Research Article

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New records of marine macroalgae for the Azores

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Abstract: The present study adds 19 species (15 Rhodophyta, one Chlorophyta and three Ochrophyta) to the Azorean marine macroalgal flora, increasing the current total of species recorded in this region to 521 (349 Rhodophyta, 76 Chlorophyta and 96 Ochrophyta), and showing that this isolated island group supports a relatively rich marine macroalgal flora. Some species fall within their known overall distributional range, whereas other found here represent a northern or southern extension to their known distribution in the Atlantic. Three species (*Antithamnionella elegans*, *Gymnophycus hapsiphorus* and *Scytosiphon dotyi*) are probable introductions to the Azores, whereas *Melanothamnus pseudoforcipatus* has an uncertain status. Six of the newly reported species were found as components of the intertidal algal turf samples, which justifies the need for continuing to examine turf samples as new discoveries can be anticipated.

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Keywords: algal turfs; biogeography; introduced species; Macaronesia; range expansion.

1 Introduction

The distribution pattern of species within and across ecosystems is determined by environmental factors (Clarke 2003) and, in the case of marine macroalgae, their biogeographical ranges are mainly determined by global temperature gradients (Lüning 1990). Well-documented changes in species abundance and distribution have increased during recent years in response to the Earth's warming and other human-mediated shifts in ecosystem structure (e.g. Barrientos et al. 2020; Lima et al. 2007; Rindi et al. 2020). Regarding macroalgae, many non-indigenous species (NIS) have been found out of their distributional range worldwide (Piñeiro-Corbeira et al. 2020; Thomsen et al. 2016; Williams and Smith 2007) and a tropicalization process has been described in temperate regions associated with the arrival of warm-water species in recent years (Osland et al. 2021; Ribeiro et al. 2019; Vergés et al. 2014).

The mid-Atlantic Ocean Azores archipelago (approximately –24°59′17″ to –31°17′42″ longitude and 36°53′2″ to 39°44′13″ latitude, Figure 1), lying between European and American coasts, has a significant role in present and past maritime traffic connections (Cardigos et al. 2006). Nearly 1200 km west of Europe, the nearest mainland, the archipelago is composed of nine islands, the Formigas islets and nearby sublittoral banks and seamounts, which spread over 500 km in a WNW–ESE direction and are organized in three groups (eastern, central, and western). The tidal range is small (<2 m, Hidrográfico 1981), and the coastline is mainly composed of irregular compact, bedrock platforms, alternating with boulder and cobble locations (Wallenstein et al. 2009a). A deep-sea floor (500–1000 m depth) occurs within about 5 km offshore (Neto et al. 2005).

The Azorean intertidal and shallow subtidal communities are primarily dominated by macroalgae. The intertidal mainly exhibits a mosaic and/or zoned distribution pattern and has a predominance of algal turfs that cover the rocks as a carpet (Wallenstein et al. 2009b). This type of growth occurs in temperate and subtropical regions in habitats subjected to a wide variety of natural stresses such

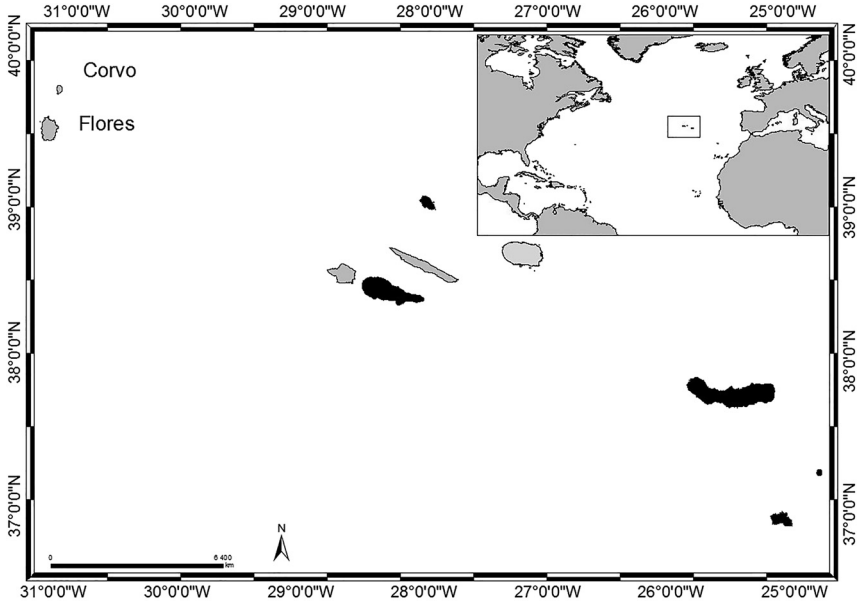

Figure 1: Geographic location of the Azores archipelago in the Atlantic Ocean with the surveyed islands in black.

as desiccation, wave-exposure, or high sediment loads (see Díaz-Tapia and Bárbara 2013, 2014 and references therein), and is also common in the intertidal assemblages of the other Macaronesian archipelagos (Tuya and Haroun 2006). Subtidal communities are mainly composed of frondose macrophytes (Neto 2001; Wallenstein et al. 2009a).

Despite the great distance of the archipelago from potential donor coastal areas in Europe, Africa and America, endemism in the Azores is low, and a locally distinct algal flora is absent (Neto et al. 2021a). Biogeographically, the Azores marine macroalgal flora has a mixed nature, with species shared with other Macaronesian archipelagos, North Africa, the Mediterranean Sea, Atlantic Europe, and the Americas (Tittley 2003; Tittley and Neto 1995, 2005, 2006; Tuya and Haroun 2009; Wallenstein et al. 2009a), and is second in species richness within the Macaronesian archipelagos after the Canary Islands and followed by Madeira and Cabo Verde (Freitas et al. 2019). According to Freitas et al. (2019), the Lusitanian biogeographical province should be redefined in several ecoregions and the Azores should be recognized as a biogeographical entity on its own, which they named the Azores ecoregion, and separated from the new Webbnesia ecoregion that comprises the archipelagos of Madeira, the Selvages and the Canary Islands.

The study of the Azorean macroalgae goes back over 180 years (Seubert and Hochstetter 1843). Initial taxonomic and biogeographic studies in the area (e.g. Prud'homme van Reine and van den Hoek 1990; Prud'homme van Reine 1998) were followed by research on species biology, ecology, the structure and functioning of intertidal and shallow subtidal communities (Neto et al. 2021a) and the taxonomic revision of herbarium material. Intensive fieldwork at locations not previously studied resulted in the recent publication of a series of checklists for different islands of the archipelago (Neto et al. 2020a–f, 2021a–c, Table 1), which confirm that the Azores host a relatively rich marine macroalgal flora.

Despite this richness, there remain some habitats and locations that were not specifically investigated. Furthermore, the species diversity of algal turfs is still poorly understood. The present study aims to contribute to fill those gaps contributing to a deeper knowledge of the Azorean macroalgal flora.

Table 1: Summary of the macroalgal flora of the Azores with information on the number of taxa per island.

	FOR	SMA	SMG	TER	GRA	SJG	PIX	FAI	FLO	COR
Rhodophyta	39	103	215	73	126	35	142	59	80	22
Chlorophyta	12	30	48	24	31	17	41	16	22	8
Ochrophyta	19	44	64	16	38	10	42	8	26	13
Total	70	177	327	113	195	62	225	83	128	43

FOR, Formigas; SMA, Santa Maria; SMG, São Miguel; TER, Terceira; GRA, Graciosa; SJG, São Jorge; PIX, Pico; FAI, Faial; FLO, Flores; COR, Corvo; Neto et al. 2020a–f, 2021a–c.

