Received: 31 March 2023 | Accepted: 5 October 2023

DOI: 10.1111/jpy.13402

RESEARCH ARTICLE

Resolving the taxonomy of the *Polysiphonia scopulorum* complex and the *Bryocladia* lineage (Rhodomelaceae, Rhodophyta)

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Funding information
Australian Biological Resources Study, Grant/Award Number: 4-G046WSD; British Phycological Society; Holsworth Wildlife Research Endowment

Editor: M.C. C Oliveira

Abstract

Cryptic diversity is common among marine macroalgae, with molecular tools leading to the discovery of many new species. To assign names to these morphologically similar species, the type and synonyms have to be examined, and if appropriate, new species must be described. The turf-forming red alga *Polysiphonia scopulorum* was originally described from Rottnest Island, Australia, and subsequently widely reported in tropical and temperate coasts based on morphological identifications. A recent study of molecular species delineation revealed a complex of 12 species in Australia, South Africa, and Europe. These species are placed in a taxonomically unresolved lineage of the tribe Polysiphonieae. The aim of this study was to resolve the genus- and species-level taxonomy of this complex and related species using molecular and morphological information. Three morphologically indistinguishable species of the complex were found at the type locality of *P. scopulorum*, preventing a straightforward assignment of the name to any of the molecular lineages. Therefore, we propose a molecularly characterized epitype. *Polysiphonia caespitosa* is reinstated for the only species found in its type locality in South Africa. We describe seven new species. Only one species of the complex can be morphologically recognized, with the other eight species indistinguishable based on morphometric analysis. The studied complex, together with another seven species currently placed in *Polysiphonia* and two *Bryocladia* species, formed a clade distinct from *Polysiphonia* sensu stricto. Based on observations of *Bryocladia cervicornis* (the generitype), we describe our seven new species in the genus *Bryocladia* and transfer another nine species from *Polysiphonia* to *Bryocladia*.

KEYWORDS
algal turfs, Ceramiales, *cox*1, cryptic diversity, epitype, new combination, new species, *Polysiphonia caespitosa*, *rbc*L, systematics

Abbreviation: ML, maximum likelihood.

INTRODUCTION

Macroalgal species are often morphologically simple and/or exhibit high levels of plasticity, which can mislead species delimitation based on morphological characters. Macroalgal surveys using molecular tools often result in the discovery of cryptic diversity, finding that morphologically circumscribed species actually involve complexes (Gomes et al., 2020; Hoshino et al., 2020; Leliaert et al., 2009, 2018). Detailed morphological investigation of these complexes often leads to diagnostic characters for the molecularly identified species, so they are pseudocryptic (Díaz-Tapia, Rodríguez-Buján, et al., 2022; Hind et al., 2014; Piñeiro-Corbeira et al., 2020; Tronholm et al., 2013; Verbruggen et al., 2006). However, morphological differences cannot always be found, and the description of true cryptic species that cannot be morphologically distinguished is becoming more frequent (Camacho et al., 2019; Díaz-Tapia et al., 2021; Díaz-Tapia, Maggs, et al., 2020; Kraft et al., 2010; Schneider et al., 2017; Soares et al., 2020).

Once molecular cryptic diversity is observed, resolving the taxonomy of the discovered lineages requires assigning validly published species names to the molecular entities. Taxonomic uncertainties in this context are often addressed by sequencing topotype or type material (Richards et al., 2021; Soares et al., 2019). However, these approaches do not always offer solutions. Type localities are not always specified or can include vast regions, such as "Australia" (e.g., Agardh, 1841). Also, some species were described based on materials from syntype localities that can be placed in distant and disjunct regions, such as *Melanothamnus ferulaceus* (Agardh, 1863). Even if type localities are unique and well-defined, uncertainties can remain after sequencing topotype material if several cryptic species are detected in sympatry (Vieira et al., 2016).

Sequencing type materials is an increasingly followed approach for resolving species-level taxonomic uncertainties, particularly among coralline red algae (Hernandez-Kantun et al., 2015; Kato et al., 2022). However, sequencing type materials in other seaweed groups is often tedious and requires authentication protocols to deal with potential contamination, and success is often reduced because the DNA is degraded in old samples (Saunders & McDevit, 2012; Vieira et al., 2016). These problems are particularly relevant in PCR-based protocols, while high-throughput sequencing techniques greatly facilitates the determination of molecular information from types (Boo et al., 2016; Hughey et al., 2017). However, even for HTS approaches, the type must be of a minimum size to ensure both a successful DNA extraction and the preservation of the specimen integrity. Many highly diverse seaweed taxa, such as the Ceramiales, Ectocarpales, and Cladophorales, include a high number of small-sized species with types that consist of minuscule amounts of material. Moreover, destructive sampling of type material is not always possible due to herbarium policies. These issues make designation of epitypes a desirable alternative to assigning available taxa names to cryptic species (Dumilag et al., 2020; Saunders & McDevit, 2012; Zuccarello et al., 2011).

The taxonomy of the red algal genus *Polysiphonia* has been historically convoluted, as clearly shown by the existence of 551 species names for a genus that currently includes 186 recognized species (Guiry & Guiry, 2023). Such accumulation of names is, at least in part, the result of the segregation and synonymization of both genera and species, mainly during the 19th and 20th centuries. The circumscription of *Polysiphonia* has been deeply modified in recent years, and integrative studies based on molecular and morphological investigations have led to the segregation or redefinition of two tribes and 18 genera (Amos et al., 2021; Díaz-Tapia, Maggs, McIvor, et al., 2017; Díaz-Tapia, Maggs, West, & Verbruggen, 2017; Savoie & Saunders, 2016, 2019; Wynne, 2018). Despite recent efforts and substantial advances, the current concept of *Polysiphonia* still consists of two distinct lineages that are resolved either as paraphyletic or monophyletic groups in phylogenies using different markers and taxon selection (Bustamante et al., 2015; Díaz-Tapia, Pasella, & Verbruggen, 2018; Díaz-Tapia, Tüney-Kizilkaya, & Taşkin, 2022; Huisman et al., 2017). One of them includes the generitype *P. stricta* and another 11 *Polysiphonia* species. The other lineage includes eight recognized species placed in *Polysiphonia* as well as two species of *Bryocladia*. Therefore, *Bryocladia* might be a candidate genus for this clade, but its generitype, *B. cervicornis*, is a poorly known species originally described from Java (Kützing, 1847), and further studies are required to determine the affinities of this species.

At the species level, the largest and most conspicuous species of *Polysiphonia*, particularly from European coasts, received much attention in foundational taxonomic accounts. Morphological forms of these species were recognized as separate species or varieties and were mostly later synonymized. For example, eight heterotypic species names are synonyms of the generitype *Polysiphonia stricta* (Guiry & Guiry, 2023). In contrast, the small (i.e., <3 cm in length) species received much less attention, and their diversity has been underestimated (e.g., Bustamante et al., 2014; Díaz-Tapia, Bárbara, Cremades, et al., 2017; Díaz-Tapia, Tüney-Kizilkaya, & Taşkin, 2022; Kim & Kim, 2015). These new inconspicuous species are particularly abundant in algal turfs, a type of assemblage composed of small seaweeds that grow densely packed. Algal turfs often include a high diversity of intermixed species that share a common habit consisting of prostrate and erect axes (Díaz-Tapia & Bárbara, 2013, 2014; Price & Scott, 1992). Turfs are highly relevant ecologically, as they are the dominant algal assemblage in tropical shallow reefs,

and their abundance is notably increasing in temperate coasts in response to the global decline of kelps and brown seaweeds canopies (Arjunwadkar et al., 2022; Filbee-Dexter & Wernberg, 2018; Littler & Littler, 2013; O'Brien & Scheibling, 2018; Reeves et al., 2022). Despite their relevance, much more work is needed to understand their biodiversity.

Unsurprisingly, one of the most extensive known red algal species complexes has been observed in a small turf-forming alga, *Polysiphonia scopulorum* (Díaz-Tapia, Ly, & Verbruggen, 2020). This species was originally described from Australia and subsequently recorded in warm and temperate regions worldwide (Díaz-Tapia & Bárbara, 2013). A first characterization of topotype material revealed the existence of at least three species identified under this name in different world regions (Huisman et al., 2017). More extensive sampling in South Africa, Australia, and southern Europe, combined with detailed morphometric analyses and molecular species delimitation using the *cox*1 and *rbc*L gene markers and three methods, has shown that the complex consists of 12 species, the majority of which are morphologically indistinguishable (Díaz-Tapia, Ly, & Verbruggen, 2020). However, the taxonomy of this species complex has not been addressed yet. The goal of this study was to resolve the taxonomy of the *Polysiphonia scopulorum* complex by assigning previous available names to discovered entities delineated based on molecular species delimitation (Díaz-Tapia, Ly, & Verbruggen, 2020) and proposing new species when needed. We also aimed to solve the generic assignment of this complex and the lineage where it was placed by studying topotype material of *Bryocladia cervicornis*.

