Journal of Applied Phycology (2020) 32:2535–2547
https://doi.org/10.1007/s10811-019-01932-4

23RD INTERNATIONAL SEAWEED SYMPOSIUM, JEJU

Molecular survey of the red algal family Rhodomelaceae (Ceramiales, Rhodophyta) in Australia reveals new introduced species

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Received: 19 July 2019 / Revised and accepted: 11 September 2019 / Published online: 7 November 2019

Abstract

Red algae are frequently dominant components of the non-native biotas in coastal areas. They often remain undetected because of morphological similarity between native and introduced species and cryptic diversity. Routine use of DNA barcodes can aid in setting baseline tabulations of native species and for detecting introduced species. We performed an extensive survey of the red algal family Rhodomelaceae in southern Australia, producing a dataset containing more than 1100 *rbc*L sequences. The objective of this study was to screen that dataset for introduced species of the tribes Polysiphoniaeae and Streblocladieae, and to provide morphological information of presumably introduced species that were not previously recorded in Australia. Molecular data and morphological observations confirmed the presence of five presumably introduced species: *Leptosiphonia brodiei*, *Melanothamnus japonicus*, *M. strictissimus*, *Polysiphonia morrowii* and *P. delicata*. *Polysiphonia morrowii* and *M. strictissimus* were detected for the first time in Australia, and *M. japonicus* and *P. delicata* were found to be more widely distributed than previously known. Somewhat unexpectedly, the distribution range of *L. brodiei* has apparently shrunk, with our survey suggesting it remains only in Tasmania. Four of these species have been reported as introduced species in other countries, but *M. strictissimus* is here recorded for the first time outside its native New Zealand. Although all five species can be considered introduced or cryptogenic, only *P. morrowii*, *M. japonicus* and *M. strictissimus* were locally abundant, and further work will be needed to assess their ability to spread and effect negative impacts on native biotas.

Keywords Cryptic introductions · Introduction vectors · *Melanothamnus* · *Polysiphonia* · Non-native species · Red algae

Introduction

Introduced species are a major threat in coastal ecosystems worldwide, and are transforming marine habitats (Carlton and Geller 1993; Molnar et al. 2008). The most recent review of the non-native seaweeds listed 346 species that were recorded as adventive or cryptogenic in one or more regions (Thomsen et al. 2016). Seaweeds are mainly introduced via hull fouling or by transfer of mollusc livestock during aquaculture activities which act as racks for the dispersal of a diverse assemblage of marine organisms (Mineur et al. 2007a, 2007b, 2008; Williams and Smith 2007). Given the increasing economic importance of the marine realm to aquaculture and commercial and touristic boating, it has been predicted that these vectors will increasingly play important roles for future introductions (Mineur et al. 2014; Thomsen et al. 2016).

The detection of introduced seaweeds is hampered by morphological similarity of introduced and native species as well as, in many cases, a complex history of different names being applied. As a result, overlooked and cryptic introductions are common, and the real number of introductions is probably being underestimated (Carlton and Geller 1993). Moreover, cryptogenic species, whose native or introduced nature cannot be determined with certainty, abound among macroalgae (Díaz-Tapia et al. 2017a; Steen et al. 2017). The family Rhodomelaceae and particularly its tribes Polysiphonieae and Streblocladieae (formerly *Polysiphonia sensu lato*) are commonly listed as introduced or cryptogenic seaweed species worldwide

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10811-019-01932-4) contains supplementary material, which is available to authorized users.

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(Williams and Smith 2007). The family is arguably the most diverse in the red algae, and it contains more introduced species than would be expected by chance (Williams and Smith 2007). Many Polysiphonieae and Streblocladieae are small (< 2 cm in length), morphologically similar and often grow as algal turfs in which many species are densely entangled to form low-lying carpets that are less conspicuous and distinguishable than larger sized seaweeds. These traits make them particularly prone to being cryptic or overlooked introductions (Díaz-Tapia et al. 2017a). The use of molecular approaches can contribute to the detection of new non-native species in such problematic taxa, and it has been proven useful for detecting seaweed cryptic introductions and determining their distributions (e.g. Zuccarello et al. 2002; Díaz-Tapia et al. 2013, 2017a; Steen et al. 2017; Manghisi et al. 2019).

In Australia, marine introductions have occurred for centuries, mainly via shipping (Hutchings 2018), and the Australian government has implemented management tools for reducing the risk of introductions via ballast water and hull fouling (Hewitt and Campbell 2007; Hutchings 2018). The risk of species introductions via shellfish livestock has also been greatly reduced by an importation ban that has been in effect since 1970 (Ogburn 2007). Moreover, protocols have been developed to survey species likely to be introduced into Australia and species that have been introduced to or are known as cryptogenic (Hayes et al. 2005). In the most recent floristic account from Australia, three species of the family Rhodomelaceae were recorded as introduced: *Chondria arcuata*, *Polysiphonia brodiei* and *P. senticulosa* (Womersley 2003). Later, *Melanothamnus japonicus* was reported for the first time in Tasmania and Western Australia in a study of this introduced species in the northwestern Atlantic, suggesting its human-mediated origin in Australia (Savoie and Saunders 2015). Our own recent work described *P. delicata* as a highly disjunct cryptogenic species from Spain and Victoria (Australia) (Díaz-Tapia et al. 2017a), and also the North Atlantic *P. devoniensis* as a new introduced species in Victoria (Díaz-Tapia et al. 2018). In a review of introduced seaweeds, *P. sertularioides* was also listed as non-native in Australia (Williams and Smith 2007), although previous Australian floristic accounts had considered that it is a widely distributed species (Womersley 1979, 2003).

Despite the efforts of the Australian government to develop management options for introduced species, a major challenge remains: the marine native biodiversity needs to be characterized in detail to allow for better detection of new introduced species (Hutchings 2013, 2018). This challenge is highly relevant for the red algae, as our knowledge of its diversity mostly relies on morpho-anatomical identifications (Womersley 1994, 1996, 1998, 2003; Huisman 2018). This is problematic, as the use of DNA barcodes in seaweed surveys has revealed cryptic diversity wherever applied (e.g. Savoie and Saunders 2016, 2019; Meynard et al., 2019), but this approach has not been systematically applied to the Australian marine flora. The few studies that have used this approach suggest the existence of large numbers of undiscovered red algal species is yet to be described in Australia (e.g. Saunders et al. 2017; Díaz-Tapia et al. 2019), thus highlighting the fact that the knowledge on the native flora is highly incomplete in a region that hosts the largest biodiversity of red algae globally (Womersley 1990).

With the aim of addressing this gap in our knowledge of Australian Rhodomelaceae, we have carried out sampling surveys using morphological identification and DNA barcodes across Western Australia, South Australia, Victoria, Tasmania and Queensland, resulting in more than 1100 *rbc*L sequences. The objective of this undertaking is to evaluate our knowledge on the biodiversity and distribution of introduced species of the tribes Streblocladieae and Polysiphonieae in Australia using this extensive sequence dataset. We also aim to characterize any detected introduced species morphologically.

Materials and methods

General sampling surveys of the family Rhodomelaceae were carried out in Queensland (Heron Island), eastern and northern Tasmania (16 sites), Victoria (49 sites), South Australia (10 sites) and Western Australia (22 sites) during 2014–2018, resulting in the collection of more than 1100 specimens. Materials for DNA extraction were preserved in silica gel desiccant. Plants for morphological study were preserved in 4% formalin seawater at 4 °C and stored in the dark. Some specimens were mounted in 20% Karo syrup (ACH Foods, Memphis, TN, USA) and 80% distilled water. Sections for microscopic observations were made by hand using a razor blade.