2 Materials and methods

The algae referred to in this paper were collected at the Azores archipelago (Figure 1) between 1993 and 2018 during field studies at littoral and sublittoral levels on the islets of Formigas and the islands of Santa Maria, São Miguel, Pico, and Graciosa. Intertidal collections were made at low tide by walking along the shores. Subtidal collections were made by scuba diving around the surveyed area. In each sampling location, whenever an unknown or potentially unrecorded species was found, it was collected manually by scraping and/or manually collecting one or two specimens into previously labelled bags. Moreover, the diversity in algal turfs was studied in detail. The species found in the turfs were morphologically identified and isolated using a dissecting microscope. Material collected was either fixed in 4–5% formalin seawater (later transferred to Kew solution, following Bridsen and Forman 1999) and/or pressed and dried. Part of the material of each species isolated from algal turfs was desiccated in silica gel for molecular studies. Voucher specimens were deposited at the Herbarium Ruy Telles Palhinha (AZB, herbarium of the University of the Azores), based at the Faculty of Sciences and Technology of the University of the Azores or the Herbarium of the University of Santiago de Compostela (SANT).

For morphological and anatomical characterization, when necessary, specimens on microscope slides were stained with aniline blue and permanently mounted using 'Karo'® corn syrup (Best Foods, Englewood Cliffs, USA). The slides included complete specimens or sections that were made by hand using a razor blade. Dried pressed specimens from earlier collections were re-hydrated and prepared for microscopic examination as above.

The whole specimens or slide preparations were observed with the naked eye and using dissecting and compound microscope Zeiss Axio Imager A1, to characterize the diagnosing structures described in the literature and compare with descriptions from other locations. Taxonomically relevant structures were measured using a calibrated micrometre eyepiece. Cell and other microscopic structure measurements, and micrographs were taken using a digital camera (Olympus model C5060, Japan) attached to light microscopes (Olympus model BX50 F, Japan), and also the optical microscope Leica DM4 B with Digital Camera Leica MC 190 HD (Leica, Germany). DNA sequences of the *rbc*L gene of selected species were obtained and assembled following methods specified in Díaz-Tapia et al. (2021) and were deposited in GenBank (see Supplementary Table S1). Sequences were used for molecularly assisted identification initially using BLAST in GenBank (Altschul et al. 1990). Subsequently, newly determined and previously published sequences of related taxa were aligned using Geneious 7.0.6 and uncorrected p-distances were analysed.

3 Results: systematic account, new species records

The new additions listed here, belonging to the Rhodophyta, Chlorophyta (Ulvophyceae) and Ochrophyta (Phaeophyceae), are alphabetically arranged within each phylum, class, order, and family. For each taxon, brief information on the diagnostic features of the Azorean material is provided, followed by data on its habitat and distribution. Illustrations are also given for some species. The systematic arrangement, nomenclature and taxonomic status follow AlgaeBase (Guiry and Guiry 2021).

Nineteen species of macroalgae (15 Rhodophyta, one Chlorophyta and three Ochrophyta) are here described for the first time for the Azores.

Rhodophyta, Florideophyceae, Bonnemaisoniales, Bonnemaisoniaceae

***Bonnemaisonia clavata* Hamel**

Type locality: Marseille (Dixon and Irvine 1977).

Specimens examined: AZB-SMG-94-229, São Miguel, Ponta Delgada, Moaçor, 1994-07-20.

Azorean material description: Thalli erect, up to 11 cm tall, reddish pink in colour, made up of erect cylindrical or slightly compressed axes. Main axes spirally branched, without hooks, from 99 to 375 µm in width and attached by a basal disc. Lateral branches with distichous and opposite arrangement, 167–204 µm in diameter at the base, decreasing rapidly in width towards the tips, where they are 62–74 µm in diameter. Male gametophytes with spermatangia formed in clavate, elongated clusters 500 µm long × 160 µm in diameter.

Habitat: Epilithic on bedrock at 12 m depth.

Distribution: *Bonnemaisonia clavata* was known only from the northeast Atlantic (from British Isles to Portugal), and the Mediterranean Sea (Rodríguez-Prieto et al. 2013). Its occurrence in the Azores extends further south its known distribution in the Atlantic.

Rhodophyta, Florideophyceae, Ceramiales, Callithamniaceae

***Aglaothamnion tripinnatum* (C.Agardh) Feldmann-Mazoyer**

Type locality: Atlantic France (Silva et al. 1996).

Specimens examined: AZB-SMG-18-83, São Miguel, Caloura, porto, 2018-06-01.

Azorean material description: Thalli robust and bright red in colour, 15–50 mm long, consisting of erect axes forming dense pyramidal tufts, attached to the substratum by interwoven rhizoidal filaments (Figure 2A). Main axis tough, enlarging from apical cells towards the base where cells are up to 95 µm long × 145 µm wide. Flaccid branches develop in an alternate distichous arrangement from the main axis and the first order of laterals develops by oblique division of the third cell from the apex. Adaxial branchlets typically curved and arising from the first two cells of lateral branches (Figure 2B), which are up to 75 µm long × 48 µm wide and decrease in size towards the apex. The studied material was vegetative.

Habitat: Epilithic on bedrock at 15 m depth.

Distribution: *Aglaothamnion tripinnatum* is widely distributed in the eastern Atlantic Ocean, the Aegean,

