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Symphyocladiella gracilis (Rhodomelaceae, Rhodophyta): A new cryptic introduction on the European coasts

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ABSTRACT

The introduction of non-native seaweed species poses significant threats to coastal ecosystems, but many introductions remain undetected due to their small size and the morphological similarity among related species. This study aims to identify specimens resembling seaweeds in the genera *Deltalsia*, *Symphyocladiella*, and *Xiphosiphonia* collected from the Eastern Scheldt in The Netherlands during a general sampling survey in March 2022. Molecular analysis using the *rbc*L gene revealed these specimens to be *Symphyocladiella gracilis*, with only 0.13% genetic divergence from sequences from Pacific North America. Morphological observations confirmed this identification, with specimens matching descriptions from the Pacific. The combination of first-order branches with both determinate and indeterminate growth, lateral branches coalescing over 1–1.3 segments, and a recessed apical cell, is unique among species found in Europe, allowing its morphological identification. This is the first record of *S. gracilis* on European coasts, representing the fifth species of the tribe Pollexfenieae introduced in this region. The species' detection near extensive Pacific oyster cultivation sites in the Eastern Scheldt, points to aquaculture as the most likely introduction pathway. These findings highlight the importance of molecular tools and taxonomic expertise for detecting cryptic introductions in small, morphologically challenging seaweed species.

1. Introduction

The introduction of marine foreign species is one of the main threats to the ecological integrity of coastal waters (Katsanevakis et al., 2016). Among non-native marine species, seaweeds have the potential to cause severe damage, as they can replace the native species at the base of these ecosystems (Maggi et al., 2015). In the last decades, European coasts have seen an increase in the number of foreign seaweed species reported (van der Loos et al., 2024). Some foreign species such as *Caulerpa taxifolia*, *Sargassum muticum*, *Undaria* pinnatifida (Maggi et al., 2015), and more recently *Rugulopteryx okamurae* (Díaz-Tapia et al., 2025; El Madany et al., 2024), have developed invasive behavior, covering large sections of the coast. These invasions have caused environmental and economic damage, harmed local species and affected fishing and touristic industries (Dijkstra et al., 2017; Schaffelke and Hewitt, 2008). All these species have relatively large thalli (> 15 cm), which makes monitoring them and their impacts feasible, as they can be visually detected *in situ* and frequently appear as beach-cast.

However, most species of macroalgae have smaller and simpler thallus architectures that make *in situ* identification to species level difficult or even impossible. For this reason, they can easily produce cryptic introductions: introductions that go unrecognized because the introduced species goes undetected or is misidentified for a native organism (Díaz-Tapia et al., 2018). This kind of introduction has received more interest in recent years, as genetic analyses have enabled easier detection, leading to the realization that they are much more common than previously acknowledged (Morais and Reichard, 2018). Seaweeds have been particularly prone to this, with species such as *Polysiphonia morrowii* (Geoffroy et al., 2012), *Ulva ohnoi* (Flagella et al., 2010), and *Caulacanthus okamurae* (Petrocelli et al., 2020) going undetected due to

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their similarity to native species. However, these species have sizes in the order of tens of centimeters, and a large portion of algal diversity is composed of even smaller species, such as those forming algal turfs, communities composed of a mixture of small macroalgae (generally < 5 cm) that grow densely entangled (Connell et al., 2014). Despite their increasing abundance worldwide, algal turfs are understudied, with little information on their specific composition. Therefore, these communities might include cryptic introduced species that require detailed morphological and genetic analyses to be detected.

The red algal family Rhodomelaceae, particularly well represented in algal turfs, includes multiple examples of cryptic and small introduced species. Such species have been often detected only when molecular tools were applied in general sampling surveys (Bustamante et al., 2019; Díaz-Tapia et al., 2023a; Piñeiro-Corbeira et al., 2020). In other cases, their abundance has increased to the point where they could no longer remain unnoticed (Sherwood et al., 2020). Despite their small size, they include examples of invasive species such as *Womersleyella setacea* or *Lophocladia trichochados* (Battelli and Rindi, 2008; Golo et al., 2024) and their potential harmfulness should not be underestimated.