DNA was extracted from silica gel–dried material following Saunders and McDevit (2012). PCR amplification was carried out for *rbc*L using the primers F57/rbcLrevNEW or F2/R1452 (Saunders and Moore 2013; Díaz-Tapia et al. 2018). Reactions were performed in a total volume of 25 μL, consisting of 5 μL 5× MyTaq reaction buffer, 0.7 μL of forward and reverse primers (10 μM), 0.125 μL MyTaq DNA Polymerase (1 U μL^{-1}) (Bioline), 17.475 μL MilliQ water and 1 μL template DNA. The PCR profile consisted of initial denaturation (93 °C for 3 min), 35 cycles of denaturation (94 °C for 30 s), primer annealing (45 °C for 30 s) and extension (74 °C for 90 s) and final extension (74 °C for 5 min). The PCR products were purified and sequenced commercially by Macrogen.

With the aim of identifying the new *rbc*L sequences, they were compared with previous data available in GenBank and our own database of European sequences using distance trees (not shown). This approach allowed us to identify the

sequences that corresponded to species known to be or potentially introduced in Australia, considering their identities and known distributions globally. Collection information and GenBank accession numbers of these sequences are provided in Table S1. We also downloaded 100 sequences from GenBank that had a similarity with these Australian sequences higher than 99% with a minimum length of 800 base pairs (Table S1). Sequences were aligned using Muscle in Geneious 6.1.8 (Kearse et al. 2012). In order to place the sequenced species in a broader phylogenetic context, 45 *rbc*L sequences of other members of the Polysiphonieae and Streblocladieae were downloaded from GenBank (Table S1). Our selection included representative species of the main lineages of these two tribes (Díaz-Tapia et al. 2017b). We selected a sequence for each species, except for the targeted taxa for which we included in the analyses a sequence per haplotype. The sequences included in the final alignment were selected after considering their quality in terms of both length and the presence of ambiguous bases. Phylogenetic trees for *rbc*L were estimated with Maximum Likelihood (ML) using RAxML 8.1.X (Stamatakis 2014). GTR-Gamma was used as the nucleotide model; branch support was estimated with 100 bootstrap replicates. Three species of *Pterosiphonia* were selected as the outgroup based on our phylogenomic analyses of the major lineages of the Rhodomelaceae which resolve a clade formed by the Herposiphonieae and Pterosiphonieae as sister to the Polysiphonieae (Díaz-Tapia et al. 2017b).

Results and discussion

Molecular identification

In the present work, we identified 60 sequences corresponding to five species known to be or potentially introduced in Australia. They corresponded to *Leptosiphonia brodiei*, *Melanothamnus japonicus*, *M. strictissimus*, *Polysiphonia morrowii* and *P. delicata* (Fig. 1). The 13 *rbc*L sequences of *L. brodiei* represented three haplotypes, with a sequence divergence of up to 0.2% (3 bp). Two of them were present in both Tasmania and Europe.

Sequences from Australia assigned to *Melanothamnus japonicus* were resolved in the phylogeny in a fully supported clade including sequences labelled as *M. akkeshiensis*, *M. flavimarinus*, *M. harveyi*, *M. japonicus*, *M. harlandii* and *M. decumbens* (henceforth the *M. japonicus/harveyi* complex; Fig. 1). The 27 Australian sequences corresponded to three haplotypes that diverged up to 0.2% (3 bp) among them and by 0–1.3% (up to 18 bp) from other species or haplotypes of the *M japonicus/harveyi* complex from Asia, North America and Europe. Two of the Australian haplotypes (H2 and H6 in Fig. 1) were exclusively found in Australia. The haplotype H2 was only found in Victoria, with H6 occurring in Victoria, Tasmania and Western Australia. The third haplotype (H3 in Fig. 1) was found in Tasmania and Victoria but had a wider distribution including New Zealand, the Atlantic North America, Japan, Korea, California and Spain.

The nine sequences of *Melanothamnus strictissimus* from Tasmania were identical and were placed in the phylogeny in a clade with four other samples from New Zealand (Fig. 1). Four haplotypes were identified in New Zealand, and Tasmanian samples were identical to haplotype 2. Sequence divergence within the *M. strictissimus* clade is up to 1% (12 bp).

The 12 *rbc*L sequences of *Polysiphonia delicata* represented two haplotypes: one found exclusively in Victoria and the other in both Spain and Tasmania. Sequence divergence within the clade is 0.1% (1 bp).

The 51 *rbc*L sequences of *Polysiphonia morrowii* represent 13 haplotypes. One of the Tasmanian sequences corresponded to haplotype 7 (Fig. 1), which is also found in Argentina, whereas the other nine Tasmanian sequences corresponded to haplotype 5 whose distribution includes New Zealand, western Asia, Pacific and Atlantic South America and Atlantic France. Sequence divergence within *P. morrowii* is up to 0.3% (6 bp).

Morphological observations and remarks

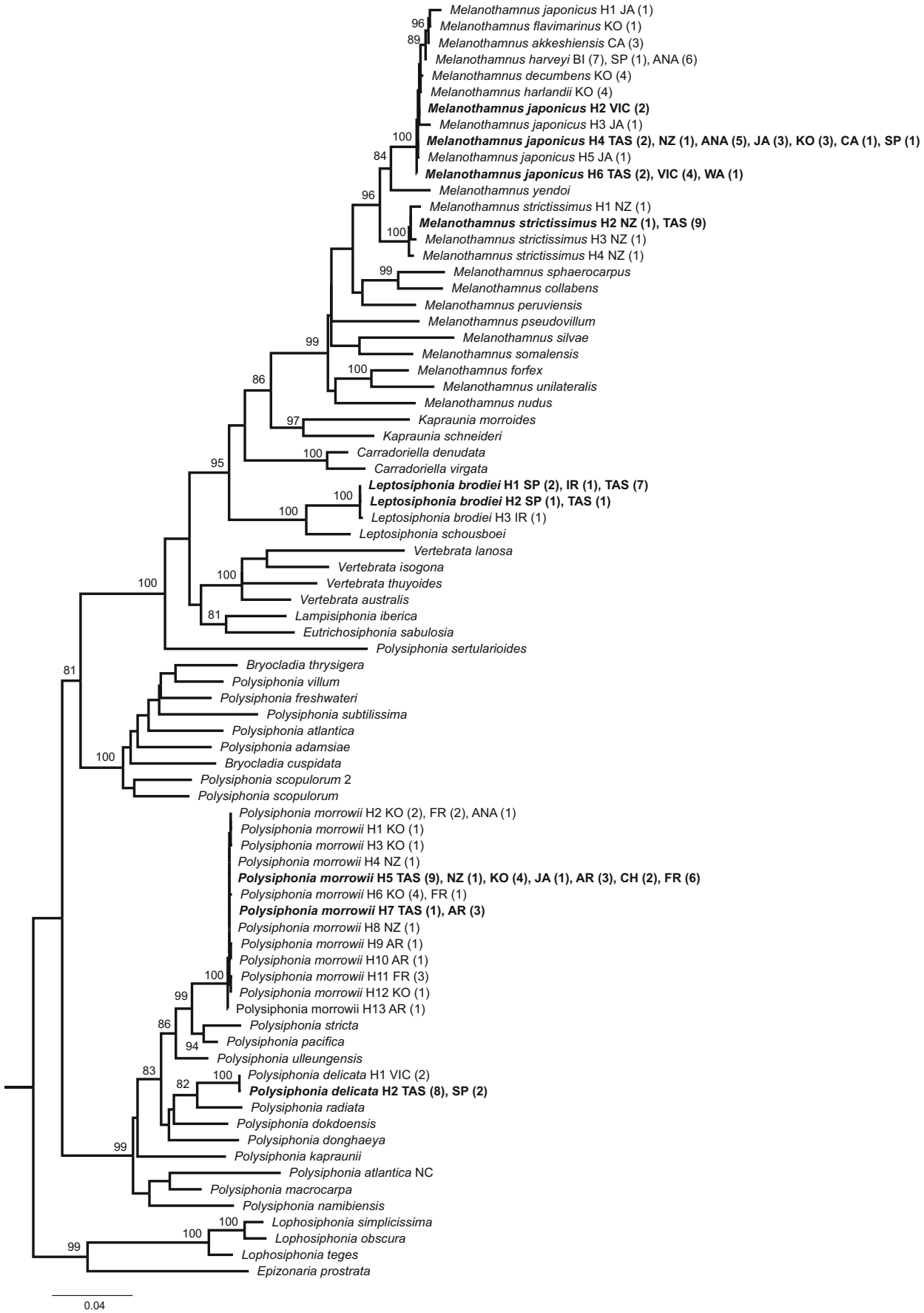
Leptosiphonia brodiei (Dillwyn) A.M.Savoie & G.W. Saunders