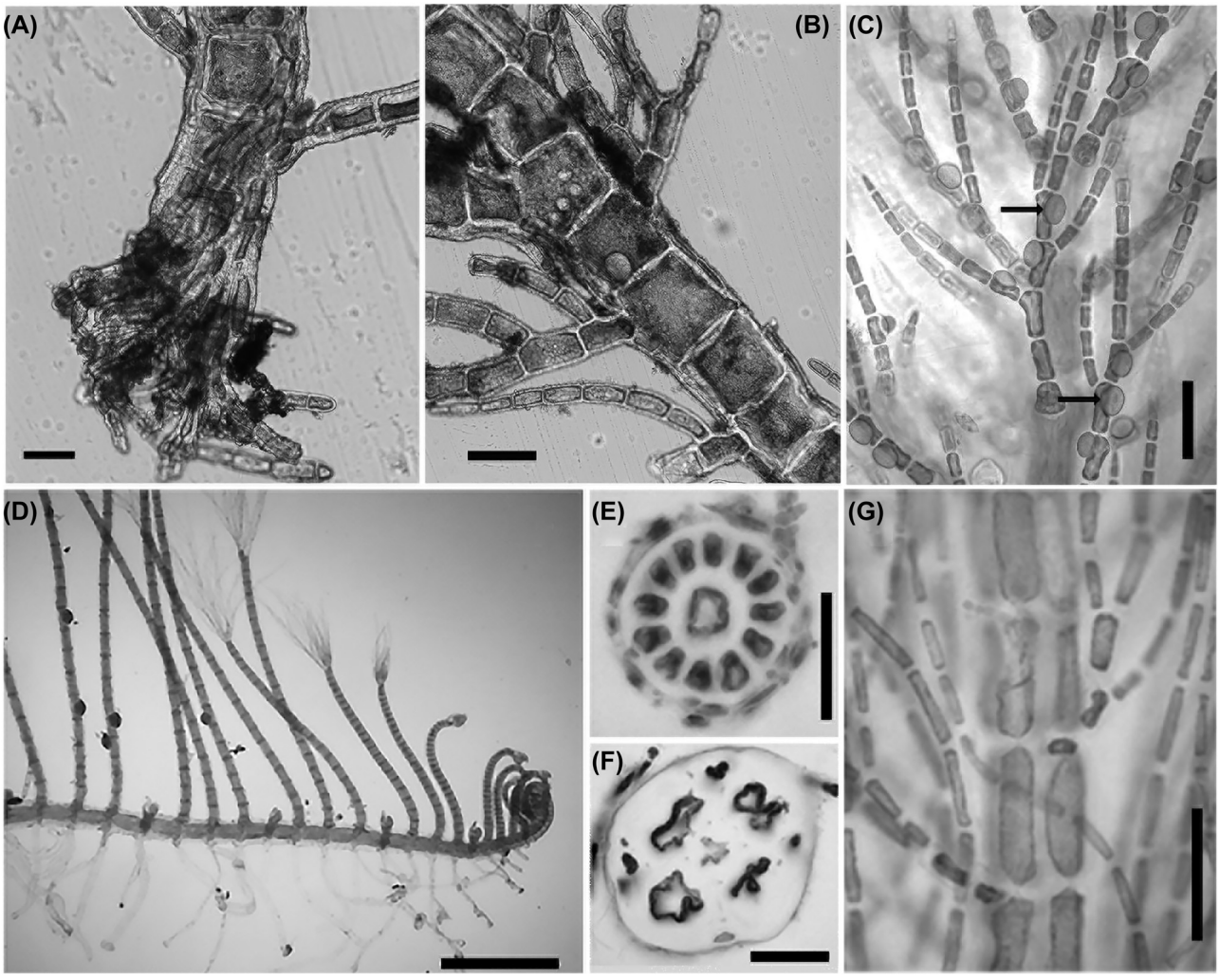

Figure 2: New red algal records from the Azores. (A and B) *Aglaothamnion tripinnatum*: vegetative frond attached by rhizoidal filaments (A, scale bar = 100 µm); adaxial branchlets typically curved arising from the first two cells of lateral branches (B, scale bar = 100 µm). (C) *Antithamnionella elegans*: filaments of vegetative fronds composed of cylindrical cells and with abundant gland cells (arrows) (C, scale bar = 50 µm). (D and E) *Herposiphonia* cf. *tenella*: prostrate axis with rhizoids and erect axes with trichoblasts in the apical parts (D, scale bar = 1 mm); cross section of an axis with 12 pericentral cells (E = scale bar 50 µm). (F and G) *Lophocladia trichoclados*: cross section of an axis with four pericentral cells (F, scale bar = 100 µm) and axis with trichoblasts on every segment in a spiral arrangement (G, scale bar = 150 µm).

Black, Caspian, Arabian and Mediterranean Seas (Guiry and Guiry 2021). Its occurrence in the Azores extends its known western distribution in the Atlantic Ocean.

Rhodophyta, Florideophyceae, Ceramiales, Ceramiaceae
***Antithamnionella elegans* (Berthold) J.H.Price *et* D.M.John**

Type locality: Golfo di Napoli, Italy (Berthold 1882).

Specimens examined: SANT-Algae 33646, São Miguel, Vila Franca do Campo, 2018-04-16.

Azorean material description: Thalli flaccid and pinkish red colour, 10 mm long, consisting of decumbent filaments with extensive prostrate systems that attach to the substratum by rhizoids, and erect filaments. Filaments composed of cylindrical cells, 40–50 µm in diameter. Axial cells bearing three whorl branches that in turn are simple or pseudodichotomously branched (Figure 2C). Gland cells are abundant (Figure 2C). The studied material was vegetative.

Habitat: Permanently submersed dock floats in a marina.

Distribution: *Antithamnionella elegans* has been reported in disjunct tropical and warm-temperate regions, including the Mediterranean, where it is considered introduced

(Verlaque et al. 2015), and the archipelagos of Madeira (Selvages Islets), Cabo Verde and the Canaries (Guiry and Guiry 2021). Its finding in the Azores in the Marina of Vila Franca do Campo suggests that it might have been introduced via hull fouling. Its presence in the Azores extends further north its known distribution in the Atlantic.

Rhodophyta, Florideophyceae, Ceramiales, Rhodomelaceae

***Herposiphonia* cf. *tenella* (C.Agardh) Ambronn**

Type locality: Sicily (Agardh 1828).

Specimens examined: SANT-Algae 33659, São Miguel, Vila Franca do Campo, pontão da Marina, 2018-04-16; SANT-Algae 33634, São Miguel, Rabo de Peixe, Calhetas, 2018-04-13; SANT-Algae 33644, São Miguel, Maia, 2018-04-13; São Miguel, Maia, 2018-04-13; SANT-Algae 33643, São Miguel, Lagoa, 2018-04-14; SANT-Algae 33641, São Miguel, baía de São Roque, 2018-04-14; SANT-Algae 33653, São Miguel, baía de São Roque, 2018-04-14; SANT-Algae 33640, São Miguel, Capelas, 2018-04-16; SANT-Algae 33638, São Miguel, Caloura, 2018-04-16; SANT-Algae 33648, São Miguel, Água de Pau, 2018-04-19.

GenBank accession numbers: OL542678-86.

Azorean material description: Thalli fairly rigid and pink in colour, 2 mm in height, consisting of extensive systems of prostrate axes that attach to the substratum by rhizoids and bear unbranched erect axes (Figure 2D). Prostrate axes exogenously branched on every segment, producing one indeterminate branch every three determinate branches. Young erect axes have trichoblasts in their apical parts (Figure 2D). Rhizoids are cut off from the pericentral cells and terminate in multicellular haptera. Axes, 50–70 μm in diameter, ecorticate, with 10–12 pericentral cells (Figure 2E). The studied material was vegetative.

Habitat: Epilithic or epiphytic on intertidal algal turfs in sand-covered bedrocks.

Distribution: *Herposiphonia tenella* has been widely reported in temperate and tropical regions, including the archipelagos of Madeira, the Canaries and Cabo Verde (Díaz-Tapia et al. 2018). Its occurrence in the Azores fits within its distribution range.

Additional observations: There is evidence that *Herposiphonia tenella* involves an unresolved species complex (Díaz-Tapia et al. 2018). The *rbc*L sequences of Azorean specimens were identical to sequences of one of the species in the complex molecularly confirmed in the Atlantic Iberian Peninsula, the Canary Islands and the Mediterranean. Even if this species complex remains unresolved and the specimens reported here might be potentially assigned to a different species name sometime, *H. tenella* is tentatively reported in the Azores. It clearly differs morphologically from *H. secunda*, the other species of the genus known in the Archipelago, the publication of *rbc*L sequences might contribute to clarify the species complex in the future as well as facilitating the clarification of the correct species name once the complex can be deciphered.

Rhodophyta, Florideophyceae, Ceramiales, Rhodomelaceae

***Lophocladia trichoclados* (C.Agardh) F.Schmitz**

Type locality: Caribbean Sea (Agardh 1828).

Specimens examined: SANT-Algae 33635, São Miguel, Rabo de Peixe, Calhetas, 2018-04-13.

GenBank accession numbers: OL624518.

Azorean material description: Thalli flaccid and delicate, pink in colour, 20 mm long, consisting of erect axes attached to the substratum by a discoid holdfast. Axes with four pericentral cells (Figure 2F), slightly corticated at the apices and densely corticated in the basal parts of the thalli, where they can reach 0.7 mm in diameter. Axes pseudodichotomously branched at irregular intervals, clothed by pigmented and persistent trichoblasts formed on every segment in a spiral arrangement (Figure 2G). The studied material was vegetative.