In the rhodomelacean tribe Pollexfenieae, the genera *Deltalsia*, *Symphyocladiella*, and *Xiphosiphonia* are characterized by a very similar outline morphology and are all represented on the European Atlantic coast. Despite extensive seaweed monitoring and comprehensive species inventories in the Netherlands, no species resembling these genera had been recorded previously. A seaweed inventory field excursion in March 2022 revealed specimens that resemble species of these genera with uncommon characteristics, leading to the suspicion that they could be a cryptic introduction. The aim of this study is to clarify the taxonomic identity of these specimens using morphological and genetic information and to assess their potential foreign origin.

2. Material and methods

A specimen morphologically resembling *Deltalsia/Symphyocladiella/Xiphosiphonia* was first observed at the location Zuidbout (51.614278, 3.960295) in the Eastern Scheldt (The Netherlands) in March 2022. Because the initial material consisted of a small fragment preserved in formalin, additional samples were collected for this study at Zuidbout (October 2022) and at Zeelandbrug, 3.5 km east of Zuidbout (51.629092, 3.914492, September 2023). Both locations are artificial dykes where the specimens were found in high abundances, covering entire surfaces of rocks from the low intertidal down to 6 m depth. Additional material (reproductive) was collected on December 2025 and January 2026. Selected specimens were separated from other species with a stereomicroscope. A fragment of a specimen was preserved in silica gel desiccant for molecular analysis, while the remaining material was preserved in 4% formalin seawater for morphological analyses. Selected thalli were mounted on semi-permanent slides with 20% corn Karo® Syrup solution (ACH Foods, Memphis, Tennessee, United States). In some samples, 1% acetic acid and 1% aqueous aniline blue were added to increase contrast. Sections for microscopic observation of the thallus structure were made by hand using a razor blade.

The silica-preserved sample was used for DNA extraction. This was done following an adapted cetyltrimethylammonium bromide (CTAB) protocol (Doyle and Doyle, 1987). The *rbc*L gene was selected for PCR amplification, as this is the most sequenced marker for Rhodomelaceae. Amplification was carried out in two segments (*rbc*L 1 and *rbc*L 2) using the primers F8/R646 and F481/R1381 (Wang et al., 2000) in a total volume of 25 μl, consisting of 2.5 μl PCR buffer, 2.5 μl dNTP's (200 μM), 1.25 μl forward primer (10 μM), 1.25 reverse primer (10 μM), 1 μl BSA (10 μg μL^{-1}), 1.25 μl Taq (1 U μL^{-1}), and 1 μl template DNA. The PCR profile consisted of an initial denaturation step (94 °C for 5 min), 35 denaturation cycles (94 °C for 1 min), primer annealing (46 °C for 1 min) and extension (75 °C for 2 min) and final extension (72 °C for 5 min). The PCR products were purified and sequenced by Macrogen (Amsterdam, The Netherlands). The obtained sequences were assembled using BioNumerics 7 (Applied Math NV, Sint-Martens-Latem, Belgium). The sequence is deposited in GenBank (accession number QB209185). The press-dried herbarium voucher is stored at the Leiden herbarium (L) (Index Herbariorum, 2026) with accession number L.4632281.