MATERIALS AND METHODS

Field and herbaria collections, morphological identification, and examination

Samples of *Polysiphonia* were collected from Europe (Atlantic Iberian Peninsula, Azores, Canary Islands, Mediterranean), Australia (Western Australia, South Australia, Victoria, Tasmania), and South Africa (Table S1 in the Supporting Information). Samples were collected using a knife to scrape intertidal algal turfs during low tide or by snorkeling in the upper subtidal. Samples were placed in plastic bags and transported to the laboratory where they were carefully cleaned and isolated using a stereomicroscope. Materials for DNA extraction were dried in silica gel desiccant. Plants for morphological examination were preserved in 4% formalin seawater at 4°C and stored in the dark. Specimens of *Polysiphonia scopulorum* were initially morphologically identified using the available references for each sampled region (Díaz-Tapia & Bárbara, 2013; Rojas-González, 1997; Stegenga et al., 1997; Womersley, 1979, 2003).

For morphological observations, wet preserved samples were mounted in 20% Karo® Syrup (ACH Foods, Memphis, Tennessee, USA) and 80% distilled water. Sections for microscopic observations were made by hand using a razor blade. Microscopic morpho-anatomical characters were studied by light microscopy. Voucher specimens were deposited in the herbaria MEL, MELU, and SANT. Herbaria abbreviations follow Thiers (2023, continuously updated).

A specimen corresponding to the type material of *Bryocladia cervicornis* was found housed at L (L.4033460) and images of this specimen have been analyzed. Moreover, a specimen of the same collection as the type (L.4033461, coll. Zollinger) was received on loan and studied in more detail. Images of the type material of *Polysiphonia scopulorum* in TCD, BM, and MEL (available https://plants.jstor.org/) were examined.

Phylogenetic analysis

A previous study of the *Polysiphonia scopulorum* complex applied molecular species delimitation methods to a data set of 135 *rbc*L and 128 *cox*1 gene sequences, resolving a consensus of 12 species whose delineation has been previously discussed (Díaz-Tapia, Ly, & Verbruggen, 2020). In order to place these 12 species in a wider phylogenetic context and resolve their taxonomy, we assembled a data set of 72 *rbc*L gene sequences (Table S1) including one sequence per haplotype of the 12 species of the *Polysiphonia scopulorum* complex (25 sequences determined in Díaz-Tapia, Ly, & Verbruggen, 2020), one sequence per species of other species of the tribe Polysiphonieae (28 sequences), and a selection of 16 species of the tribe Streblocladieae. Likewise, we assembled a data set of 64 *cox*1 gene sequences (Table S1) including one sequence per haplotype of the 12 species of the *Polysiphonia scopulorum* complex (32 sequences determined in Díaz-Tapia, Ly, & Verbruggen, 2020), one sequence per species of other species of the tribe Polysiphonieae (18 sequences), and a selection of 14 species of the tribe Streblocladieae. Three species of the tribe Pterosiphonieae were selected as the outgroup based on phylogenomic analyses of the family Rhodomelaceae (Díaz-Tapia, Maggs, West, & Verbruggen, 2017). Length of sequences ranged between 704–1467 and 562–1617 bp in the *rbc*L and *cox*1 gene data sets, respectively. Sequences of each gene were aligned using MUSCLE in Geneious 6.1.8 (Kearse et al., 2012). Models of nucleotide evolution were selected for each data set based on the Bayesian Information Criterion using ModelFinder in IQ-Tree (Kalyaanamoorthy et al., 2017). Maximum-likelihood (ML) phylogenetic trees were inferred in

IQ-TREE v2.1.2 (Minh et al., 2020) using the model GTR+F+I+G4 (Tavaré, 1986), and branch support was determined using 1000 non-parametric bootstrap replicates (Felsenstein, 1985) and ultrafast bootstrap (Hoang et al., 2018).

RESULTS

Phylogenetics

The species of the tribe Polysiphonieae grouped into three highly supported clades in the *rbc*L gene phylogeny (Figure 1). The first included the genera *Epizonaria* and *Lophosiphonia*. The second is composed of 12 *Polysiphonia* spp. including the generitype *P. stricta*. The third clade, indicated *Bryocladia* in Figure 1, includes the species of the *Polysiphonia scopulorum* complex, several other species currently placed in the genus *Polysiphonia*, two species of *Bryocladia*, and *Streblocladia camptoclada*.

Within the *Bryocladia* clade, our focus in this paper, "*Polysiphonia*" *scopulorum* was shown to contain several species-level entities, in line with the species delimitation results presented by Díaz-Tapia, Ly, and Verbruggen (2020) based on molecular species delineation using two molecular markers and three methods (GMYC, PTP, and ABGD). Species "*Polysiphonia*" *scopulorum* 2–6 were placed in a highly supported clade, and "*P.*" *scopulorum* 1 was inferred as sister to that clade, but this relationship was unsupported. "*Polysiphonia*" *scopulorum* 7 was resolved with high support as sister to "*P.*" *adamsiae*, while relationships of the remaining four species of the complex were unresolved. Among them, only "*P.*" *scopulorum* 10 and 11 were inferred as sister, while "*P.*" *scopulorum* 8 and 9 were inferred as sister to other species of "*Polysiphonia*."

The *cox*1 gene phylogeny (Figure S1 in the Supporting Information) lacked some species for which data were unavailable, and the topology was congruent compared with the *rbc*L gene phylogeny. "*Polysiphonia*" *scopulorum* 1 and 3–6 were resolved in a moderately supported clade, while phylogenetic relationships among the remaining species were unresolved.

Redefining *Bryocladia*

Based on our phylogenetic analyses and further reasoning provided below, we propose the transfer of nine *Polysiphonia* species to the genus *Bryocladia* and the description of seven new species of the "*Polysiphonia*" *scopulorum* complex within *Bryocladia*.

The type material of *Bryocladia cervicornis* (L4033460) consisted of a small and fragile specimen unavailable for loan, but images of the voucher were examined (Figure 2a). Handwritten notes in the envelope of this specimen clearly stated that it belonged to the Kützing herbarium and corresponded to the specimen number 2380 of the Zollinger collection from Java used in the original description (Kützing, 1847) and that was subsequently illustrated (Kützing, 1864, Tab. Phyc. XIV. 15). In addition to this specimen, the voucher L4033461 was also labeled as *B.cervicornis* and belonged to the Zollinger collection (number 2411) from Java. The habit of this specimen is similar to the type material, and its main characters agree with Kützing's (1847, 1864) description and illustrations (Figure 2b). In addition to the previously described characters for the species, we could determine a key character, as rhizoids in *B.cervicornis* are in open connection with the pericentral cells (Figure 2c). The combination of characters seen in *B.cervicornis* strongly suggest its affinity with the *Bryocladia* clade in Figure 1.

New combinations resulting from the transfer of the *Polysiphonia* species to *Bryocladia* are included in Table 1. According to our phylogeny, *Streblocladia camptoclada* is also placed in this clade. However, the sequence included in our tree is from a South African specimen, and the type locality of this species is Callao, Peru. Relationships between Pacific South American and South African populations of this species and their respective generic placement require further study, and we refrain from transferring this based on the current evidence. On the contrary, we included in Table 1 the transfer of *Polysiphonia rudis*, as the placement of this species in the *Bryocladia* clade has been molecularly confirmed (Huisman et al., 2017) even though its sequence is not publicly available.

According to our results, the description of the genus *Bryocladia* requires emendation to include the species here transferred and described:

Bryocladia F. Schmitz, in Schmitz & Falkenberg, 1897: 442.

Description: Thalli consisting of prostrate and erect axes. Rhizoids in open connection with pericentral cells, unicellular. Axes ecorticate, with 4, 6–8, or 9–12 pericentral cells. Erect axes with branches predominantly endogenous or exogenous depending on the species. Trichoblasts deciduous when present.