Habitat: Epilithic on tidepools at the low intertidal.

Distribution: *Lophocladia trichoclados* has a wide distribution, including the archipelagos of Madeira (Salvages Islets), Cabo Verde and the Canaries (Guiry and Guiry 2021). Its occurrence in the Azores fits within its distribution range.

Additional observations: The Azorean DNA sequences of the *rbc*L gene diverged from specimens from the Canary Islands (AF083380) and Florida (AF465819) by 0.95%. This sequence divergence indicates a close similarity of specimens from different Atlantic regions, but further DNA sequences would be required for more reliable comparisons, as the two sequences available in GenBank contain several ambiguous bases. Therefore, the relatively high levels of sequence divergence found with respect to the Azorean specimen might be related to the poor quality of these sequences.

Rhodophyta, Florideophyceae, Ceramiales, Rhodomelaceae

***Lophosiphonia simplicissima* Díaz-Tapia**

Type locality: Niembro, Spain (Díaz-Tapia and Bárbara 2013).

Specimens examined: SANT-Algae 33636, São Miguel, Rabo de Peixe, Calhetas, 2018-04-13; SANT-Algae 33642, São Miguel, baía de São Roque, 2018-04-14.

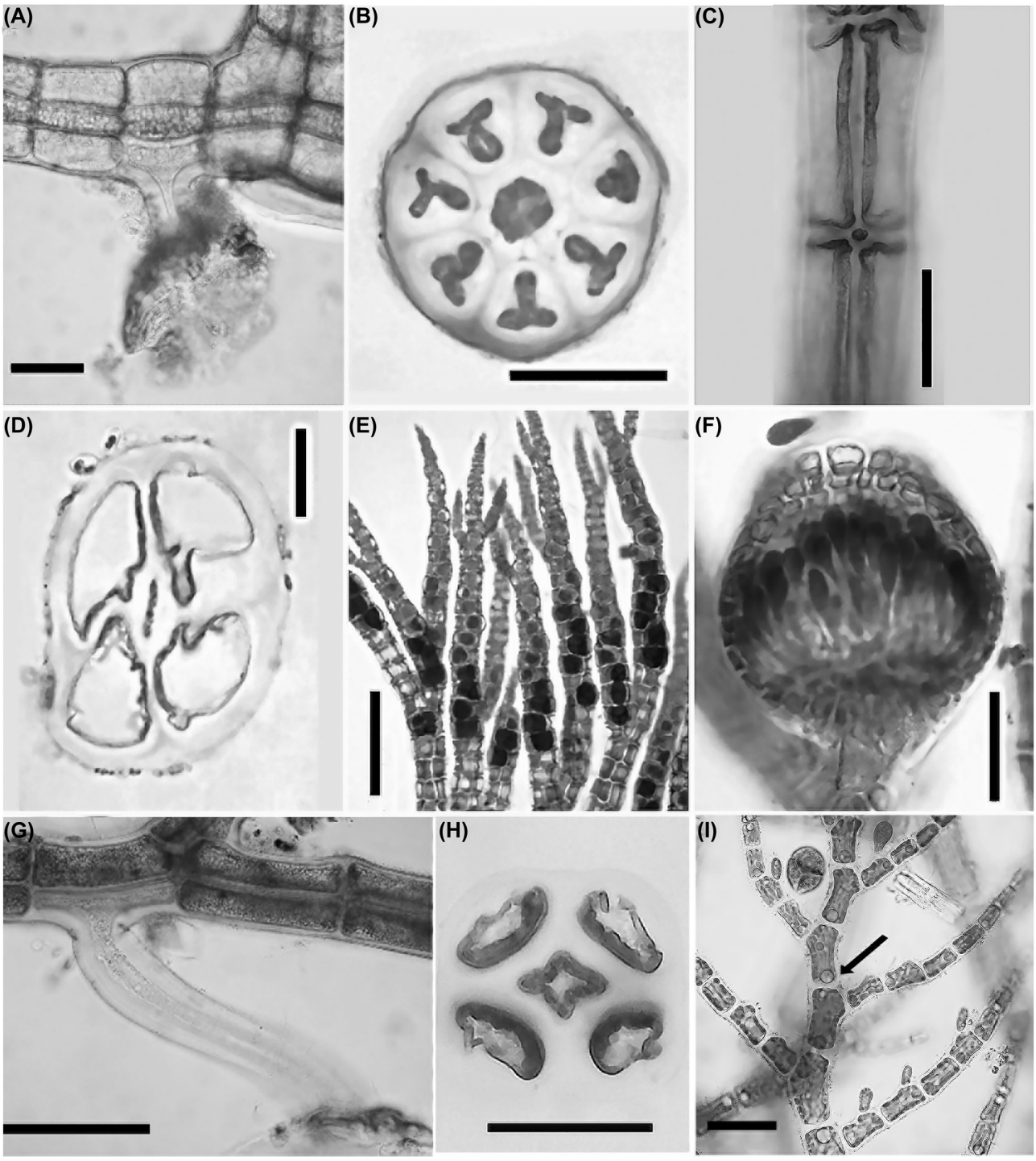

Figure 3: New red algal records from the Azores. (A and B) *Lophosiphonia simplicissima*: unicellular rhizoid in open connection with a pericentral cell (A, scale bar = 50 µm); cross section of an axis with seven pericentral cells (B, scale bar = 50 µm). (C–F) *Melanothamnus pseudoforcipatus*: pericentral cells with plastids only on radial cell walls (C, scale bar = 100 µm); cross section of an axis with four pericentral cells (D, scale bar = 50 µm); apical parts of erect axes with tetrasporangia in compact spiral series (E, scale bar = 300 µm); cystocarp with cells of the ostiole larger than cells below (F, scale bar = 150 µm). (G and H) *Polysiphonia* cf. *villum*: prostrate axis with a rhizoid in open connection with a pericentral cell (G, scale bar = 100 µm); cross section of an axis with four pericentral cells (H, scale bar = 30 µm). (I) *Gymnophycus hapsiphorus*: alternate-distichously branched erect filament with refractive vesicles located near pit-connections (arrow) and a mature tetrasporangium (I, scale bar= 50 µm).

GenBank accession numbers: OL542690-1.
Azorean material description: Thalli fairly rigid and black in colour, 10 mm long, consisting of extensive systems of prostrate axes that attach to the substratum by rhizoids and bear erect axes. Rhizoids unicellular and in open connection with the pericentral cells (Figure 3A). Axes ecorticate, 60–100 μm in diameter, with (6-) 7 pericentral cells (Figure 3B). Erect axes unbranched or scarcely branched endogenously at irregular intervals and occasionally bear spirally arranged trichoblasts at their apices. The studied material was vegetative.
Habitat: Epiphytic on intertidal algal turfs in sand-covered bedrocks.
Distribution: *Lophosiphonia simplicissima* was known only in the Iberian Peninsula (Díaz-Tapia and Bárbara 2013). The two Azorean DNA sequences of the *rbc*L gene were identical to the available sequence from the Iberian Peninsula. Its occurrence in the Azores extends its known western distribution in the Atlantic Ocean.