To assess the identity of this sample and analyze its phylogenetic position within the tribe Pollexfenieae, all the available sequences for species of this tribe were downloaded from GenBank and were aligned with ours using the MAFFT method (Katoh et al., 2002; Katoh and Standley, 2013) through the MAFFT plugin 1.5.0 in Geneious Prime 2026.0.2 (https://www.geneious.com/). Genetic divergence among sequences was analyzed when < 0.8% regarding our newly determined sequence. For phylogenetic reconstruction, a single sequence per species was retained in the final alignment, selecting the longest one when more than one was available. However, sequences with a divergence < 0.8% regarding our newly determined sequence, were included in the tree as different haplotypes. A maximum-likelihood phylogeny for *rbc*L was inferred using IQ-TREE 3.0.1 (Nguyen et al., 2014). As a constraint, the chloroplast genome-based tree described in Díaz-Tapia et al. (2023a) was used. The best-fit substitution model, TN + F + I + R3, was selected with ModelFinder as implemented in IQ-TREE. Branch support was assessed with 1000 ultrafast bootstrap replicates.

3. Results

3.1. Phylogeny

The sequence of the *rbc*L gene of the sample collected from The Netherlands was 0.13% (1–2 bp) divergent from the three sequences of *Symphyocladiella gracilis* (Kylin) D.Bustamante, B.Y.Won, S.C.Lindstrom & T.O.Cho available in GenBank (KU564473, KU564480, KX419777, as *Symphyocladia plumosa*). The phylogenetic tree constructed for the tribe Pollexfenieae (Fig. 1) resolved a highly supported clade including the sequences of species of the genus *Symphyocladiella*. This genus included nine species, eight taxonomically recognized, and the newly determined sequence from The Netherlands was placed in a highly supported clade with two other sequences of *S. gracilis* from British Columbia and California. Among congeners, the least divergent species was *S. dendroidea* (0.99%, 11 bp). Therefore, molecular information indicates that the specimens from The Netherlands belong to the species *S. gracilis*.

3.2. Morphological observations of specimens from The Netherlands

Thalli forming turfs up to 40 mm high (Fig. 2a, b), dorsiventral, composed of an extensive system of prostrate axes bearing erect axes dorsally and rhizoids ventrally that attach to the substratum (Fig. 3a, b). Erect axes with a distinct main axis, bearing 1–2 orders of alternate branches formed every two segments (Fig. 3a, c). Thalli dark red in color, with a rigid texture.

Axes cylindrical or subcylindrical, composed of an axial central cell surrounded by 6–8 pericentral cells, ecorticate (Fig. 3d, e). Prostrate axes growing from a domed apical cell 20–30 μm in diameter, increasing to 110–170 μm in diameter in median parts, with segments 1.3 length/diameter ratio. Rhizoids growing from the pericentral cells of the prostrate axes, up to two per segment, cut off from the pericentral cells, composed of a filament 50–90 μm in diameter and 190–540 μm in length and a terminal multicellular discoid pad.

Erects axes growing from prostrate ones at irregular intervals, with domed apical cells 17.5–25 μm in diameter increasing to 100–170 μm in diameter in medial and basal parts, with segments 1.2 length/diameter ratio. First order branches of determinate or indeterminate growth. Lateral branches of determinate growth with triangular apical cells once growth is complete. Apical cells of the main axes and young lateral branches overtopped by lateral branches (Fig. 3f). Branches of the first order coalesce with main axis over 1.1–1.3 segments (Fig. 3g).

Procarps formed in apical parts of erect axes, replacing a determinate branch (Fig. 3h). Cystocarps globular (Fig. 3i) to slightly urceolate,