Type species: *Bryocladia cervicornis* (Kützing) F.Schmitz in Schmitz & Falkenberg, 1897: 442.

Other species: Seven new species described below and species listed in Table 1.

Shared features of the "*Polysiphonia*" *scopulorum* complex

The 135 specimens of "*Polysiphonia*" *scopulorum* collected during our sampling surveys of the family Rhodomelaceae in South Africa, Australia, and southern Europe were morphologically identifiable as "*Polysiphonia*" *scopulorum*. We describe the morphological characters shared among the nine species

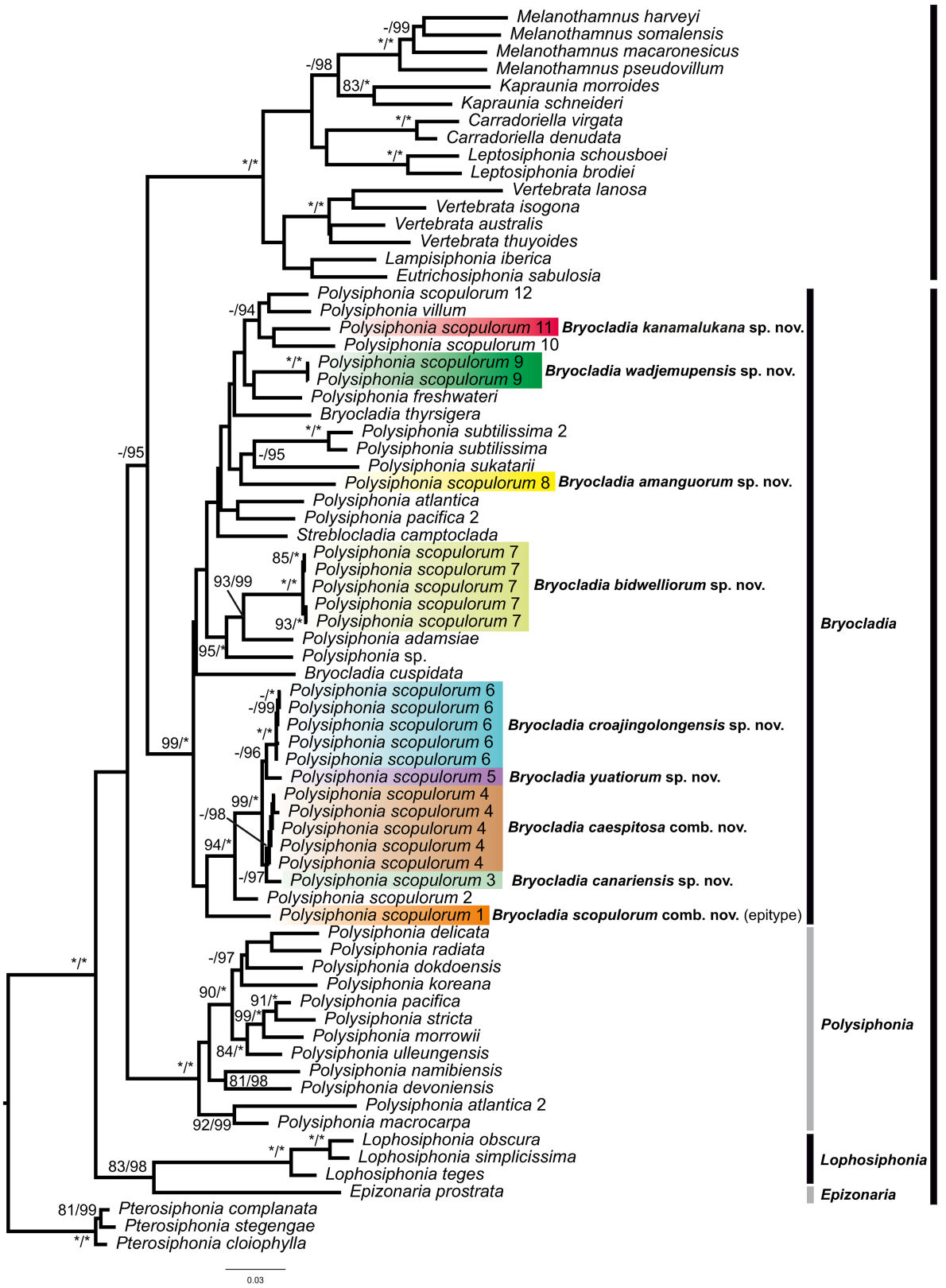

FIGURE 1 Maximum-likelihood phylogeny of the tribe Polysiphonieae based on *rbc*L gene sequences. Branch support values are indicated on branches as non-parametric/ultrafast bootstrap when ≥80% and ≥95%, respectively; asterisks represent full support. [Color figure can be viewed at wileyonlinelibrary.com]

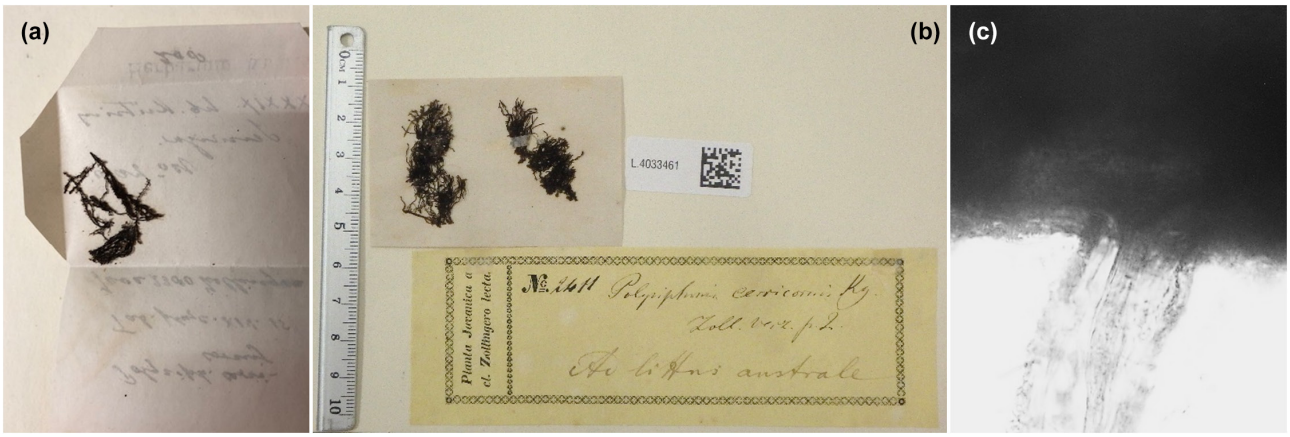

FIGURE 2 *Bryocladia cervicornis*. (a) Type material (L.4033460). (b) Topotype specimen of the Zollinger collection (L.4033461). (c) Rhizoid in open connection with the pericentral cell (specimen L.4033461). [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 New combinations in the genus *Bryocladia* of species that are not part of the *B. scopulorum* complex, followed by basionyms and synonyms.