Selected homotypic synonyms: *Polysiphonia brodiei* (Dillwyn) Sprengel.

Description: Detailed morphological and anatomical descriptions of Australian representatives were provided in Womersley (1979, 2003).

Habitat and distribution in Australia: *Leptosiphonia brodiei* was abundantly collected in southeastern Tasmania in the course of this study (Fig. 2).

Remarks: *Leptosiphonia brodiei* is a native from the North Atlantic and was reported to be an adventive species in South Australia, Tasmania and Victoria in the most recent floristic accounts from southern Australia based on morphological identifications (Womersley 2003, as *Polysiphonia*). Molecular data determined in our study confirm these identifications, as the two haplotypes detected in Australia were identical to haplotypes of the species from Europe. The species was only found in Tasmania during our surveys, but was not present in our collections from South Australia and Victoria, where it was recorded in the 1950s–1990s. Apparently, these populations were extirpated or, at least, their abundance has been highly reduced to the point they are not easily detectable at present. Outside Australia, this species has been reported as introduced in New Zealand, Japan and Korea


Melanothamnus japonicus H1 JA (1)
Melanothamnus flavimarinus KO (1)
Melanothamnus akkeshiensis CA (3)
Melanothamnus harveyi BI (7), SP (1), ANA (6)
Melanothamnus decumbens KO (4)
Melanothamnus harlandii KO (4)
Melanothamnus japonicus H2 VIC (2)
Melanothamnus japonicus H3 JA (1)
Melanothamnus japonicus H4 TAS (2), NZ (1), ANA (5), JA (3), KO (3), CA (1), SP (1)
Melanothamnus japonicus H5 JA (1)
Melanothamnus japonicus H6 TAS (2), VIC (4), WA (1)
Melanothamnus yendoi
Melanothamnus strictissimus H1 NZ (1)
Melanothamnus strictissimus H2 NZ (1), TAS (9)
Melanothamnus strictissimus H3 NZ (1)
Melanothamnus strictissimus H4 NZ (1)
Melanothamnus sphaerocarpus
Melanothamnus collabens
Melanothamnus peruviensis
Melanothamnus pseudovillum
Melanothamnus silvae
Melanothamnus somalensis
Melanothamnus forfex
Melanothamnus unilateralis
Melanothamnus nudus
Kapraunia morroides
Kapraunia schneideri
Carradoriella denudata
Carradoriella virgata
Leptosiphonia brodiei H1 SP (2), IR (1), TAS (7)
Leptosiphonia brodiei H2 SP (1), TAS (1)
Leptosiphonia brodiei H3 IR (1)
Leptosiphonia schousboei
Vertebrata lanosa
Vertebrata isogona
Vertebrata thuyoides
Vertebrata australis
Lampisiphonia iberica
Eutrichosiphonia sabulosia
Polysiphonia sertularioides
Bryocladia thrysigera
Polysiphonia villum
Polysiphonia freshwateri
Polysiphonia subtilissima
Polysiphonia atlantica
Polysiphonia adamsiae
Bryocladia cuspidata
Polysiphonia scopulorum 2
Polysiphonia scopulorum
Polysiphonia morrowii H2 KO (2), FR (2), ANA (1)
Polysiphonia morrowii H1 KO (1)
Polysiphonia morrowii H3 KO (1)
Polysiphonia morrowii H4 NZ (1)
Polysiphonia morrowii H5 TAS (9), NZ (1), KO (4), JA (1), AR (3), CH (2), FR (6)
Polysiphonia morrowii H6 KO (4), FR (1)
Polysiphonia morrowii H7 TAS (1), AR (3)
Polysiphonia morrowii H8 NZ (1)
Polysiphonia morrowii H9 AR (1)
Polysiphonia morrowii H10 AR (1)
Polysiphonia morrowii H11 FR (3)
Polysiphonia morrowii H12 KO (1)
Polysiphonia morrowii H13 AR (1)
Polysiphonia stricta
Polysiphonia pacifica
Polysiphonia ulleungensis
Polysiphonia delicata H1 VIC (2)
Polysiphonia delicata H2 TAS (8), SP (2)
Polysiphonia radiata
Polysiphonia dokdoensis
Polysiphonia donghaeya
Polysiphonia kapraunii
Polysiphonia atlantica NC
Polysiphonia macrocarpa
Polysiphonia namibiensis
Lophosiphonia simplicissima
Lophosiphonia obscura
Lophosiphonia teges
Epizonaria prostrata
0.04

◀ **Fig. 1** Phylogenetic tree estimated with ML analysis of *rbc*L sequences. Values at nodes indicate bootstrap support (BP) (only shown if ≥ 80). Species and haplotypes found in Australia are in boldface. The different haplotypes for each species are numbered (H1–13) and numbers in parentheses indicate the number of sequences available from each country or region. Codes for countries/regions: ANA, Atlantic North America; AR, Argentina; BI, British Isles; CA, California; CH, Chile; FR, France; JA, Japan; KO, Korea; NZ, New Zealand; SP, Spain; TAS, Tasmania; VIC, Victoria; WA, Western Australia

(Maggs and Hommersand 1993; Adams 1991; Womersley 2003; as *Polysiphonia*).

Melanothamnus japonicus (Harvey) Díaz-Tapia & Maggs (Fig. 3)

Homotypic synonyms: *Polysiphonia japonica* Harvey; *Neosiphonia japonica* (Harvey) M.-S.Kim & I.K.Lee.

Other currently accepted species in the *M. japonicus/harveyi* complex include *M. akkeshiensis* (Segi) A.M.Saunders & G.W.Saunders, *M. flavimarinus* (Kim & Lee) Díaz-Tapia & Maggs, *M. harveyi* (Bailey) Díaz-Tapia & Maggs, *M. harlandii* (Harvey) Díaz-Tapia & Maggs and *M. decumbens* (T.Segi) Díaz-Tapia & Maggs. If they would be considered taxonomic synonyms, *M. harveyi* would predate other names.