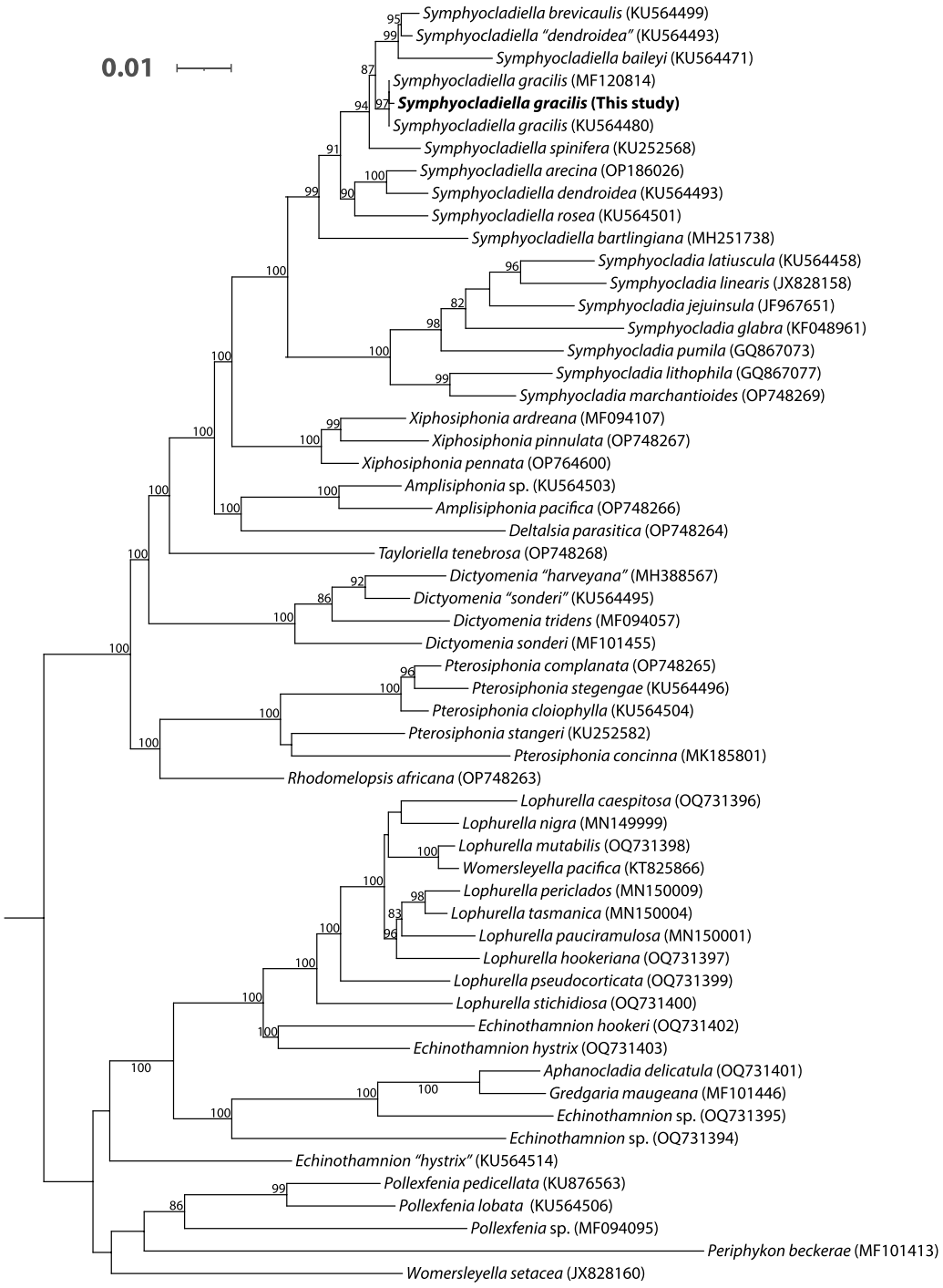


Fig. 1. Maximum likelihood phylogeny of the tribe Pollexfenieae based on the *rbc*L gene constrained with a base tree of 24 species based on whole chloroplast genomes (outgroup not shown for visibility). The consensus sequence of the samples collected in this study is highlighted in bold. Bootstrap support values shown when above 80%.

470–510 μm high and 470–490 μm in diameter; carpospores clavate, 84–118 × 20–34 μm. Tetrasporangia borne on last-order branches, forming straight series, subsphaerical, 46–66 × 50–66 μm, tetrahedrically divided (Fig. 3j).