Binomial in *Bryocladia* Basionym Synonyms	Type material Type locality
***Bryocladia adamsiae* (Womersley) Díaz-Tapia comb. nov.** *Polysiphonia adamsiae* Womersley, 1979, *Australian Journal of Botany* 27, p. 503, figure 13e–h.	Holotype: AD35678 Orford, Prosser Bay, Tasmania, Australia
***Bryocladia atlantica* (Kapraun & J.N.Norris) Díaz-Tapia comb. nov.** *Polysiphonia atlantica* Kapraun & J.N.Norris 1982, In Rützler, K. & Macintyre, I.G. (eds) The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize. I. Structure and Communities, *Smithsonian Contributions to the Marine Sciences 12,* p. 226, figure 207 a–c. *Polysiphonia macrocarpa* Harvey in Mackay 1836, p. 206, not *P. macrocarpa* (C. Agardh) Sprengel 1827.	Syntypes: TCD (as *P. macrocarpa* Harvey) Portstewart & Miltown Malbay, Ireland
***Bryocladia caespitosa* (M.A. Pocock) Díaz-Tapia comb. nov.** *Falkenbergiella caespitosa* M.A. Pocock, 1953, *Journal of the Linnean Society of London, Botany* 55, p. 41, figures 4, 7–9, pl. 9. *Polysiphonia caespitosa* (M.A. Pocock) Hollenberg (1968, p. 79).	Holotype: GRA13957 Muizenberg, False Bay, Cape Province, South Africa
***Bryocladia freshwateri* (D.E.Bustamante, B.Y.Won & T.O.Cho) Díaz-Tapia comb. nov.** *Polysiphonia freshwateri* D.E. Bustamante, B.Y. Won & T.O. Cho 2015, *European Journal of Phycology* 50, p. 332, figures 1–20.	Holotype: CUK10427 Yeonji-ri, Uljin-eup, Uljin-gun, Gyeonsangbuk-do, Korea
***Bryocladia rudis* (Hooker f. & Harvey) Díaz-Tapia comb. nov.** *Polysiphonia rudis* Hooker f. & Harvey 1845, In Hooker, J.D. (ed.) *The botany of the Antarctic voyage of H.M. discovery ships Erebus and Terror, in the years 1839–1843, under the command of Captain Sir James Clark Ross, Kt., R.N., F.R.S.,* etc. *by Joseph Dalton Hooker, M.D., R.N., F.L.S., assistant surgeon of the "Erebus" and botanist to the expedition. Vol. 1. Flora antarctica. Part I. Botany of Lord Auckland's Group and Campbell's Island*, p. 183.	Possible syntypes: BM1082279-82 Auckland Island, New Zealand
***Bryocladia scopulorum* (Harvey) Díaz-Tapia comb. nov.** *Polysiphonia scopulorum* Harvey, 1855, *Transactions of the Royal Irish Academy* 22, p. 540.	Holotype: TCD Rottnest Island, Western Australia
***Bryocladia subtilissima* (Montagne) Díaz-Tapia comb. nov.** *Polysiphonia subtilissima* Montagne, 1840, *Annales des Sciences Naturelles, Botanique, Seconde Série* 13, p. 199.	Holotype: PC French Guiana
***Bryocladia sukatarii* (Díaz-Tapia, Tuney & E.Taskin) Díaz-Tapia comb. nov.** *Polysiphonia sukatarii* Díaz-Tapia, Tuney & E.Taskin 2022, *Phycologia* 61, pp. 267–268, figures 2–10.	Holotype: EGE43731 Serçin, Lake Bafa, Turkey
***Bryocladia villum* (J.Agardh) Díaz-Tapia comb. nov.** *Polysiphonia villum* J. Agardh, 1863, *Species genera et ordines algarum, seu descriptiones succinctae specierum, generum et ordinum, quibus algarum regnum constituitur. Volumen secundum: algas florideas complectens. Part 2, fasc. 3*. p. 941. *Polysiphonia scopulorum* var. *villum* (J.Agardh) Hollenberg (1968, p. 81).	Isotype: US00164816 "*Americae tropicae*", probably Pacific Mexico

recognized in this complex along with the details of these characters and measurements in each species (Table 2).

Thalli were dorsiventral, consisting of extensive prostrate systems that bear rhizoids ventrally, erect axes dorsally, and produce further prostrate axes laterally (Figure 3a–d). Erect axes were up to 15 mm in length, unbranched or scarcely branched pseudodichotomously at irregular intervals (Figure 3a–d); tetrasporophytes were often more densely branched at the apical parts. Thalli were brownish red to black in color, with a fairly rigid texture.

Axes were composed of a small axial cell and four pericentral cells, without cortical cells (Figure 3e). Prostrate axes grew from a dome-shaped apical cell (Figure 3f). They lacked trichoblasts and formed a branch initial on every segment or several segments apart, some of which subsequently originated endogenous branches (Figure 3f), that is, branches formed after the division of the pericentral cells. Lateral and ventral branches produced further prostrate axes, while dorsal branches produced erect axes (Figure 3g). Rhizoids were formed several segments apart or one per segment, in open connection with the pericentral cells (Figure 3h). Rhizoids were unicellular, consisting of a filament often terminated in a discoid pad (Figure 3i).

Erect axes grew from a dome-shaped apical cell (Figure 3j). Apices of erect axes were often damaged but had resumed apical growth (Figure 3k). Erect axes were unbranched or bore sparse endogenous, occasionally exogenous, branches at irregular intervals (Figure 3l,m). Trichoblasts ranged from absent to profusely developed, formed on every segment, rarely several segments apart, in a spiral arrangement, dichotomously branched up to four orders, with uninucleate cells (Figure 3n). They were deciduous and left conspicuous scar cells when shed (Figure 3o).

Gametophytes were dioecious. Spermatangial branches formed at the apices of the erect axes, replacing trichoblasts, spirally arranged on every segment (Figure 4a). They were cylindrical, incurved, and lacked sterile apical cells when mature (Figure 4b). Most spermatangial branches replaced one of the branches of a trichoblasts, but they often replaced the two basal branches (Figure 4c). Procarps formed on determinate laterals, at the apices of erect axes. They were composed of a supporting cell, a four-celled carpogonial branch, a basal and two lateral sterile cells (Figure 4d). Mature cystocarps formed near the middle of erect axes and were ovoid and with an apical ostiole (Figure 4e–g). Carpospores were clavate (Figure 4e–g).

Tetrasporangia formed on erect axes and lateral branches, in the apices of erect axes, rarely at mid parts, which are often more profusely branched than vegetative axes (Figure 4h). One tetrasporangium was formed per segment, arranged in straight or slightly spiral series (Figure 4i–k). Tetrasporangia were subspherical, with two presporangial cover cells and a postsporangial cover cell (Figure 4m), the last absent in *Bryocladia bidwelliorum* (Figure 4l).

Description of new species in the "*Polysiphonia*" *scopulorum* complex

Our phylogenetic results, in line with the species delimitation results from Díaz-Tapia, Ly, and Verbruggen (2020), showed clear evidence that "*Polysiphonia*" *scopulorum* consists of multiple species. Here, we propose an epitype for "*P.*" *scopulorum* among the three molecular species found in its type locality, provide a molecular characterization of topotype material of *Bryocladia caespitosa*, and formally describe seven new species within the genus *Bryocladia*. Since these species are morphologically indistinguishable, with the exception of *P. bidwelliorum*, we propose a diagnosis based on molecular sequences only.

Bryocladia scopulorum (Harvey) Díaz-Tapia comb. nov. (Figures 3a, 5)

BASIONYM: *Polysiphonia scopulorum* Harvey, 1855, *Transactions of the Royal Irish Academy* 22, p. 540.

HOMOTYPIC SYNONYMS: *Lophosiphonia scopulorum* (Harvey) Womersley 1950, *Transactions of the Royal Society of South Australia* 73, p. 188; *Vertebrata scopulorum* (Harvey) Kuntze 1891, *Revisio generum plantarum. Pars II*., p.929.

EPITYPE (designated here): Turf with sterile specimens collected from Parakeet Beach, Rottnest Island, on 17.iii.2015, leg. Pilar Díaz-Tapia & Joana F. Costa, PD1655, MELUA 132369a.

LECTOTYPE: TCD (Harvey, Travelling Set no. 187; designated in Parnell et al., 2010).

ISOLECTOTYPES: BM 001067671, MEL 517744.

GENBANK ACCESSION NUMBERS OF THE EPITYPE: MT676285 (*rbc*L); MT676017 (*cox*1).

TYPE LOCALITY: Rottnest Island, Western Australia, Australia (Harvey, 1855).

HABITAT AND DISTRIBUTION: Intertidal turfs growing on sand-covered rocks. Molecularly confirmed only from the type locality.

A detailed description of this species is provided in Huisman et al. (2017) and measurements of the epitype are provided in Table 2.

Bryocladia caespitosa (Pocock) Díaz-Tapia comb. nov. (Figures 3b,e,i, 4b, 6)

BASIONYM: *Falkenbergiella caespitosa* Pocock, 1953, *Journal of the Linnean Society of London, Botany* 55, p. 41, figures 4, 7–9, pl. 9.

TABLE 2 Measurements of morphological characters for the species of the "*Polysiphonia*" *scopulorum* complex.