Rhodophyta, Florideophyceae, Ceramiales, Rhodomelaceae
***Melanothamnus pseudoforcipatus* Díaz-Tapia**
Type locality: Rande, Spain (Díaz-Tapia et al. 2017).
Specimens examined: SANT-Algae 33654-5, São Miguel, baía de São Roque, 2018-04-15; SANT-Algae 33660, São Miguel, Vila Franca do Campo, 2018-04-18.
GenBank accession numbers: OL542687-9.
Azorean material description: Thalli fairly rigid and dark red to brown in colour, 16 mm long, decumbent, consisting of extensive systems of prostrate axes that attach to the substratum by rhizoids and erect axes. Axes with four pericentral cells (Figure 3C and D), ecorticate, and exogenously and pseudodichotomously branched at irregular intervals. Erect axes 200–300 μm in diameter in the basal parts, usually have spirally arranged trichoblasts in their apical parts, one per segment. In vegetative young branches, pseudodichotomous branches give a forcipate aspect to the apices. Rhizoids cut off from the pericentral cells and cells with plastids that lie only on the radial walls (Figure 3C). Tetrasporophytes bear subspherical tetrasporangia in compact spiral series (Figure 3E) at the apical parts of the erect axes. Female gametophytes bear globose cystocarps, with cells of the pericarp surrounding the ostiole larger than cells below (Figure 3F).
Habitat: Intertidal algal turfs in sand-covered bedrocks.
Distribution: *Melanothamnus pseudoforcipatus* was known only from a single site on the northwestern Iberian Peninsula, placed close to aquaculture facilities, which led to qualify the species as cryptogenic (Díaz-Tapia et al. 2017). Whether it is native or introduced in Azores is unknown. Its occurrence in the Azores extends further south its known distribution in the Atlantic.
Additional observations: *Melanothamnus pseudoforcipatus* was found forming tufts on the northwestern Iberian Peninsula and only vegetative specimens have been observed (Díaz-Tapia et al. 2017). The three Azorean DNA sequences of the *rbc*L gene were identical to the available sequence from the Iberian Peninsula. The finding of this species as part of the Azorean algal turfs contrasts with the tufts originally described and provides evidence that its growth form can be variable. Studied material was fertile, and reproductive structures are here described for the first time.

Rhodophyta, Florideophyceae, Ceramiales, Rhodomelaceae
***Polysiphonia* cf. *villum* J.Agardh**
Type locality: Mexico (Agardh 1863).
Specimens examined: SANT-Algae 33650, São Miguel, praia do Pópulo, 2018-04-12.
GenBank accession numbers: OL542692.
Azorean material description: Thalli flaccid and pink in colour, 8 mm long, decumbent, consisting of extensive systems of prostrate axes that attach to the substratum by rhizoids and bear erect axes unbranched or endogenously irregularly branched. Rhizoids in open connection with the pericentral cells (Figure 3G) and erect axes lack trichoblasts. Axes with four pericentral cells (Figure 3H), ecorticate and 50–70 μm in diameter. The studied material was vegetative.
Habitat: Intertidal algal turfs in sand-covered bedrocks.
Distribution: *Polysiphonia villum* has been recorded in disjunct temperate and tropical regions (Díaz-Tapia et al. 2018). Its occurrence in the Azores fits within its distributional range.
Additional observations: Molecular data revealed that *P. villum* is a complex of at least two species, one that has been molecularly characterized in the Caribbean, Brazil and Australia (recorded as *P. villum* or *P. scopulorum var. villum* by Díaz-Tapia et al. 2018, Huisman et al. 2017, Mamoozadeh and Freshwater 2011) and the other in Pacific North America (Savoie and Saunders 2019, recorded as *P. scopulorum* var. *villum*). The three Azorean DNA sequences of the *rbc*L gene from the Azores were identical to the eight available sequences from the North Atlantic and differed by 0.2–0.6% from sequences from Brazil and Australia, indicating that the Azorean specimen corresponds to the species that has been molecularly confirmed in the Atlantic Iberian Peninsula, Australia, Brazil, and the Caribbean (Díaz-Tapia et al. 2018;

Mamoozadeh and Freshwater 2011). Even if this species complex remains unresolved and the specimens reported here are assigned to a different species at some point, we tentatively report this species in the Azores. It clearly differs morphologically from the other species of the genus reported in the Archipelago and the publication here of *rbc*L sequences might contribute to clarify the species complex in the future as well as facilitating the clarification of the correct species name once the complex can be deciphered.

Rhodophyta, Florideophyceae, Ceramiales, Rhodomelaceae

***Pterosiphonia complanata* (Clemente) Falkenberg**

Type locality: Cádiz, Spain (Roxas Clemente y Rubio 1807).

Specimens examined: AZB-SMG-02-242, São Miguel, Ribeira Grande, 2002-08-10; AZB-SMG-10-40; São Miguel, Ferraria, 2010-07-29.

Azorean material description: Thalli brownish red in colour, 7–9 cm long and 7–12 cm wide, consisting of flabellate to cylindrical tufts composed of few to many compressed erect axes up to 620 µm in diameter. Branching complanate, alternate distichous, up to 5–6 orders; the lateral branches arise at intervals of 3–4 segments and coalesce with the main axis. Lateral branches up to 320 µm near the base and 130 µm towards the apex. The studied material was vegetative.

Habitat: Intertidal at mid to low shore levels.

Distribution: *Pterosiphonia complanata* is known from the eastern Atlantic Ocean, including Madeira Island (Guiry