4. Discussion

Molecular analyses of undetermined specimens of the tribe Pollexfenieae from The Netherlands revealed that they corresponded to *Symphyocladiella gracilis*. This is the first record of the species on European coasts, as it was previously only known from the pacific coasts of North America, from California to southeast Alaska (Savoie and Saunders, 2016; Scagel et al., 1989). This finding significantly expands the distribution area of the species.

4.1. Identity of the specimens

Symphyocladiella gracilis has been unequivocally identified using molecular information, as our *rbc*L sequences were only up to 0.13% divergent regarding sequences from Pacific North America, and at least



Fig. 2. *Symphyocladiella gracilis*. (a) Tuft found *in situ* during low tide. (b) Close up of a thallus *in situ*. Photos by Mick Otten.

0.88% divergent regarding other species in the Pollexfenieae. Our morphological studies further support this finding, as the characters observed in our material agree with previous descriptions of the species (Kylin, 1925; Savoie and Saunders, 2016).

The specimens collected in the Netherlands largely morphologically resemble several species occurring on European coasts, primarily *Symphyocladiella dendroidea* and *S. arecina*, as well as *Deltalsia parasitica* and the three species of the genus *Xiphosiphonia*. However, a detailed examination of their morphological characters enables *S. gracilis* to be differentiated from these species (Table 1).

Species of *Xiphosiphonia*, as well as *Symphyocladiella arecina*, can be distinguished from *S. gracilis* because they have determinate first-order branches resulting in a well-defined linear outline morphology, while both determinate and indeterminate branches are present in the currently examined specimens. *Symphyocladiella dendroidea* has lateral branches that coalesce with the main axes for over 1.5 segments, higher than the 1–1.3 segments in *S. gracilis*. It is also a larger species, reaching up to 7 cm (vs 4 cm), with more branching orders and erect axes that are occasionally corticate at the base. Finally, *Deltalsia parasitica* is the most similar species morphologically, but can be distinguished by its apical cells, which are mostly in line with the apices of nearby determinate branches, unlike in *S. gracilis*, for which the apical cell is recessed in relation to adjacent branches.

4.2. *Symphyocladiella gracilis: a new introduced species in Europe*

Until now, the presence of *Symphyocladiella gracilis* had only been reported from the western coast of North America (Savoie and Saunders, 2016). Although a disjunct natural distribution spanning both regions cannot be ruled out, it is unlikely given the high genetic similarity between North American and European specimens, the low genetic variability among the European specimens, and the fact that most *Symphyocladiella* species are restricted to the Pacific. Together, these point to a human-mediated introduction.

In Europe, *S. gracilis* is known only from the Netherlands. Its small size and close morphological similarity to related taxa may have hindered its detection elsewhere, so it may have reached other European coasts first and remain unnoticed there. Given its native distribution, with water temperatures ranging from 3ºC in winter in Alaska and 22ºC in summer in California (NOAA, 2026), other European regions may also provide suitable environmental conditions for the establishment of this species. However, its absence from the Dutch flora before this study is well supported.

The Dutch seaweed flora has been documented through several complementary sources. Extensive observation datasets come from the Strandwerkgemeenschap (2026), which has surveyed seaweeds along the Dutch coast since 1931, with monthly surveys in the Eastern Scheldt; Stichting ANEMOON (2026), which monitors intertidal and subtidal assemblages; and individual citizens recording observations on platforms such as Observation.org. More than 10 000 seaweed specimens collected in the Netherlands since 1949 and housed at the Leiden herbarium (L) (Index Herbariorum, 2026) have been examined during the revision of the Dutch checklist, and the ARISE project (ARISE, 2026) has DNA-barcoded hundreds of Dutch seaweed samples. These data have been used to compile the checklist of Dutch seaweeds (Stegenga et al., 1997), first published in 1997 and regularly updated since, and a recent report (Van der Loos and Helfferich, 2026) summarizing more than 41 000 records. None of these sources include *Symphyocladiella*. Morphologically similar genera such as *Deltalsia* and *Xiphosiphonia* do occur in the Netherlands, but their records and vouchers are well characterized, making it unlikely that *S. gracilis* was previously overlooked under these names. This, together with the rapid increase in biomass of *S. gracilis* at the site of first detection and at neighbouring sites, indicates a recent introduction.