	Bryocladia amanguorum	*B. bidwelliorum*	*B. caespitosa*	*B. canariensis*	*B. croajingolongensis*	*B. kanamalukana*	*B. scopulorum*	*B. wadjemupensis*	*B. yuatiorum*
Thallus height (mm)	10	7	10	8	15	5	15	7	6
Prostrate axes									
Apical cell diameter (μm)	18	20–25	25–28	20–25	20–25	20	20	18	22
Diameter (μm)	50–75	80–140	70–100	45–90	60–110	45–55	70–120	30–70	70–110
Segments Length/ Diameter	0.6–1	0.5–1.2	0.5–1.5	(0.4-) 1–1.4 (–1.8)	0.8–1.7 (–2.14)	1.2–2	0.5–1.14	0.7–1.5	1.1–1.4
Rhizoids									
Length (μm)	150–450	250–750 (–1200)	90–500	225–450 (–700)	50–300	30–60	100–300	45–450	100–500
Diameter of the filament (μm)	15–45	25–60	20–100	20–40	25–70	20–40	20–50	15–50	30–50
Erect axes									
Apical cell diameter (μm)	13	17.5–25	25	20–23	22–25	15–18	25	15–18	17.5–30
Diameter (μm)	45–70	70–110	50–90	40–60	50–90	35–45	70–100	35–50	(60)-80–130
Segments Length/ Diameter	0.4–0.8	0.4–1.1	(0.4-)0.7–1.5	1.4–2.2	0.6–1.8 (–2.4)	(0.8-) 1–1.6	0.5–1.4	0.7–1.6	0.4–0.9 (–1.4)
Trichoblasts									
Length (μm)	300	1100	–	500	300–1500	240–5000	-	50–63	75–400
Diameter of basal cell (μm)	13–25	20–38	–	17–35	17–28	17–23	-	10–12.5	17–20
Spermatangial branches									
Length (μm)	-	150–225	–	160–250	160–250	–	–	–	–
Diameter (μm)	-	30–60	–	30–55	37–55	–	–	–	–
Cystocarps									
Length (μm)	300	400–520	–	310–420	300–500	200–330	–	–	–
Diameter (μm)	230	300–500	–	270–380	200–400	140–250	–	–	–
Carpospores									
Length (μm)	–	67–93	–	62–88	55–80	40–65	–	–	–
Diameter (μm)	-	15–28	–	17–30	15–33	10–30	–	–	–
Tetrasporangia									
Size (μm)	43–45×45–53	20–30×15–30	–	22–27×25–27	17–35×17–28	30–35×35–43	–	–	47–50×50–63
Cover cells	3	2	–	3	3	3	–	3	3

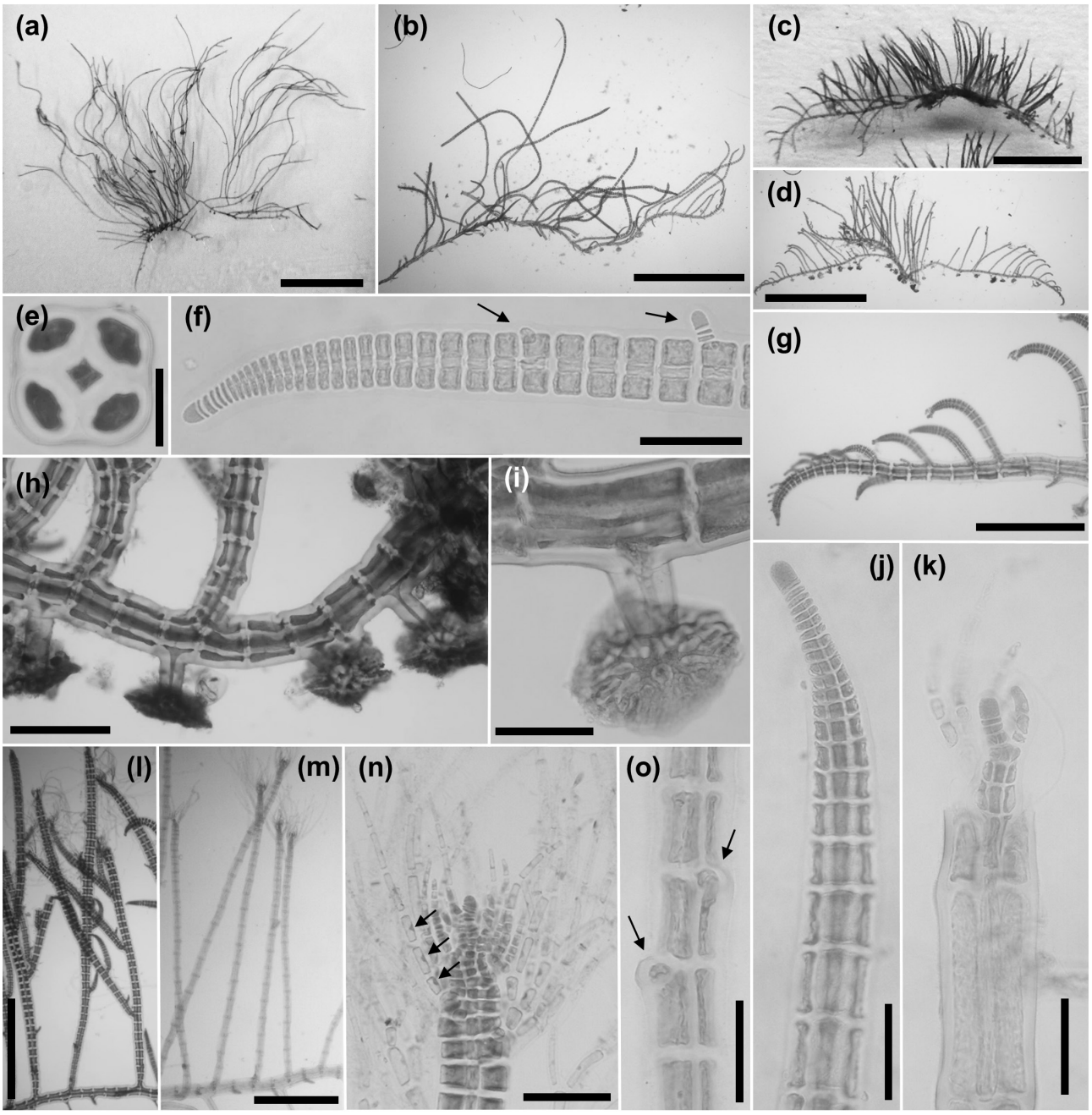

FIGURE 3 *Bryocladia scopulorum* complex: vegetative morphology. (a) Habit of the epitype of *Bryocladia scopulorum*. (b) Habit of topotype material of *Bryocladia caespitosa*. (c) Habit of *Bryocladia bidwelliorum* sp. nov. (d) Habit of *Bryocladia croajingolongensis* sp. nov. (e) Cross-section of an axis with a central axial cell and four pericentral cells. (f) Apex of a prostrate axis bearing young endogenous branches (arrows). (g) Apex of a prostrate axis bearing dorsally erect axes and producing lateral branches. (h) Prostrate axis bearing rhizoids ventrally and erect axes dorsally. (i) Rhizoid in open connection with the pericentral cell. (j) Apical cell of an erect axis. (k) Damaged erect axis resuming growth. (l) Erect axes with endogenous branches irregularly arranged. (m) Unbranched erect axes. (n) Apex of an erect axis with profusely developed trichoblasts composed of uninucleate cells (arrows show nuclei). (o) Erect axis with scar cells of trichoblasts (arrows). (e, i), *B. caespitosa*; (f), *B. wadjemupensis*; (g), *B. croajingolongensis*; (h, m, n), *B. bidwelliorum*; (j, l), *B. canariensis*; (k), *B. amanguorum*; (o), *B. kanamalukana*. Scale bars: (a) = 5 mm; (b, c, d) = 3 mm; (e, o) = 40 μm; (f, j, k) = 50 μm; (g) = 400 μm; (h) = 260 μm; (i, n) = 100 μm; (l) = 900 μm; (m) = 1.7 mm.

HOMOTYPIC SYNONYMS: *Polysiphonia caespitosa* (Pocock) Hollenberg, 1968, *Brittonia* 20, p. 79.

GENBANK ACCESSION NUMBERS OF TOPOTYPE MATERIALS: MT676175-78 (*rbc*L); MT676032-4 (*cox*1).

TYPE LOCALITY: Muizenberg, False Bay, Cape Province, South Africa (Pocock, 1953).