Description: Plants predominantly erect, forming dense tufts 2–2.5 cm high, the axes much-branched (Fig. 2a), attached by short prostrate axes or dense masses of rhizoids that develop proximally. Anchoring rhizoids cut off from the pericentral cells. Erect axes with four pericentral cells, ecorticate or corticate basally, growing from rounded apical cells, with segments 90–350 μm in diameter and 0.67–0.86 *L*/*D* (Fig. 2b). Main axes irregularly or pseudodichotomously branched, sometimes at wide angles and bearing laterals in an irregularly spiral pattern, the axes usually densely branched to four or more orders (Fig. 2a, c). Branches replacing trichoblasts. Trichoblasts abundant, borne on every segment in a one-fourth spiral (Fig. 2b, d), up to three times branched, composed of uninucleate cells and leaving conspicuous scar cells when shed. Plastids elongate to ribbon-like or convoluted, lying only on radial walls of pericentral cells so that the outer walls appear transparent (Fig. 2e). Plants dioecious. Cystocarps globular (Fig. 2f), 250–490 μm high and 200–400 μm in diameter; carposporangia clavate.

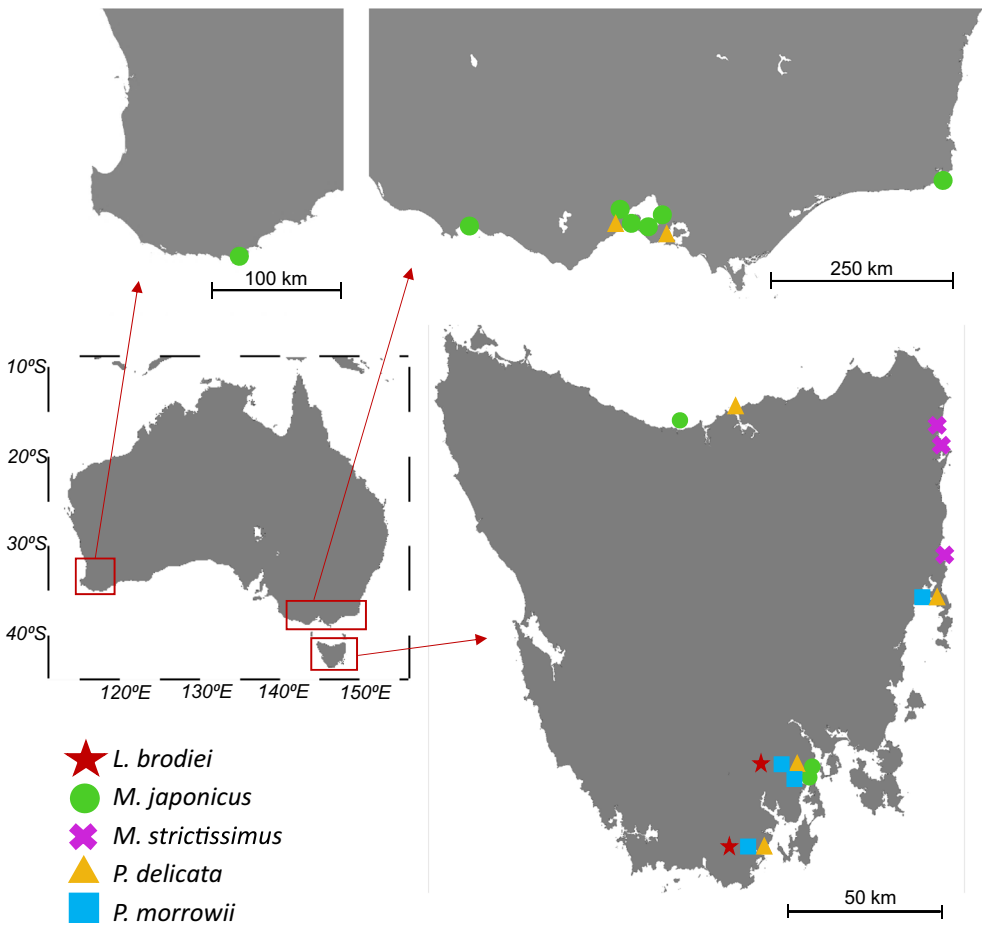


Fig. 2 Distribution of *Leptosiphonia brodiei*, *Melanothamnus japonicus*, *M. strictissimus*, *Polysiphonia delicata* and *P. morrowii* in Australia

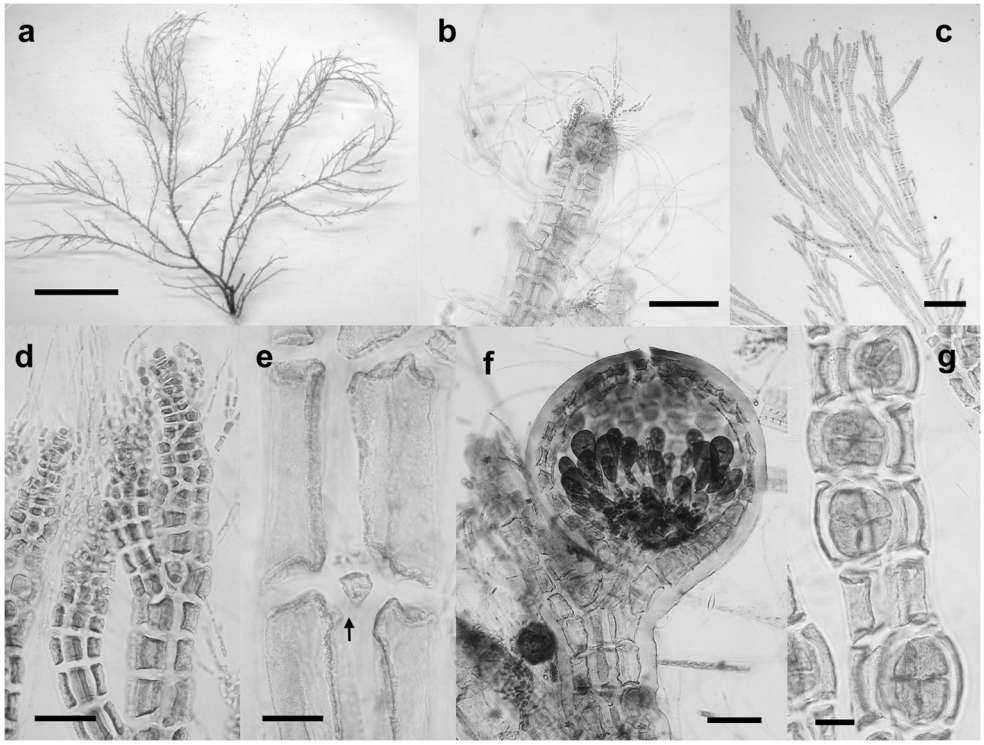


Fig. 3 *Melanothamnus japonicus*. **a** Habit. **b** Apical part of an erect axis with abundant trichoblasts. **c** Apical part of an erect axis with abundant branches. **d** Apex of an erect axis, bearing trichoblasts on every segment. **e** Pericentral cells with convolute plastids lying only on radial cell walls, and a scar cell of a trichoblast (arrow). **f** Cystocarp. **g** Tetrasporangia in spiral series. Scale bars: **a** 1 cm; **b** 200 μm; **c** 700 μm; **d f** 100 μm; **e**, **g** 50 μm

Tetrasporangia formed in the last three orders of branching, in spiral series, ellipsoid when mature, 90–150 μm long × 60–80 μm wide (Fig. 2g).