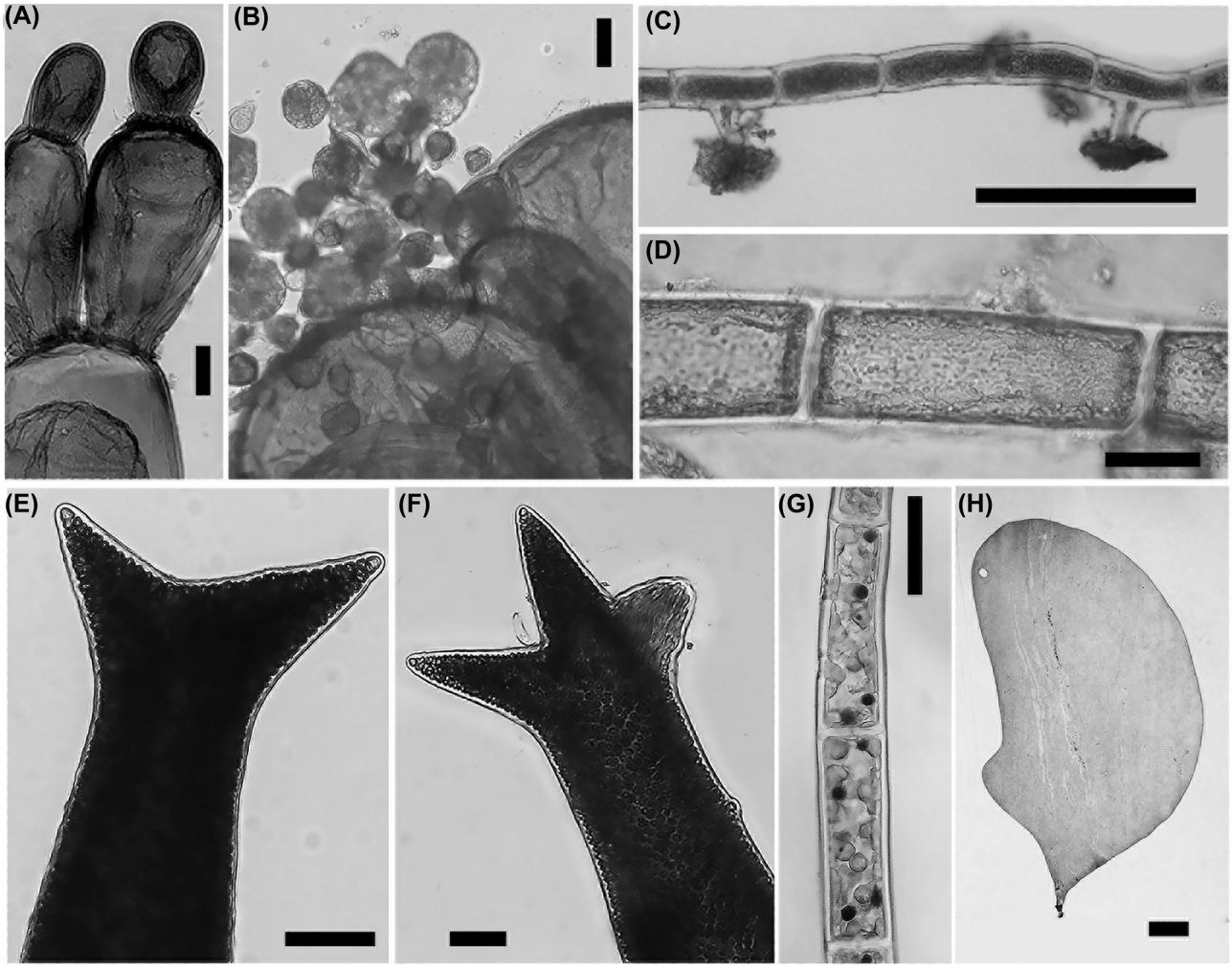

Figure 4: New red algal records from the Azores. (A and B) *Griffithsia opuntioides*: ellipsoidal to cylindrical cells (A, scale bar = 100 µm); tetraspores in clusters in terminal tetrasporangia (B, scale bar = 50 µm). (C and D) *Ptilothamnion sphaericum*: prostrate axis with unicellular rhizoids inserted in a median position on cells (C, scale bar = 300 µm); erect filament composed of barrel-shaped cells (D, scale bar = 50 µm). (E and F) *Hypnea valentiae*: forked (E, scale bar = 50 µm) or three-pointed stellate branchlets (F, scale bar = 50 µm), with acute apices with small apical cells. (G) *Rhodothamniella floridula*: filament composed of cylindrical cells containing several chloroplasts, each with one pyrenoid (G, scale bar = 35 µm). (H) *Sebdenia canariensis*: thalli with rounded lobes and a smooth margin (H, scale bar = 1 cm).

and Guiry 2021). Its occurrence in the Azores extends its known distribution in the North Atlantic Ocean.

Rhodophyta, Florideophyceae, Ceramiales, Wrangeliaceae

***Griffithsia opuntioides* J.Agardh**

Syntype localities: In the Mediterranean Sea (Agardh 1842).

Specimens examined: AZB-GRW-06-206, Graciosa, Praia, Ponta da Doca, 2006-06-04; AZB-PIX-07-798, Pico, Lajes do Pico, 2007-07-16; AZB-PIX-07-811, Pico, Lajes do Pico, 2007-07-16.

Azorean material description: Thallus filamentous, 1.4–2.8 cm long, ecorticate, erect, pseudodichotomously branched, attached to the substrate by unicellular rhizoids developed from the prostrate basal filaments. Ellipsoidal to cylindrical cells (Figure 4A), the terminal ones 490 µm long x 196 µm wide. Vegetative cells 1764 µm long × 294 µm wide on average, narrower at the base (332–431 µm wide) and wider towards the tips (941–1172 µm wide). Tetrasporangia tetrahedrally divided, 30–91 µm in diameter, borne in terminal clusters with an involucre (Figure 4B).

Habitat: Epilithic on low intertidal crevices (AZB-PIX-07-798) and rocks (AZB-PIX-07-811), and on boulders at 12 m depth (AZB-GRW-06-206).

Distribution: *Griffithsia opuntioides* is widely distributed in temperate, subtropical, and tropical marine waters (Guiry and Guiry 2021). Its occurrence in the Azores fits within its distributional range.

Rhodophyta, Florideophyceae, Ceramiales, Wrangeliaceae

***Gymnophycus hapsiphorus* Huisman *et* Kraft**

Type locality: Gneering Shoal, Queensland, Australia (Huisman and Kraft 1983).

Specimens examined: SANT-Algae 33647, São Miguel, Vila Franca do Campo, Marina, pontão, 2018-04-16.

Azorean material description: Thalli flaccid and pinkish red in colour, 40 mm long, consisting of short prostrate systems that attach to the substratum by rhizoids and erect filaments. These later are alternate-distichously branched (Figures 3I), 70–90 µm in diameter in basal parts, and composed of cylindrical cells that contain refractive vesicles located near pit-connections (Figure 3I). Tetrasporangia sessile, borne adaxially, subspherical, 20–25 × 25–35 µm (Figure 3I).

Habitat: Permanently submersed dock floats in a marina.

Distribution: *Gymnophycus hapsiphorus* has been reported in Australia and the Canary Islands (Afonso Carrillo and Sansón 1999; Huisman and Kraft 1983). In the Azores, it was found only in a marina, suggesting that it has been probably introduced via hull fouling. Its finding in the Azores extends further north its known distribution in the Atlantic.

Rhodophyta, Florideophyceae, Ceramiales, Wrangeliaceae:

***Ptilothamnion sphaericum* (P.Crouan *et* H.Crouan *ex* J.Agardh) Maggs *et* Hommersand**

Type locality: Brest, France (Agardh 1851).

Specimens examined: SANT-Algae 33661, São Miguel, Vila Franca, 2018-04-17; SANT-Algae 33651, São Miguel, praia do Pópulo, 2018-04-12.

Azorean material description: Thalli fairly rigid and pinkish red colour, 7 mm long, consisting of extensive systems of prostrate filaments that attach to the substratum by rhizoids (Figure 4C) and bear erect filaments unbranched or irregularly branched. Filaments composed of barrel-shaped cells (Figure 4C and D), 50–70 µm in diameter. Rhizoids unicellular and inserted in a median position on cells (Figure 4C). The studied material was vegetative.

Habitat: Intertidal algal turfs in sand-covered bedrocks.

Distribution: *Ptilothamnion sphaericum* has been reported only in southern Europe, from the southern British Isles and northwestern France to the southern Iberian Peninsula (Díaz-Tapia and Bárbara 2011, 2014; Maggs and Hommersand 1993). Its finding in the Azores extends its known western distribution in the Atlantic.

Rhodophyta, Florideophyceae, Gigartinales, Cystocloniaceae

***Hypnea valentiae* (Turner) Montagne**

Type locality: Red Sea (Turner 1809).

Specimens examined: AZB-SMG-17-28, São Miguel, Ponta Delgada, baía de São Roque, 2017-04-17.

Azorean material description: Thallus cartilaginous, brownish red, 1.5 cm long, composed of terete axes (118–180 µm in diameter), with branches repeatedly alternated, becoming bushy. Branches covered by spine-like to cornuted branchlets (90–140 µm in diameter) interspersed with forked (Figure 4E) or three-pointed stellate branchlets (Figure 4F), with acute apices with small apical cells.

Habitat: Epilithic on bedrock at 5 m depth.