HABITAT AND DISTRIBUTION: Intertidal turfs growing on sand-covered rocks. Molecularly confirmed in South Africa, the Azores, Atlantic Iberian Peninsula,

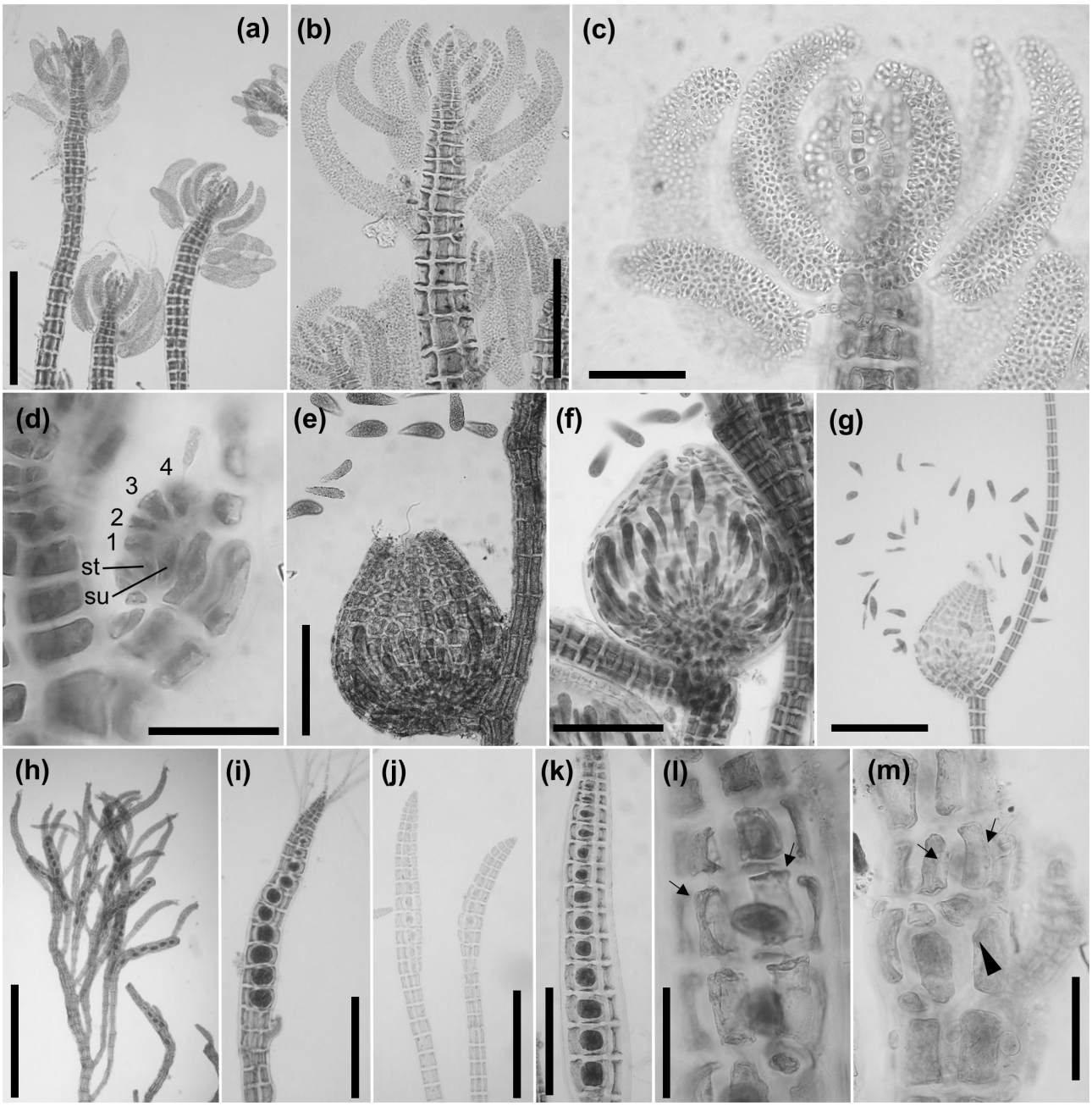

FIGURE 4 *Bryocladia scopulorum* complex: reproductive morphology. (a) Apex of erect axes with spermatangial branches. (b) Spermatangial branches without sterile apical cells. (c) Spermatangial branches formed on the two branches of trichoblasts. (d) Procarp with a supporting cell (su), a sterile basal cell (st) and a four-celled carpogonial branch (1–4). Figs (e–g) Cystocarps. (h) Profusely branched erect axes with series of tetrasporangia. (i–k) Apices of erect axes with tetrasporangia. (l–m) Tetrasporangia with two presporangial cover cells (arrows) and a postsporangial cover cell (arrowhead) in Fig. (m). (a, c, f, k, l), *B. bidwelliorum*; (b), *B. caespitosa*; (d, h, i), *B. croajingolongensis*; (e, m), *B. canariensis*; (g), *B. kanamalukana*; (j), *B. wadjemupensis*. Scale bars: (a) = 300 μm; (b, e, f, j, k) = 200 μm; (c) = 60 μm; (d) = 30 μm; (g) = 250 μm; (h) = 1 mm; (i) = 300 μm; (l, m) = 50 μm.

and French Mediterranean, and known in a single site in South Australia (Yorke Peninsula).

Detailed descriptions of this species from South Africa and Atlantic Iberian Peninsula are provided in Pocock (1953, as *Falkenbergiella*) and Díaz-Tapia & Bárbara (2013, as *Polysiphonia*), respectively. Measurements of topotype materials are provided in Table 2.

Bryocladia amanguorum Díaz-Tapia sp. nov. (Figures 3k, 7)

DIAGNOSIS: Distinguished from other species in the complex only by DNA data, with sequences of the holotype MT676281 (*rbc*L) and MT676132 (*cox*1) as reference for the species.

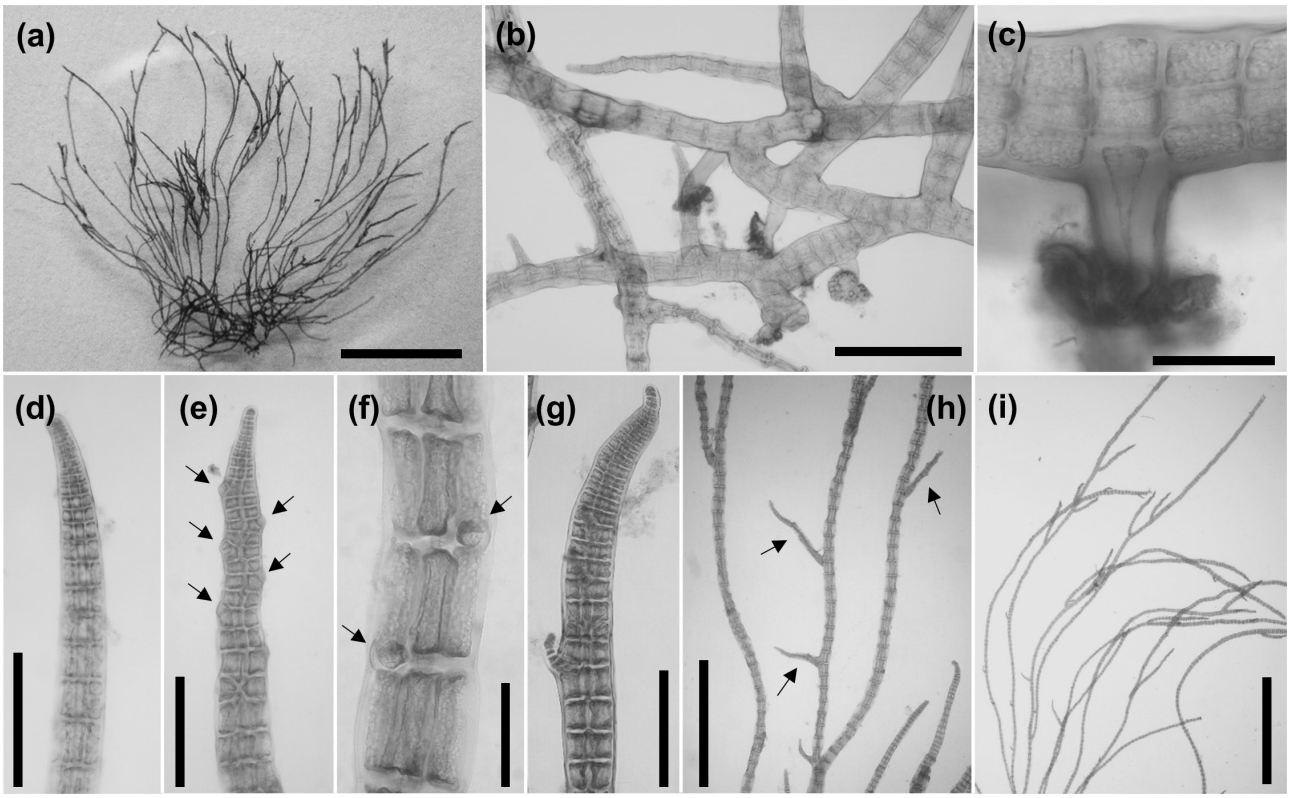

FIGURE 5 Epitype of *Bryocladia scopulorum*. (a) Habit. (b) Prostrate axes. (c) Rhizoid in open connection with the pericentral cell. (d–e) Apex of an erect axis without (d) or with (e) trichoblast initials on every segment (arrows). (f) Scar cells of trichoblasts (arrows). (g) Apex of an erect axis with endogenous young branches. (h) Basal parts of erect axes with adventitious branches (arrows). (i) Apical parts of erect axes scarcely branched at irregular intervals. Scale bars: (a) = 5 mm; (b, e, g) = 170 μm; (c, f) = 80 μm; (d) = 150 μm; (h) = 1 mm; (i) = 2 mm.