Habitat and distribution in Australia: *Melanothamnus japonicus* was collected in Western Australia (one site), in the southwestern coast in Tasmania (three sites) and in several sites in Victoria where it was particularly frequent in Port Phillip Bay (Fig. 2). It was abundantly found growing on intertidal rocks, epiphytically on a variety of intertidal host species (*Codium* sp., *Sargassum* sp., seagrasses), as well as on human-made substrata (pontoons or jetty piles) up to 0.5 m depth.

Remarks: The combination of morphological characters observed in *Melanothamnus japonicus* from Australia (thalli erect, rhizoids cut off from the pericentral cells, four pericentral cells with segments over 300 μm in diameter and longer than its width, axes ecorticate and longer than 2 cm, branches replacing trichoblasts and absence of multicellular propagules) differs from most species previously recorded in the study area (Womersley 2003). *Polysiphonia succulenta* Harvey is the only Australian species that also has these characters, but it can be distinguished because it is usually grey in colour and composed of conspicuously swollen cells, whereas *M. japonicus* is brownish-red with less swollen cells (Womersley 2003; Nam and Kang 2012; PD pers. obs.). The observed morphological characters of *M. japonicus* in Australia agree with previous descriptions of this species in eastern Asia (Nam and Kang 2012, as *Neosiphonia japonica*). Moreover, a majority of newly determined sequences for Australian specimens were identical to two haplotypes assigned to *M. japonicus* from Asia, New Zealand and Europe. Molecular and morphological evidence thus support the identification of the Australian specimens as *M. japonicus*. The recognition of different species in the clade here referred to as *M. japonicus/harveyi* complex has varied among authors (McIvor et al. 2001, as *Polysiphonia*; Savoie and Saunders 2015, as *Neosiphonia*). Therefore, the species here studied should be assigned to *M. harveyi* if the complex is considered a single species (McIvor et al. 2001) or to *M. japonicus* if six species are recognized in the complex (Savoie and Saunders 2015). We have recorded this species in Australia as *M. japonicus* following the current taxonomic treatment in AlgaeBase (Guiry and Guiry, 2019).

The absence of *Melanothamnus japonicus* in previous Australian floristic accounts (Womersley 1979, 2003), together with its documented history of introductions in several temperate locations including New Zealand, Atlantic and Pacific North America, Atlantic Spain and the Mediterranean Sea (Savoie and Saunders 2015; Wolf et al. 2018), indicates that it is likely to have been introduced in Australia as well. This agrees with conclusions of previous molecular studies of the *M. harveyi/japonicus* complex that included specimens collected in 2010 from a site in Tasmania (Tinderbox) and one in Western Australia (Albany) (Savoie and Saunders 2015). Moreover, a sequence of *M. japonicus* from a site in Victoria was available in GenBank (Díaz-Tapia et al. 2017b, as *M. harveyi*). The results of our study confirm the presence of this species in the previously explored sites in Tasmania and

Western Australia in 2010 (Savoie and Saunders 2015) after 5 and 7 years, respectively, evidencing well-established populations in these sites. Moreover, our study showed that *M. japonicus* is also present in at least other two sites in southeastern and northern Tasmania and that its distribution covers much of the Victorian coast, being particularly frequent in Port Phillip Bay (Fig. 3).

Melanothamnus strictissimus (J.D.Hooker & Harvey) Díaz-Tapia & Maggs (Fig. 4)

Homotypic synonyms: *Polysiphonia strictissima* J.D.Hooker & Harvey.

Description: Plants predominantly erect, forming dense tufts 1.5–3 (−7) cm high, with abundantly branched axes (Fig. 4a) and attached by short prostrate axes or a dense mass of rhizoids that develop at basal parts of thalli. Rhizoids cut off from the pericentral cells (Fig. 4b). Axes with four pericentral cells, corticate at basal parts, growing from rounded apical cells, with segments 90–350 μm in diameter and 0.5–0.9 *L*/*D*. Main axes irregularly or pseudodichotomously branched, bearing laterals in an irregularly spiral pattern, usually densely branched to four or more orders. Branches replacing trichoblasts. Trichoblasts abundant, borne on every segment in a one-fourth spiral, branched up to three times (Fig. 4c), composed of uninucleate cells, deciduous and leaving conspicuous scar cells when shed. Plastids elongate to ribbon-like or convoluted, lying only on radial walls of pericentral cells so the outer walls appear transparent. Plants dioecious. Spermatangial branches occupying one branch of a trichoblast, 100–300 μm long and 30–150 μm in diameter, cylindrical (Fig. 4e), with 1–2 sterile apical cells when mature. Cystocarps globular, 100–600 μm high and 90–600 μm in diameter (Fig. 4f); carposporangia clavate. Tetrasporangia in spiral series, ellipsoid when mature, 60–90 μm long × 50–95 μm wide (Fig. 4g).

Habitat and distribution in Australia: *Melanothamnus strictissimus* was collected from four sites from the northern and northwestern coasts of Tasmania (Fig. 2). It was found growing abundantly and mostly epiphytically on intertidal turf-forming species from sand-covered rocks.

Remarks: *Melanothamnus strictissimus* is morphologically indistinguishable from *M. japonicus*, so much so that DNA sequences are needed for separating this pair of sister species. In fact, *M. japonicus* in New Zealand was designated as a cryptic introduced species because of its resemblance to the native species *M. strictissimus* (McIvor et al. 2001). As is true of *M. japonicus*, *M. strictissimus* differs from any other species previously recorded in Australia (Womersley 2003; see remarks for *M. japonicus*), although specimens from Australia match previous descriptions for the species in New Zealand, its type locality (Adams 1991; Nelson 2013; as *Polysiphonia*). Furthermore, *rbc*L sequences of Tasmanian specimens were identical to one haplotype of *M. strictissimus* from New