Distribution: Since its original description from the Red Sea, this species has been reported worldwide in tropical and subtropical seas. Introduced into the Mediterranean, probably via oysters, it was first found at Etang de Thau, France, in 1996 (Verlaque et al. 2015). Its occurrence in the Azores fits within its distribution range.

Additional observations: Morphological characters observed in the Azorean specimens agree with specimens of the species from other regions (Afonso Carrillo and Sansón 1999). The diagnostic stellate branchlets of this taxon, which were observed in the specimens here described, are not always present leading to common potential misidentification (Tsiamis and Verlaque 2011). Their absence can cause confusion with specimens of *Hypnea musciformis*, although the axes tips of the latter are mostly unbranched and attenuate, whereas those of *H. valentiae* are densely ramified throughout (Schneider and Searles 1991). Molecular tools are showing that *Hypnea* may contain species complexes, while other species exhibit a high morphological plasticity that has led to an overestimation of diversity in some regions (de Jesus 2019; Nauer et al. 2015). Therefore, records of *Hynea valentiae* and other congeners should be ideally confirmed using molecular information. Unfortunately, we could not obtain DNA sequences from Azorean specimens, but the species is here recorded based on its distinctive morphological characters.

Rhodophyta, Florideophyceae, Palmariales, Rhodothamniellaceae

***Rhodothamniella floridula* (Dillwyn) Feldmann**

Syntype localities: Galway and Antrim, Ireland (Dillwyn 1809).

Specimens examined: SANT-Algae 33652, São Miguel, praia do Pópulo, 2018-04-12; SANT-Algae 33637, São Miguel, Rabo de Peixe, Calhetas, 2018-04-13; SANT-Algae 33645, São Miguel, Maia, 2018-04-13; SANT-Algae 33658, São Miguel, Ponta Delgada, baía de São Roque, 2018-04-15; SANT-Algae 33639, São Miguel, Caloura, 2018-04-16; SANT-Algae 33662, São Miguel, Vila Franca do Campo, 2018-04-18.

Azorean material description: Thalli pinkish red in colour, forming dense robust turfs up to 20 mm in thickness and composed of extensive systems of densely entangled prostrate and erect uniseriate fragile filaments. Filaments 20–30 μm in diameter, unbranched or irregularly branched, and composed of cylindrical cells containing 3–8 chloroplasts, each with one pyrenoid (Figure 4G). The studied material was vegetative.

Habitat: Intertidal algal turfs in sand-covered bedrocks.

Distribution: *Rhodothamniella floridula* has been reported in Atlantic Europe, Madeira, Tristan da Cunha, southern South America, southern Africa, and Australia (Díaz-Tapia and Bárbara 2014, Guiry and Guiry 2021). Its finding in the Azores extends its known western distribution in the North Atlantic Ocean.

Rhodophyta, Florideophyceae, Sebdeniales, Sebdeniaceae

***Sebdenia canariensis* Soler-Onís, Haroun *et* Prud'homme**

Type locality: Las Lanzas, Canary Islands, Spain (Soler-Onis et al. 1995).

Specimens examined: AZB-SMG-94-81, São Miguel, São Vicente Ferreira, 1994-07-08; AZB-SMG-94-498, São Miguel, São Vicente Ferreira, 1994-06-06; AZB-SMG-96-125, São Miguel, São Roque, 1996-07-11; AZB-SMG-96-232, São Miguel, São Vicente Ferreira, 1996-07-16; AZB-SMG-96-365a, São Miguel, Lagoa-piscina, 1996-07-25; AZB-PIX-07-1243, Pico, Canal da Madalena, 2007-07-25; AZB-PIX-07-1319, Pico, Manhenha, 2007-07-27.

Azorean material description: Thalli foliose, 4–32 cm long, soft, gelatinous but firm, attached to the substratum through a small disc (3 mm in diameter) from which a short cylindrical stipe (5–8 mm long) develops. Thalli reddish in colour (but turning yellowish when dried as herbarium specimens), with a swollen base, which develops into either a round large single blade (Figure 4H), or a pseudodichotomous blade with rounded lobes and a smooth margin. In cross section, medulla composed of interwoven dichotomously branched filaments (193–321 μm in length) and surrounded by a three-layered cortex. Outer cortical cells pigmented, isodiametric, 3.7–13.7 μm, and inner cells hyaline, 44 × 70 to 50 × 91 μm. Gland cells (18–23 μm in diameter) develop from the medullary filaments. Stellate cells (body 26–60 μm in diameter) are frequently observed among the medullary filaments. Tetrasporangia subspherical, cruciately divided, 21–23 μm in diameter and spread among cortical cells on both blade surfaces.

Habitat: Epilithic on subtidal rocks at 10–20 m depth.

Distribution: *Sebdenia canariensis* was known from the Canaries and Cabo Verde (Guiry and Guiry 2021). Its occurrence in the Azores extends further north its known distribution in the Atlantic.

Chlorophyta, Ulvophyceae, Bryopsidales, Dichotomosiphonaceae

***Avrainvillea canariensis* A.Gepp *et* E.S.Gepp**

Type locality: Gran Canaria, Canary Islands, Spain (Gepp and Gepp 1911).

Specimens examined: AZB-SMA-17-01 and AZB-SMA-17-02, Santa Maria, emissores, 2017-07-17.

Azorean material description: Thalli solitary, greenish fan-shaped, up to 5 cm in height, composed of an elongated, simple, and somewhat compressed rhizoidal base, and a paddle-shaped, thin, and very lightly zoned frond with a spongy structure. Siphonous organization, composed

of cylindrical, green or golden green siphons, not differentiated in utricles, and sometimes exhibiting slightly flattened dichotomies.
Habitat: Lowshore rockpools with sand influence.
Distribution: This new record of the Macaronesian endemic *A. canariensis* (Ribeiro et al. 2019) in the Azores represents a northern expansion of the species' known range.

Ochrophyta, Phaeophyceae, Ectocarpales, Chordariaceae
***Nemacystus flexuosus* (C.Agardh) Kylin**
Type locality: Gibraltar, Spain (Agardh 1824).
Specimens examined: AZB-SMG-93-149a-c, São Miguel, São Vicente Ferreira, 1993-07-22; AZB-SMG-12-25, São Miguel, São Roque, 2012-03-14.
Azorean material description: Thalli erect, up to 10 cm in length, pseudoparenchymatous, filiform and cylindrical, entangled, and slender with alternate irregular branching. Branches wider near the base (1.5 mm), becoming progressively slender towards the tips (0.1 mm). Thalli brown, although somewhat greenish under water, gelatinous but firm. Medulla uniaxial, composed of rectangular cells, surrounded by a cortex composed of short assimilatory filaments, not compressed and with constant diameter (6–8 μm), with basal cells oblong to cylindrical, middle cells elongated and oval, and terminal cells often elongated, up to 13.4 μm in length. Phaeophycean hairs present. Fertile material bears both cylindrical and uniseriate plurilocular pedicellate sporangia and unilocular sporangia about 21 × 16 μm.
Habitat: Epilithic in rockpools (AZB-SMG-12-25) and on subtidal rocks at 7 m depth (AZB-SMG-93-149a-c).
Distribution: *Nemacystus flexuosus* is distributed in the Mediterranean, eastern Atlantic including the Canaries, Selvages and Madeira (Guiry and Guiry 2021). Its occurrence in the Azores extends further north its known distribution in the Atlantic.