The introduction pathway cannot be determined with certainty, as the species was found once naturalized and established. However, it is plausible to hypothesize that the introduction of *Symphyocladiella gracilis* in The Netherlands is related to aquaculture activities. Two main introduction vectors account for most seaweed introductions worldwide: marine traffic and aquaculture (Hewitt et al., 2007). Introductions associated with aquaculture are in general initially restricted to areas where non-native species are cultivated, leading to the formation of introduction hotspots. A well-known example is the Thau Lagoon (southern France), where dozens of non-native seaweeds have been detected in Europe for the first time (Boudouresque et al., 2010; van der Loos et al., 2024; Verlaque, 2001). Over time, some of these species have spread beyond cultivation areas and, in some cases, become invasive, as illustrated by the recent expansion of *Rugulopteryx okamurae* (García-Gómez et al., 2020). In the case of the Thau lagoon, as well as many other aquaculture-related seaweed introductions in Europe, they are linked to the cultivation of the Pacific oyster (*Magallana gigas*). The Dutch coast is another region where the pacific oyster has been extensively cultivated (Troost, 2010) particularly in the Eastern Scheldt where specimens of *S. gracilis* were detected, making this the most likely introduction pathway.

Alternatively, the introduction of *S. gracilis* to The Netherlands may be related to navigation. Marine traffic can transport organisms via biofouling or ballast water. Although initiatives such as the Ballast Water Management Convention (IMO, MEPC, 2004) and the Biofouling Guidelines proposed by the International Maritime Organization (IMO, MEPC, 2023) aim to reduce species transfers, their implementation has been limited and uneven across regions, and introductions through these vectors are still common (David and Gollasch, 2015; Hewitt et al., 2009). This vector seems unlikely for *S. gracilis*, however. There are no major ports in the Eastern Scheldt, and access from the sea is only