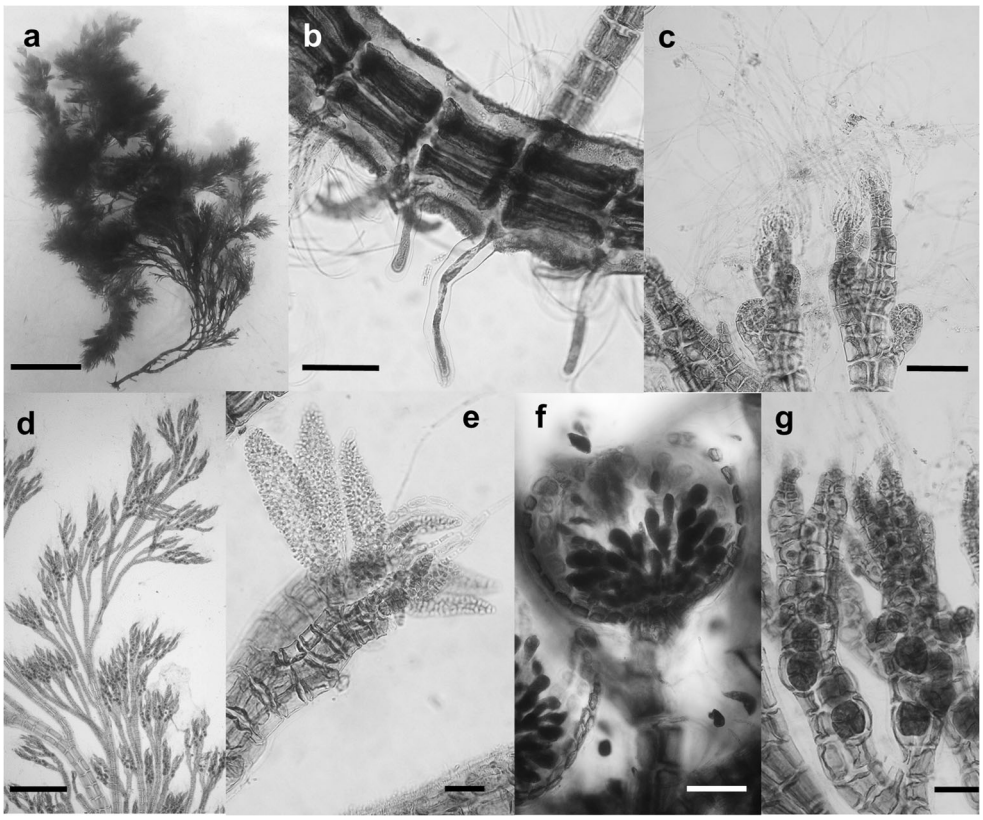


Fig. 4 *Melanothamnus strictissimus*. **a** Habit. **b** Rhizoids cut off from the pericentral cells. **c** Apex of erect axes with abundant trichoblasts. **d** Apical part of an erect axis with abundant branches. **e** Spermatangial branches. **f** Cystocarp. **g** Tetrasporangia in spiral series. Scale bars: **a** 1 cm; **b**, **e**, **g** 100 μm; **c** 150 μm; **d** 1 mm; **f** 200 μm

Zealand. Therefore, molecular and morphological data strongly support the presence of *M. strictissimus* in Tasmania, the first record of this species outside New Zealand (Adams 1991; Nelson 2013). Considering the absence of this species in previous floristic accounts from Tasmania (Womersley 1979, 2003) and its presence in several sites of the northeastern coast that are up to 65 km apart, the evidence suggest that it is most probably a recently introduced species in Australia. It is not entirely impossible that it is a native that was overlooked in the past in Australia, as the distribution of several red algae includes both New Zealand and Tasmania (e.g. Womersley 2003). Based on our data, it is not possible to ascertain whether it is native or introduced, so we propose that *M. strictissimus* should be considered a cryptogenic species in Australia.

It is interesting that both *Melanothamnus japonicus* and *M. strictissimus* were locally abundant in Tasmania, but with complementary distributions (Fig. 2), a phenomenon that could be the result of differential patterns of dispersal of propagules of these introduced species across Tasmania. Alternatively, their distribution could be the result of competitive exclusion between both species (i.e. species competing for the same limiting resource cannot coexist; Hardin 1960). *Melanothamnus strictissimus* and *M. japonicus* are closely related, morphologically indistinguishable and share the same habitat (mostly epiphytic on a variety of intertidal seaweeds). Their competition for the same ecological niche might thus impede their coexistence. The prevalence of one or the other species could be explained by the chance factor of colonization timing, so that the first colonizer would occupy the ecological niche and somehow prevent the successful settlement of the second species. Alternatively, sites where each one of the species was found slightly differ in wave exposure, suggesting that *M. strictissimus* may be more competitive in sites with higher levels of wave exposure, whereas *M. japonicus* might be restricted to more sheltered conditions. Ecological interactions between native and introduced species have received considerable attention, and examples of competitive exclusion of native species are provided in several studies (Casas et al. 2004; Scheibling and Gagnon 2006). The potential role of competitive exclusion in shaping the abundance and distribution of multiple introduced species has been less studied (Lohrer and Whitlatch 2002). Further work of a more ecological focus is needed to better understand interactions between *M. japonicus* and *M. strictissimus* in Tasmania.

Polysiphonia delicata Díaz-Tapia (Fig. 5)

Description: Thalli forming discrete turfs 1 (−7) cm high (Fig. 5a), initially organized radially but becoming decumbent and dorsiventral when developing rhizoids in basal parts that form extensive prostrate systems (Fig. 5b). Axes ecorticate, with four pericentral cells. Prostrate axes bearing unicellular rhizoids in open connection with the pericentral cells (Fig. 5c). Erect axes 15–75 μm in diameter, composed of segments 1.3–2.3 *L*/*D*. Trichoblasts sparse, the scar cells spirally arranged every two to three segments. Branches arising independent of trichoblasts. Gametophytes dioecious. Spermatangial branches borne on suprabasal cells of modified trichoblasts and replacing them, cylindrical with a sterile apical filament of four to six cells, 200–425 μm long and 50–25 μm in diameter (Fig. 5d). Mature cystocarps ovoid to round, 100–240 μm high and 100–200 μm in diameter (Fig. 5e); carposporangia clavate. Tetrasporangia in lateral branches forming straight series, ellipsoid, 5–25 μm in diameter (Fig. 5f).

Habitat and distribution in Australia: *Polysiphonia delicata* was previously recorded only in Victoria (Díaz-Tapia et al. 2017a), but in the present study it was also collected in four sites from the northern and southwestern coasts of Tasmania (Fig. 2) where it grew on human-made substrata (jetty piles, pontoons) as well as on intertidal rocks or as an epiphyte. It was rare in all of the studied sites.

Remarks: Morphological observations agree with the original description of *Polysiphonia delicata* and differ from other recognized species in Australia (Díaz-Tapia et al. 2017a). Newly determined *rbc*L sequences were identical to one of the previously known haplotypes of this species from its type locality in Spain. Therefore, the newly sequenced specimens can be confidently assigned to *P. delicata*. It was recently described as a new cryptogenic species (i.e. its native or introduced origin is uncertain), after observations from Victoria (Australia) and northwestern Spain (Díaz-Tapia et al. 2017a). Its occurrence in Tasmania expands its range in Australia, and like previous records of the species, most specimens in Tasmania were collected growing on human-made structures, a type of habitat that often hosts introduced species (Arenas et al. 2006). However, some specimens of *P. delicata* were epiphytes of *Sargassum* sp. or grew on intertidal rocks, suggesting the naturalization of this species is occurring in some Tasmanian locations. One of these specimens was considerably longer (7 cm) than the previous length observed in the species (27 mm) (Díaz-Tapia et al. 2017a).