Ochrophyta, Phaeophyceae, Ectocarpales, Scytosiphonaceae
***Scytosiphon dotyi* M.J.Wynne**
Type locality: San Mateo County, California, USA (Wynne 1969).
Specimens examined: AZB-FOR-90-10, Formigas, ponta Norte, 1990-06-05; AZB-SMG-04-22, São Miguel, Caloura, Cerco, 2004-03-25.
Azorean material description: Thalli brownish, tufted, 3.5–4.3 cm long, pseudoparenchymatous, attached by a discoid holdfast. Thalli tubular, hollow, without constrictions and with diffuse intercalary growth. Phaeophycean hairs absent as well as ascocyst-like cells among sporangia. Surface cells small and irregular, 5–7.5 μm in diameter. Fertile material with uniseriate plurilocular sporangia, 15–25 μm long and 3–5 μm wide at the base and 8 μm at the tip.
Habitat: Epilithic on mid (AZB-SMG-04-22) and low (AZB-FOR-90-10) intertidal rocks.
Distribution: *Scytosiphon dotyi* has been recorded from the Mediterranean Sea (where it was introduced, arriving in the Adriatic Sea between 1960 and 1970, Verlaque et al. 2015), the northeastern Atlantic, the North Pacific and Asia (Guiry and Guiry 2021; Taşkın 2012). Already recorded in the Canary Islands, its occurrence in the Azores is a northwestern extension of its known distribution in the eastern North Atlantic.

Ochrophyta, Phaeophyceae, Sporochnales, Sporochnaceae
***Sporochnus anomalus* (Pallas) M.J.Wynne**
Type locality: Not given by Pallas (1766).
Specimens examined: AZB-SMA-05-236, Santa Maria, Baía do Raposo, 2005-06-29; AZB-SMA-05-262a-d, Santa Maria, Ilhéu de São Lourenço, 2005-07-01.
Azorean material description: Thallus erect, up to 20 cm tall, composed of terete branched axes, from which arise lateral branches up to 13 cm long. Numerous determinate tufted branchlets develop on axes and branches, which are composed of a long stalk (4.3 mm at the base, 0.7 mm at the tip, and up to 300 μm in diameter), an elongated cylindrical receptacle (0.4–0.5 mm long, 0.3–0.4 mm wide) and a terminal cluster of filaments extending from an apical pit.
Habitat: Epilithic on subtidal rocks at 6–30 m depth.
Distribution: *Sporochnus anomalus* is distributed in Baja California and Gulf of California, the Mediterranean and the Canaries (Guiry and Guiry 2021). Its occurrence in the Azores represents a northern expansion of the known range of the species in the Atlantic.

4 Discussion

The 19 species newly reported here (15 Rhodophyta, one Chlorophyta and three Ochrophyta) increase the current total of species recorded in Azores to 521 (349 Rhodophyta, 76 Chlorophyta and 96 Ochrophyta), and show that the Azorean macroalgal flora remains incompletely known. They also indicate that the mid-Atlantic Azores archipelago supports a relatively rich marine macroalgal flora and confirm the Azores as a suitable geographic location for the settlement of macroalgae with different biogeographical affinities.

The distribution of *Bonnemaisonia clavata*, *Melanothamnus pseudoforcipatus* and *Ptilothamnion sphaericum*,

known from the northeast Atlantic, can now be extended further south in the Atlantic. On the other hand, there is an extension of the known north-western distribution in the Atlantic for *Antithamnionella elegans*, *Lophosiphonia simplicissima*, *Pterosiphonia complanata*, *Gymnophycus hapsiphorus*, *Rhodothamniella floridula*, *Nemacystus flexuosus*, *Scytosiphon dotyi* and *Sporochnus anomalus*. Moreover, the records of *Sebdenia canariensis* and *Avrainvillea canariensis* considerably extend their known distributions in the Atlantic to the north. The presence on the Azores of the remaining macroalgae newly reported here (*Aglaothamnion tripinnatum*, *Herposiphonia tenella*, *Lophocladia trichoclados*, *Polysiphonia villum*, *Griffithsia opuntioides* and *Hypnea valentiae*) was not unexpected as it fits within their distribution range.

The northern expansion in the Atlantic of species known from warm-water areas can be considered as a signal of global warming effects on the benthic communities in the Macaronesia region, as reported for the species *Cladophora lehmanniana* (Lindenberg) Kützing, *Sargassum furcatum* Kützing, and *Avrainvillea canariensis* that were recently found in Madeira (Ferreira et al. 2012; Ribeiro et al. 2019). This situation has also been observed in the Canary Islands, where the proportion of tropical elements in the marine flora has increased in recent years (Afonso-Carrillo et al. 2007; Cassano et al. 2008).

Only two isolated specimens of the mesophotic species *Avrainvillea canariensis* were found in the Azores and were restricted to low shore tidepools with sand influence. The Azorean specimens are smaller than those reported from the Canaries and Madeira, where the species forms scattered patches at depths below 25 m (Afonso-Carrillo et al. 1984; Ribeiro et al. 2019). It is likely that the species may occur in other locations in the Azores and, therefore, further exploration is recommended to evaluate its potential spread and to investigate the occurrence of a possible new marine subtidal assemblage in the soft subtidal bottoms of the mesophotic zone of the Azores.

Two of the species reported as introduced in other locations [*Antithamnionella elegans* in the Mediterranean, Madeira and Cabo Verde and *Gymnophycus hapsiphorus* in the Canary Islands (Afonso-Carrillo and Sansón 1999; Guiry and Guiry 2021; Verlaque et al. 2015)] were collected in marinas, suggesting they might also have been introduced in the Azores via hull fouling.

Although our knowledge of seaweed diversity and biogeography still largely relies on information derived from morphological identifications, the use of molecular tools is revealing that cryptic diversity is common among algae. Together, molecular species delimitation and morphological studies can, therefore, resolve hidden introductions or complexes of cryptic species (e.g. Díaz-Tapia et al. 2018; Hoshino et al. 2021). This was the case for two of the newly reported species in Azores that belong to unresolved species complexes (*Herposiphonia tenella*, Díaz-Tapia et al. 2018, *Polysiphonia villum*, Savoie and Saunders 2019). The molecular analyses performed, coupled with the morphological identifications made, helped to clarify species identification even if resolving the taxonomy of these complexes requires further work.

Recent investigations have indicated that a significant level of undiscovered cryptic diversity is likely to be found in algal turfs (Díaz-Tapia et al. 2020a, b). Turf assemblages are dominant in sand-covered rocks, a particularly stressful habitat for benthic macroalgae. This type of assemblage is widely distributed along the Azorean coasts but their flora is still poorly known. Research developed in the present study revealed that six of the newly reported species were found as components of the intertidal algal turf samples (*Herposiphonia tenella, Lophosiphonia simplicissima, Melanothamnus pseudoforcipatus, Polysiphonia villum, Ptilothamnion sphaericum* and *Rhodothamniella floridula*). Previous work by one of the present authors has already reported four other new species for the Azorean algal turf, namely *Polysiphonia scopulorum* complex Harvey (Díaz-Tapia et al. 2020a), *Vertebrata cymatophylla* (Børgesen) Muñoz-Luque and Díaz-Tapia and the newly discovered species *Melanothamnus macaronesicus* Rodríguez-Buján and Díaz-Tapia (Rodríguez-Buján et al. 2021) and *V. barbarae* Muñoz-Luque and Díaz-Tapia (Díaz-Tapia et al. 2021) which are endemic to Macaronesia and the Azores, respectively. This justifies the need for continued prospecting of turf samples as new discoveries can be anticipated.

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