HOLOTYPE (designated here): Turf with female gametophytes and tetrasporophytes collected on 21.iii.2015, leg. Pilar Díaz-Tapia & Joana F. Costa, PD1722; MELUA 132373a.

TYPE LOCALITY: Green Head, Western Australia, Australia.

ETYMOLOGY: "*amanguorum*" refers to Amangu, the traditional owners of the land from which this species is described.

HABITAT AND DISTRIBUTION: Intertidal turfs growing on sand-covered rocks. Only known at its type locality.

Bryocladia bidwelliorum Díaz-Tapia sp. nov. (Figures 3c,h,m,n, 4a,c,g,k,l, 8)

DIAGNOSIS: Distinguished from other species in the complex because it has four pericentral cells and tetrasporangia with two cover cells; sequences of the holotype MT676253 (*rbc*L) and MT676115 (*cox*1) as reference for the species.

HOLOTYPE (designated here): Turf with female gametophytes and tetrasporophytes, collected on 9.xi.2016, leg. Pilar Díaz-Tapia, PD2739; MEL 2457666.

TYPE LOCALITY: Pebbly beach, Mallacoota, Victoria, Australia.

ETYMOLOGY: "*bidwelliorum*" refers to Bidwell, the traditional owners of the land that includes the type locality of this species.

OTHER SPECIMENS EXAMINED: PD954; SANT 35655; Glaneuse Reef, Point Lonsdale, Victoria, Australia; 2.xii.2014; sterile specimens. PD1043; MELUA 132362a; Kilcunda, Victoria, Australia; 23.xii.2014; tetrasporophytes. PD1117; SANT 35656; Killarney Beach, Victoria Australia; 27.xii.2014; female gametophytes and tetrasporophytes. PD 1282; MELUA 132365a; Tween Reefs, Inverloch, Victoria, Australia; 19.i.2015; sterile specimens. PD3200; MELUA 132375a; Boat Harbour, Tasmania, Australia; 2.xi.2017; sterile specimens. PD3289; MELUA 132381a; Wynyard, Tasmania, Australia; 4.xi.2017; tetrasporophytes. PD3335; MELUA 132382a; George Town, Tasmania, Australia; 5.xi.2017; male gametophpytes. PD4638; MEL 2524095; Cable Bay, South Australia, Australia; 29.x.2018; sterile specimens. PD4690; SANT 35657; Pondalowie Bay, South Australia, Australia; 30.x.2018; tetrasporophytes.

HABITAT AND DISTRIBUTION: Intertidal sand-covered rocks. From the Yorke Peninsula (South Australia) to Mallacoota (Victoria), and Tasmania.

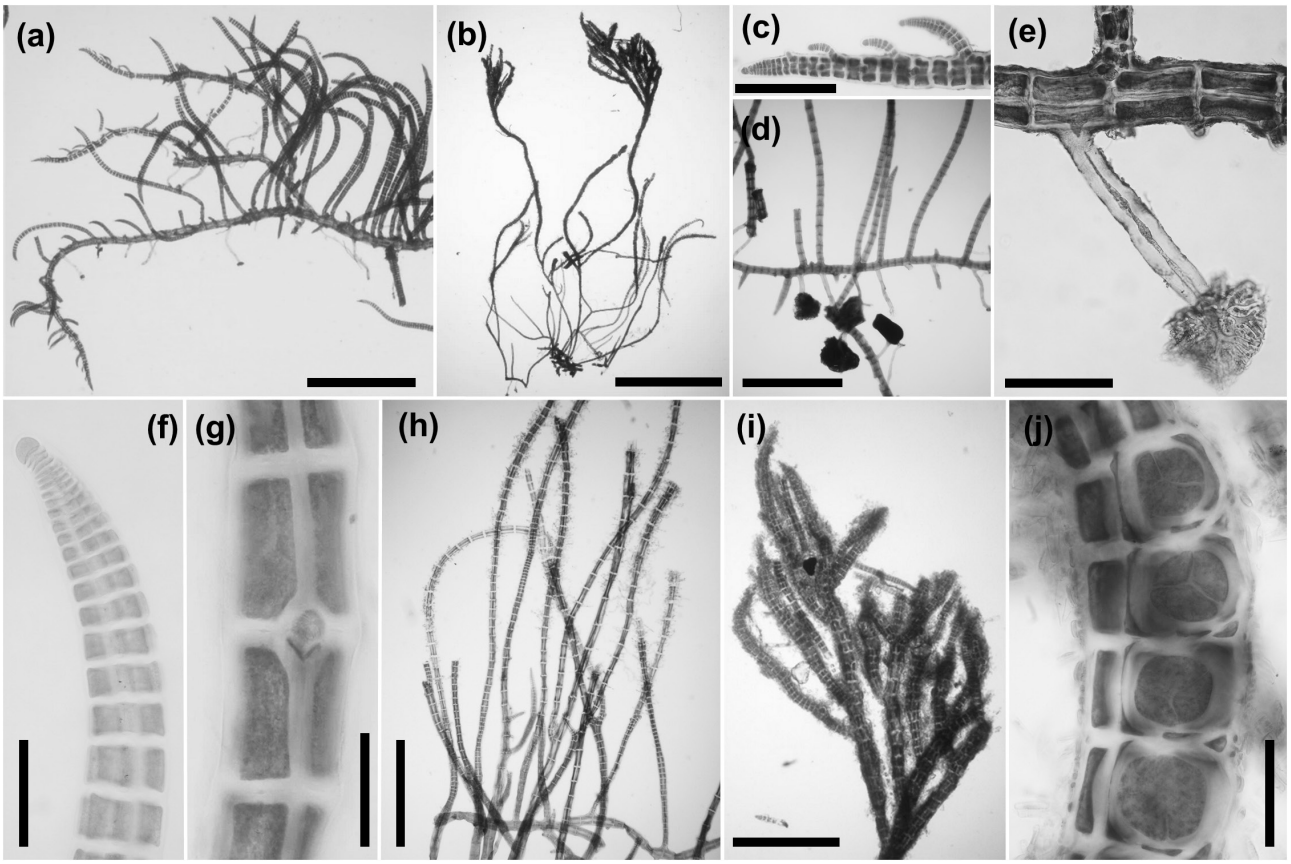

FIGURE 6 *Bryocladia caespitosa* from South Africa. (a–b) Habit. (c) Apex of a prostrate axis with young endogenous branches. (d) Prostrate axes. (e) Rhizoid in open connection with the pericentral cell. (f) Apex of an erect axis. (g) Erect axis with a scar cell of a trichoblast. (h) Erect axes unbranched or with adventitious branches at basal parts. (i) Apex of an erect axis profusely branched, with tetrasporangia. (j) Detail of tetrasporangia. Scale bars: (a) = 1.4 mm; (b) = 2.8 mm; (c) = 450 μm; (d) = 800 μm; (e) = 150 μm; (f, j) = 75 μm; (g) = 50 μm; (h, i) = 750 μm.

Bryocladia canariensis Díaz-Tapia sp. nov. (Figures 3j,l, 4e,m, 9)

DIAGNOSIS: Distinguished from other species in the complex only by DNA data, with sequences of the holotype MT676169 (*rbc*L) and MT676027 (*cox*1) as reference for the species.

HOLOTYPE (designated here): Turf with male and female gametophytes and tetrasporophytes collected on 14.vi.2018, leg. Pilar Díaz-Tapia & Laura Muñoz Luque, PD4344; SANT 35602.