Polysiphonia morrowii Harvey (Fig. 6)

Description: Thalli forming dense tufts (Fig. 6a) 5–10 (−25) cm high, consisting of interwoven prostrate axes and erect axes spirally branched mostly every four segments (Fig. 6b). Lower axes sometimes bearing series of short reflexed branchlets (Fig. 6c). Axes ecorticate, with four pericentral cells. Plastids discoid. Prostrate axes bearing rhizoids in open connection with the pericentral cells (Fig. 6e). Erect axes growing from acutely pointed apical cells (Fig. 6d), increasing to 60–140 μm in diameter, segments 0.8–2.7 *L*/*D*. Trichoblasts absent. Plants dioecious. Cystocarps urceolate, 400–600 μm

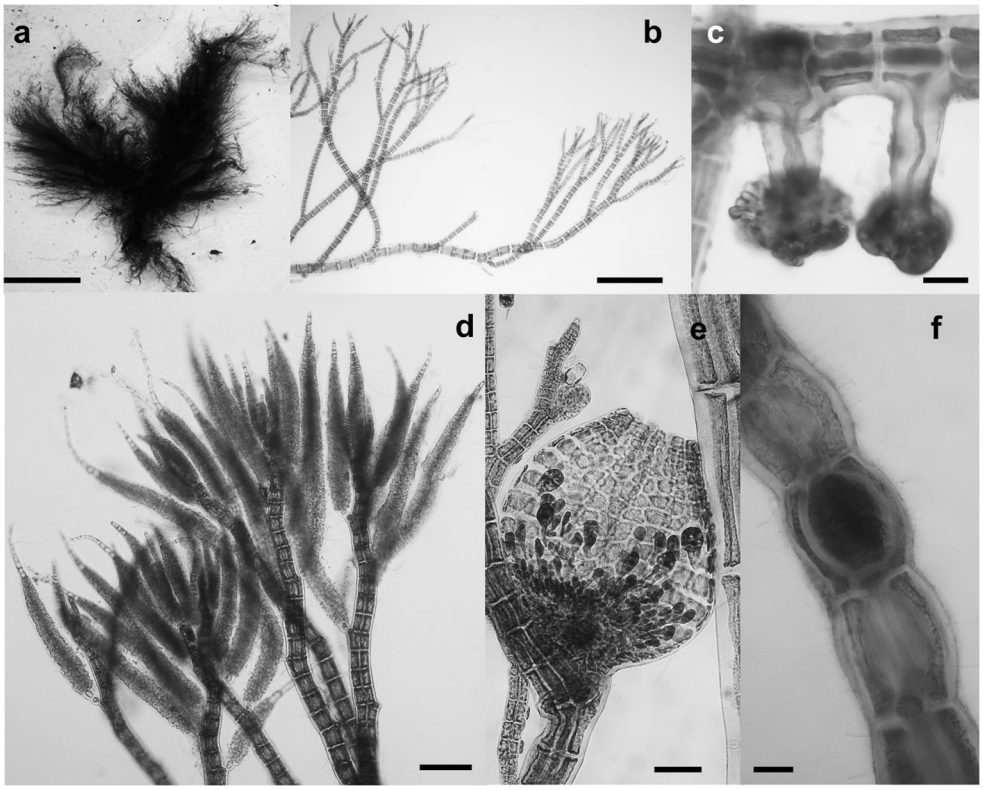


Fig. 5 *Polysiphonia delicata*. **a** Turf. **b** Habit. **c** Rhizoids in open connection with the pericentral cells. **d** Spermatangial branches with an apical filament of sterile cells. **e** Cystocarp. **f** Tetrasporangium. Scale bars: **a** 2 cm; **b** 400 μm; **c**, **e**–**f** 50 μm; **d** 10 μm

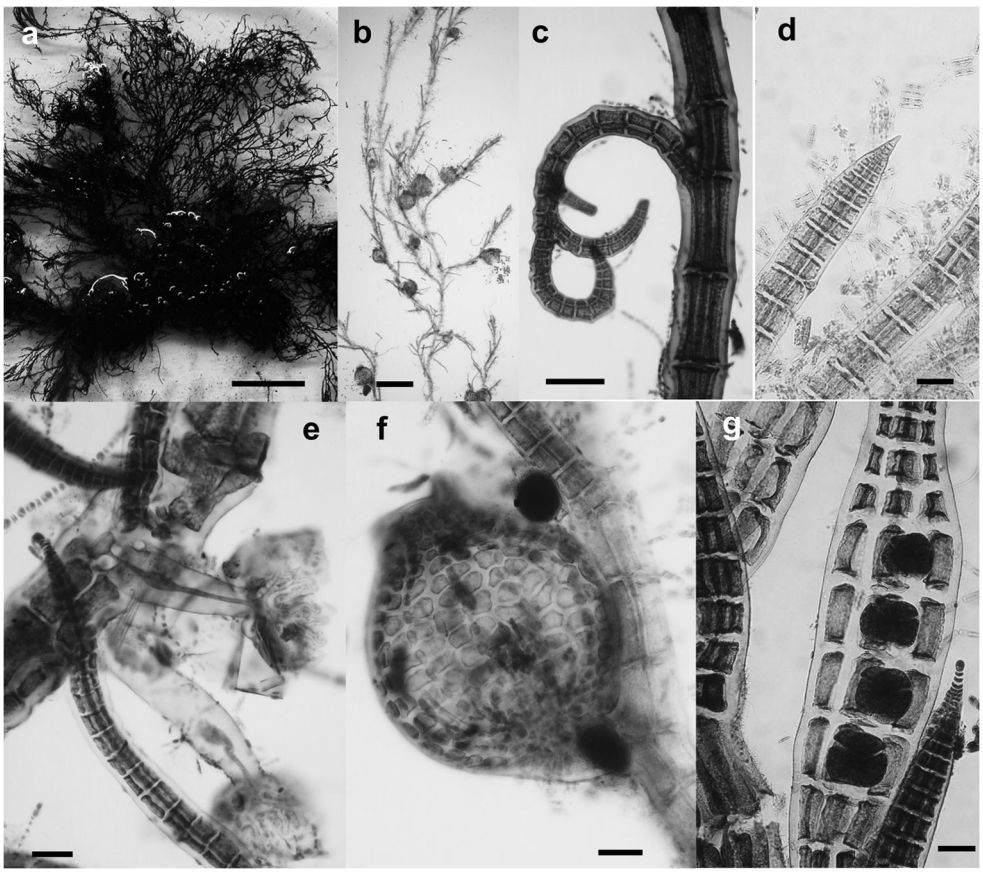


Fig. 6 *Polysiphonia morrowii*. **a** Turf. **b** Erect axes. **c** Basal incurved lateral branches. **d** Apices of branches with pointed apical cells. **e** Rhizoids in open connection with the pericentral cells. **f** Urceolate cystocarp. **g** Tetrasporangia in straight series. Scale bars: **a** 1 cm; **b** 1 mm; **c** 200 μm; **d**–**g** 50 μm

high and 250–450 μm in diameter (Fig. 6f). Tetrasporangia borne in last 2–3 branching orders in straight series, ellipsoid, 55–70 μm in diameter (Fig. 6g).

Habitat and distribution in Australia: *Polysiphonia morrowii* was collected in four sites from the western coast of Tasmania (Fig. 2), where it was found growing abundantly on intertidal rocks and in pools.

