of Green Turtle Cay, Abaco Islands, Bahamas (Lapointe *et al.* 2005); 5) in 2010, *Caulerpa verticillata* J. Agardh, was recorded at Esterito and La Concha in the southwestern Gulf of California, overgrowing coral reefs (Pérez-Estrada *et al.* 2013); 6) in 2015, the invasive strain of *Caulerpa taxifolia* (identical to the New South Wales, specimen illustrated by Creese *et al.* 2004) colonised Rarotonga Island, Cook Islands, Pacific Ocean (pers. com. Hilary Ayrton, Ministry of Marine Resources, Cook Islands); 7) in 2021, *Caulerpa brachypus* f. *parvifolia* and *Caulerpa parvifolia*, native to the Indo-Pacific, were detected outside their native range and are rapidly spreading north of New Zealand on coral reefs (D'Archino *et al.* 2021; Scarrott 2024); and 8) since 2021, *Caulerpa prolifera*, native to the tropical Atlantic and Mediterranean, has colonised two sites in California: San Diego Bay and Newport Beach (Waters *et al.* 2024).

These introductions point to two primary pathways: maritime transport (ballast water or anchors) and the tropical aquarium trade, as *Caulerpa* species are attractive and commonly used ornamental algae. While effective control of ballast water and anchors-mediated dispersal, from all vessels is challenging, increasing awareness among aquarists and coastal aquarium managers about the invasive potential of these algae would be beneficial. Accordingly, stricter regulations prohibiting their possession have been implemented in France, the United States, and Australia.

Acknowledgements
We would like to thank Godelieve E. Van As for her assistance in locating the algae colonies in Villefranche Bay. We also thank the anonymous reviewers and the editor-in-chief for their valuable work.

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Submitted 26 March 2026;
accepted on 3 July 2026;
published on 30 July 2026.