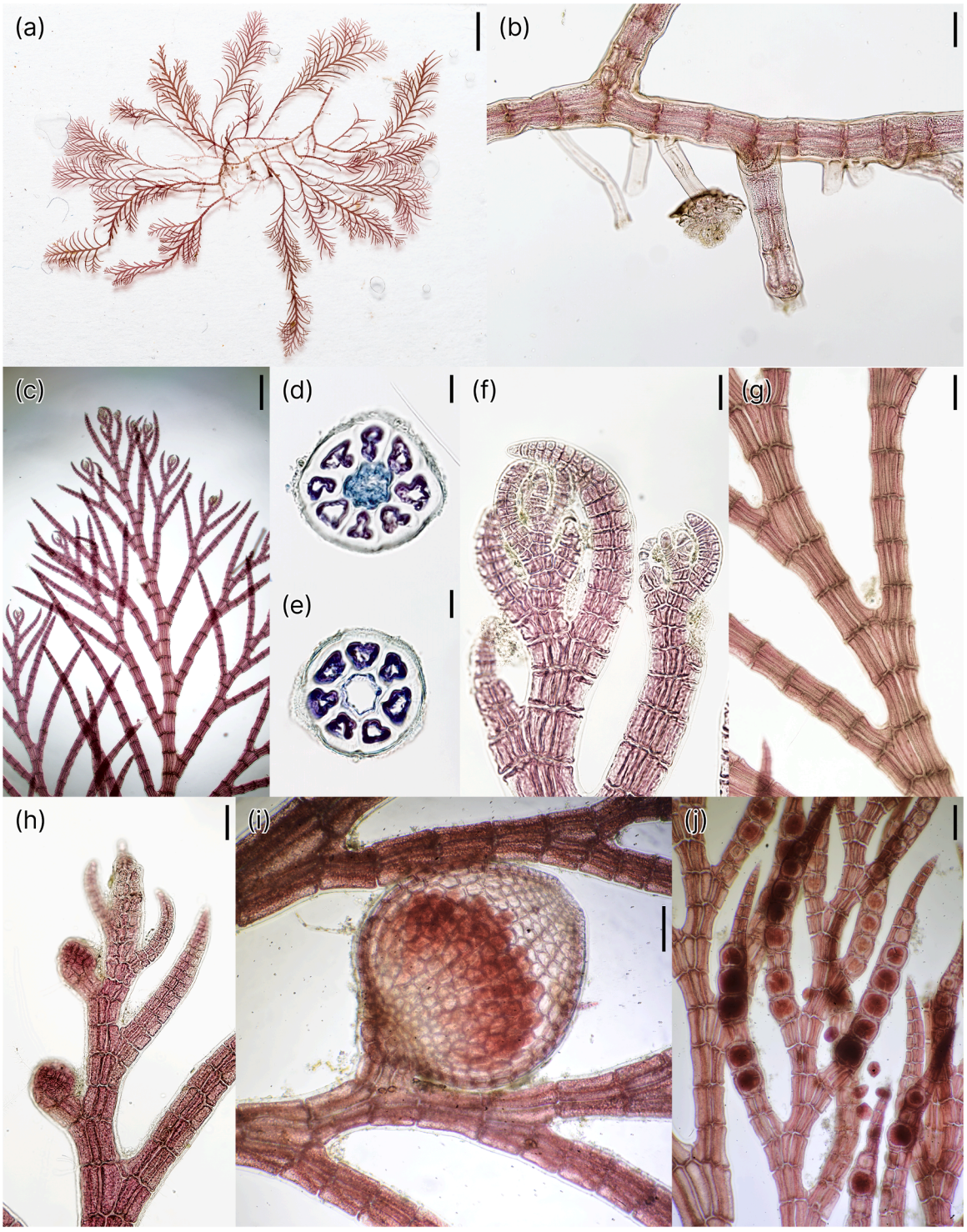


Fig. 3. *Symphyocladiella gracilis*. (a) Habit. (b) Prostrate axis with rhizoids. (c) Apical part of an erect axis bearing alternate branches every two segments. (d, e) Cross sections of erect axes showing an axial cell surrounded by pericentral cells. (f) Apex of an erect axis. (g) Main erect axis bearing determinate branches. (h) Young cystocarps. (i) Mature cystocarp. (j) Braches with tetrasporangia. Scale bars: (a) 2 mm. (b, f, g, h, i, j) 100 μm. (c) 200 μm. (d, e) 10 μm. Images (a-h) correspond to materials collected on September 2023, and (i, j) on December 2025. Photos (i-j) by Mart Karremans.

possible through the Roompotsluis, the navigation lock in the storm surge barrier, which is limited to vessels of up to 95 m in length (Rijkswaterstaat, 2026).The landward connections are also restricted by locks designed for inland navigation. Therefore, traffic in the Eastern Scheldt consists of small vessels rather than ocean-going ships, making direct transport from the native range of *S. gracilis* very unlikely.

However, when and where *S. gracilis* was introduced to Europe remains unknown. European Union regulations currently restrict the introduction of non-native species for aquaculture in order to minimize the risk of importing invasive species and diseases (The Council of the European Union, 2022). Several scenarios could explain the arrival of *S. gracilis* despite these regulations. First, the species may have been introduced before the regulations came into force and remained undetected until now, although this seems unlikely, as discussed above.

Table 1 Comparison of the main morphological characters distinguishing Symphyocladia gracilis from morphologically similar species of Symphyocladia, Dasysiphonia and Xiphosiphonia. NL, the Netherlands; NA, North America. Values in parentheses indicate infrequent states. Branching coalescence is expressed as the number of cells over which branches are coalescent with the main axis.