Remarks: Molecular data show that the two haplotypes of *Polysiphonia morrowii* from Australia are identical to some of those of this species from other regions, including Japan, its type locality. Accordingly, we have identified the Australian specimens as *P. morrowii*. The combination of its morphological characters (thalli > 2 cm, ecorticate axes with four pericentral cells, rhizoids in open connection with the pericentral cells, trichoblasts absent and the apical cells sharply pointed) differs from most species of the genus previously recorded in Australia (Womersley 2003). *Polysiphonia senticulosa* is the only species with these characters, which has been recorded as an adventive species in Victorian harbours (Womersley 2003). The distinction between *P. senticulosa* Harvey (type locality in Washington state, USA) and *P. morrowii* is unclear and has been much discussed (e.g. Nelson and Maggs 1996; D'Archino et al. 2013; and references therein). *Polysiphonia senticulosa* was recorded as an introduced species in Europe, Australia and New Zealand between the late 1960s and the 1990s based solely on morphological characters (Maggs and Stegenga 1998; Nelson 1999; Womersley 2003). More recently, *P. morrowii* was recorded for the first time as introduced in the Mediterranean Sea, again based on its morphology (Curiel et al. 2002). Subsequently, it has been recorded in France, Chile, Canada, Argentina and New Zealand using morphological and molecular evidence that included sequences of *P. morrowii* from its type locality in Asia (Kim et al. 2004; Geoffroy et al. 2012; D'Archino et al., 2013; Croce and Parodi 2014; Savoie and Saunders 2019). By contrast, molecular data of *P. senticulosa* from Washington are not available, and whether these taxa represent different or a single species needs reassessment. Interestingly, we did not find *P. senticulosa* or *P. morrowii* in our surveys in Port Phillip Bay (Victoria), where the former was found during the late 1960s and 1970s, suggesting that this population has apparently been extirpated or at least largely reduced to the point where the species is not easily detectable. Conversely, *P. morrowii* was found for the first time in the eastern Tasmania in 2017. Considering its absence in Australia in previous floristic accounts despite being morphologically distinct from native species, and that it has been considered introduced in several regions worldwide, it should be included on the list of introduced species in Australia.

General discussion

Our extensive survey of Australian Rhodomelaceae is based on DNA barcodes and has resulted in several new insights into the occurrence and distribution of species likely introduced to this region. Two species, *Polysiphonia morrowii* and *Melanothamnus strictissimus*, are recorded for the first time in Australia, primarily in Tasmania, and we conclude that they are introduced and cryptogenic, respectively. We have expanded the range of the cryptogenic species *P. delicata* in Australia, as it has now been detected in Tasmania following its earlier record in Victoria in 2014 (Díaz-Tapia et al. 2017a). The morpho-anatomical identification of *P. brodiei* was confirmed with molecular data and our results suggest that its distribution appears to have now largely contracted to Tasmania (Womersley 2003). Similarly, *P. senticulosa*, which was most recently recorded in Victoria 43 years ago (Womersley 2003), was not detected in our surveys in that state or in South Australia. Conversely, the distribution of the introduced *M. japonicus* in Australia is wider than previously reported, as it now extends to Western Australia as well as to Tasmania and Victoria. This makes *M. japonicus* the most widespread introduced rhodomelacean in Australia, as other non-native species of this family are restricted to just one or two states (Womersley 2003).

The most likely introduction and spread vectors for the species studied here, as for most seaweeds, are aquaculture activities and shipping (Williams and Smith 2007). Unsurprisingly, the introduced species that we report were most frequently found growing on pontoons in marinas, in piers or in sites close to harbours or aquaculture facilities. At the same time, these species have been naturalized in Australia and all of them were also found in natural habitats. Significantly, the frequency of introduced species was considerably higher in Tasmania (56% of the explored sites) than that in other Australian regions (4.5% and 12.2% of the explored sites in Western Australia and Victoria, respectively). Among the five surveyed states in Australia, Tasmania accounts for the largest aquaculture production (Mobsby and Koduah 2017), which might have contributed to the increased spread of non-native species propagules compared with that in states where aquaculture intensity is lower. Also, the importation of mollusc livestock for aquaculture in the past might have acted as the introduction vector for some species, as it presumably has done for other marine organisms (Gregory et al. 2012). However, our surveys in South Australia have failed to detect any of the introduced rhodomelaceans studied here, despite aquaculture production in that state being, like in Tasmania, among the highest in Australia (Mobsby and Koduah 2017). This suggests that environmental conditions in Tasmania may facilitate the establishment of the studied introduced species. Sea-surface temperatures are higher and persist longer in South Australia compared with those in Tasmania (Foster et al. 2014), and differences in the frequency of introduced rhodomelacean species in both states might be related to this environmental factor.

The discovery of *Polysiphonia morrowii* and *Melanothamnus japonicus* in Australia, as well as the presence of the primarily European *Leptosiphonia brodiei*, is not

surprising, as they have been recognized as introduced species for more than a decade and, since then, have been detected in several other countries (Maggs and Hommersand 1993; Savoie and Saunders 2015; Geoffroy et al. 2016; Wolf et al. 2018). This adds these species to the list of certainly introduced seaweeds that have been discovered in a range of widely separated localities within relatively short timeframes, such as *Undaria pinnatifida*, *Gracilaria vermiculophylla* and *Codium fragile* subsp. *fragile* (Epstein and Smale 2017; Krueger-Hadfield et al. 2016; Verbruggen et al. 2017). Only a few of these species are morphologically distinctive or form conspicuous populations. By contrast, most introduced seaweeds are inconspicuous or cryptic and are thus easy to overlook. This is certainly the case for *P. delicata*, which forms small turfs on artificial substrata or intertidal rocks, and *M. strictissimus*, which is morphologically indistinguishable from *M. japonicus*. The detection of these (and many other) introduced seaweeds requires identification by expert taxonomists and the use of both reliable morphological and molecular data. Recent surveys of the family Rhodomelaceae in Australia have led to the discovery of five new introduced species over a time span of less than 5 years (Savoie and Saunders 2015; Díaz-Tapia et al. 2017a, 2018; this work). This contrasts with the previous recognition of only three introduced species in the most species-rich red algal family in Australia (Womersley 2003). Most probably, these five species were introduced in Australia long before first being recorded, but have only come to attention as the true diversity of this taxonomic group has been revealed using molecular approaches. Our results thus further highlight the importance of conducting diversity surveys by expert taxonomists with the aim of improving our knowledge of native species and the detection of new introductions (Hutchings 2013, 2018). A further increase in the rate of discovery of both native and introduced algal species could be achieved through metabarcoding (Oliveira et al. 2018). We consider this approach very promising for mixed algal turfs, as the small, cryptic species in this habitat are very labour-intensive targets for traditional biodiversity surveys like the one we carried out here. For such systems, metabarcoding could provide a less laborious first-pass molecular screening of the species composition before traditional examination of those localities that the metabarcodes indicate to contain new biodiversity.

The distinction between introduced and invasive species is not always straightforward, as the latter are often defined as non-native species that become excessively abundant and cause negative ecological and/or economic harm outcomes (Williams and Smith 2007). Three of the species reported in this study (*Melanothamnus japonicus*, *M. strictissimus* and *Polysiphonia morrowii*) were particularly abundant in the sites where they were found, and accordingly, further studies are needed to assess their ability to spread and their potential negative impacts on native marine assemblages in order to determine whether they should be considered invasive and in need of control.

Acknowledgements We thank Joana Costa, Kyatt Dixon, Margaret Brookes and Guadalupe Bribiesca-Contreras and the Parks Victoria and Bush Blitz teams for assistance in the field.

Funding information P.D.T. acknowledges support from the postdoctoral program "Axudas de apoio á etapa de formación posdoutoral, Xunta de Galicia" (ED481D2017/011). C.P.C. and P.D.T. received funding from Xunta de Galicia within the program "Axudas para a consolidación e estruturación de unidades de investigación competitivas do SUG" (grants GPC2015/025, ED431D 2017/20, ED431B 2018/49). Funding for the field and molecular work in eastern Victoria, including participation in a Bush Blitz expedition, a Bush Blitz Strategic Taxonomy Grant (TTC216-03) and a National Taxonomy Research Grant (RFL213-08), was provided by the Australian Biological Resources Study. Sampling in Western Australia and Tasmania was made possible through funding from the Holsworth Wildlife Research Endowment.

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