	S. gracilis (NL)	*S. gracilis* (NA)	*S. dendroidea*	*S. arecina*	*D. parasitica*	*X. pennata*	*X. ardreana*	*X. pinnulata*
Thallus size (cm)	1–4	2–4	1–7	1–3	Up to 5	1–4	2–4	1–3
Number of pericentral cells	6–8	8	7–12	8–9	6–8	5–6	7–10	6–7 (8)
Cortication	No	No	Base of larger specimens	No	No	No	No	No
First order branches growth	Determinate and indeterminate	Determinate and indeterminate	Determinate and indeterminate	Determinate (indeterminate)	Indeterminate	Determinate	Determinate	Determinate
Branching order	2	2–3	3	2–3	3–4	1 (2)	1 (2)	1 (2)
Branching coalescence (segments)	1.1–1.3	1	1.5–2.5	2–3	0.7–1.3	1.5–2.5	2.5–3.5	0.5–1.5
Apical cell recessed	Yes	Yes	Yes	Yes	In line	Yes	Yes	Yes
Trichoblasts in vegetative axes	Absent	Absent	Present	Absent	Absent	Absent	Absent	Absent
References	This work	1, 5	3, 6	4, 7	2,7	2, 8	2, 8	2, 9

1. Kylin (1925), as Pterosiphonia), 2. Maggs and Hommersand (1993), as Pterosiphonia), 3. Uwai and Masuda (1999), as Pterosiphonia tanakae), 4. Díaz-Tapia (2013), 5. Savoie and Saunders (2016), as Symphyocladia plumosa), 6. Bustamante et al. (2019), 7. Díaz-Tapia et al. (2023b), 8. Díaz-Tapia & Bárbara (2013), as Pterosiphonia)) and 9. PD pers. obs.

Second, the regulations may reduce the risk of introductions without eliminating it entirely. Finally, the regulations may not always be enforced, as previously reported for the Thau Lagoon (van der Loos et al., 2024).

Our findings bring the total number of introduced species in the rhodomelacean tribe Pollexfenieae to six. Other species in this tribe that have been reported as introduced include *Lophurella stichidiosa*, *Symphyocladiella dendroidea*, *Womersleyella setacea*, *Symphyocladia marchantioides*, as well as *Xiphosiphonia pinnulata* considered as non-native in some regions (Díaz-Tapia et al., 2023b; van der Loos et al., 2024). This lineage therefore appears prone to introductions, consistent with Williams and Smith (2007), who identified Rhodomelaceae as the family with the highest number of introduced species. Therefore, this is a good candidate group to consider when assessing the occurrence of introduced species. In the case of *S. gracilis*, it is probably more widespread in Europe than is currently recognized and further studies in other regions are required to detect its potential occurrence.

5. Conclusions

Symphyocladiella gracilis is a newly introduced species to the European coast. Due to its high morphological similarity to other species in the region, this species can be considered a cryptic introduction, and its detection has been only possible after the application of molecular tools. Once it was molecularly identified, morphological characters were found that distinguish it from other similar European species.

This study highlights the importance of accurate monitoring of non-native species to prevent biological invasions and associated biodiversity loss. However, the difficulty of monitoring and identifying seaweed species, especially small, simple, and morphologically variable species (Verbruggen, 2014), hinders this process, leading to the appearance of cryptic introductions. Molecular tools and taxonomic expertise are therefore crucial for effective monitoring, especially DNA barcoding using widely available markers such as *rbc*L in red algae.

CRediT authorship contribution statement

Antón Vázquez-Arias: Writing – original draft, Visualization, Formal analysis, Conceptualization. **Luna van der Loos:** Writing – review & editing, Investigation, Conceptualization. **Frank Perk:** Writing – review & editing, Investigation. **Javier Autón:** Investigation, Formal analysis. **Pilar Díaz-Tapia:** Writing – review & editing, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Genetic data is available on GenBank

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