TYPE LOCALITY: Castillo de Ágila, Lanzarote, Canary Islands, Spain.

ETYMOLOGY: "*canariensis*" refers to the name of the Macaronesian archipelago where the type locality of the species is found.

OTHER SPECIMENS EXAMINED: PD4332, SANT 35600, Caleta de Famara, Lanzarote, Canary Islands, Spain, 13.vi.2018, sterile plants; PD4339, SANT 35601, Castillo de Águila, Lanzarote, Canary Islands, Spain, 14.vi.2018, male and female gametophytes and tetrasporophytes; PD4396, SANT 35596, Puerto del Carmen, Lanzarote, Canary Islands, Spain, 15.vi.2018, tetrasporophytes.

HABITAT AND DISTRIBUTION: Intertidal turfs growing on sand-covered rocks in sites with moderate to high wave exposure. Molecularly confirmed only in Lanzarote.

Bryocladia croajingolongensis Díaz-Tapia sp. nov. (Figures 3d,g, 4d,h,i, 10)

DIAGNOSIS: Distinguished from other species in the complex only by DNA data, with sequences of the holotype MT676238 (*rbc*L) and MT676070 (*cox*1) as reference for the species.

HOLOTYPE (designated here): Tetrasporophytes and sterile plants collected on 13.xi.2016, leg. Pilar Díaz-Tapia, PD2869; MEL 2457778.

TYPE LOCALITY: Shipwreck Creek, Victoria, Australia.

ETYMOLOGY: "*croajingolongensis*" refers to the Croajingolong National Park, which includes the type locality of the species.

OTHER SPECIMENS EXAMINED: PD899; SANT 35658; Queenscliff, Victoria, Australia; 1.xii.2014; tetrasporophyte. PD770; SANT 35659; 13th beach, Victoria,

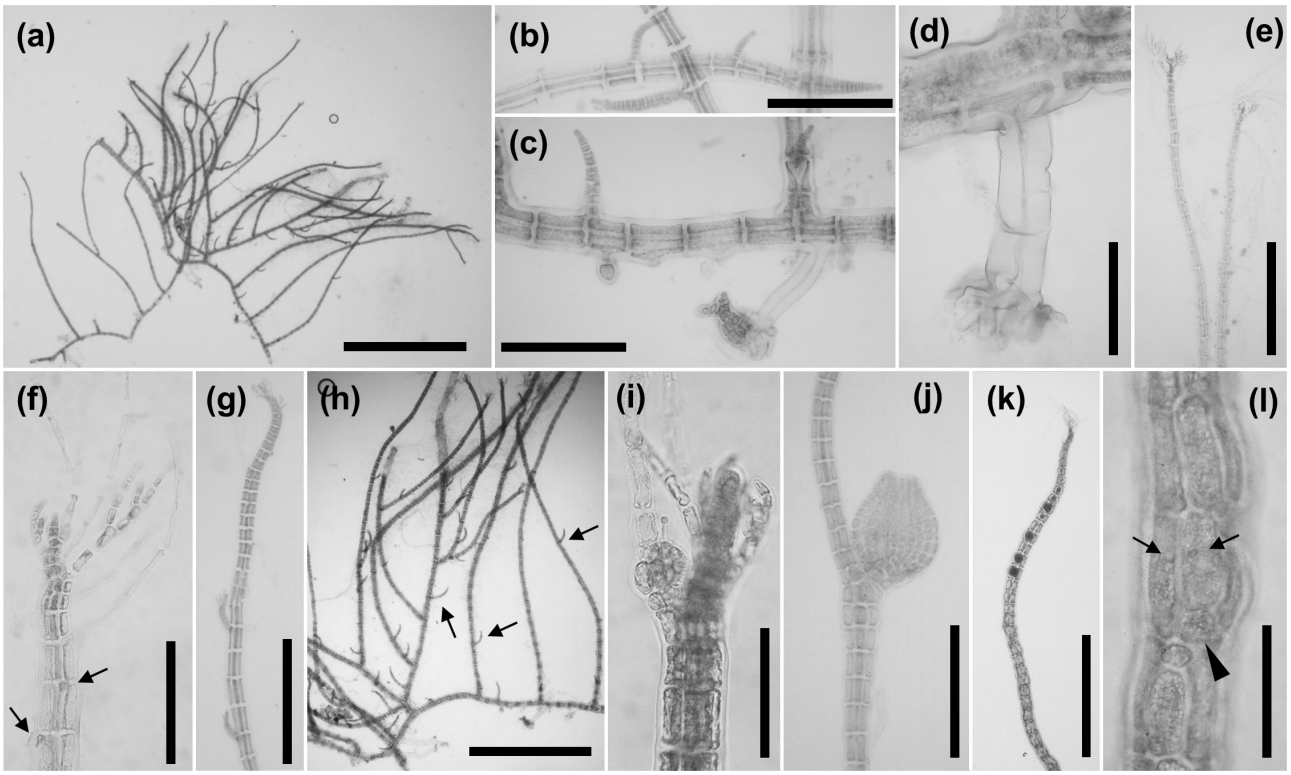

FIGURE 7 *Bryocladia amanguorum* Díaz-Tapia sp. nov. (a) Habit. (b) Apex of a prostrate axis bearing young erect axes. (c) Prostrate axis with rhizoids. (d) Rhizoid in open connection with the pericentral cell. (e) Apex of erect axes. (f) Apex of an erect axis with trichoblasts or their scar cells (arrows) on every segment spirally arranged. (g) Erect axis with young adventitious branches. (h) Basal parts of erect axes with adventitious branches (arrows). (i) Procarp. (j) Cystocarp. (k) Erect axis with tetrasporangia. (l) Tetrasporangia with two presporangial (arrows) and one postsporangial (arrowhead) cover cells. Scale bars: (a) = 1.7 mm; (b, c) = 200 μm; (d, f) = 100 μm; (e) = 400 μm; (g, j) = 350 μm; (h) = 1 mm; (i, l) = 80 μm; (k) = 1 mm.

Australia; 9.xii.2014; male and female gametophytes and tetrasporophytes. PD2716; MEL 2457647A; Bastion Point, Victoria, Australia; 8.xi.2016; female gametophytes. PD2813; MEL 2457729A; Bastion Point, Victoria Australia; 11.xi.2016; male and female gametophytes. PD3197; MELUA 132374a; 2.xi.2017; Boat Harbor, Tasmania, Australia; tetrasporophytes. PD3326; SANT 35660; George Town, Tasmania, Australia; 5.xi.2017; sterile specimens. PD3486; SANT 35661; Bicheno, Tasmania, Australia; 9.xi.2017; tetrasporophytes.

HABITAT AND DISTRIBUTION: Intertidal turfs growing on sand-covered rocks. Molecularly confirmed in Australia from the Yorke Peninsula (South Australia) to Mallacoota (Victoria), and Tasmania.

Bryocladia kanamalukana Díaz-Tapia sp. nov. (Figures 3o, 4g, 11)

DIAGNOSIS: Distinguished from other species in the complex only by DNA data, with sequences of the holotype MT676280 (*rbc*L) and MT676133 (*cox*1) as reference for the species.

HOLOTYPE (designated here): Turf with female gametophytes and tetrasporophytes collected on 5.xi.2017, leg. Pilar Díaz-Tapia & Joana F. Costa, PD3337; SANT 35662.

TYPE LOCALITY: George Town, Tasmania, Australia.

ETYMOLOGY: "*kanamalukana*" refers to the indigenous name of the Kanamaluka river that flows into the sea near to the type locality of the species.

HABITAT AND DISTRIBUTION: Intertidal sand-covered rocks. Only known at its type locality.

Bryocladia wadjemupensis Díaz-Tapia sp. nov. (Figures 3f, 4j, 12)

DIAGNOSIS: Distinguished from other species in the complex only by DNA data, with sequences of the holotype MT676275 (*rbc*L) and MT676126 (*cox*1) as reference for the species.

HOLOTYPE (designated here): Turf of sterile specimens collected on 15.iii.2015, leg. Pilar Díaz-Tapia & Joana F. Costa, PD 1617; SANT 35663.

TYPE LOCALITY: Rottnest Island, Western Australia, Australia.

OTHER SPECIMEN EXAMINED: PD1868; SANT 35664; Gladstone, Queensland, Australia; 13.v.2015; tetrasporophyte.

ETYMOLOGY: "*wadjemupensis*" refers to the indigenous name of Wadjemup island that is the type locality of the species.

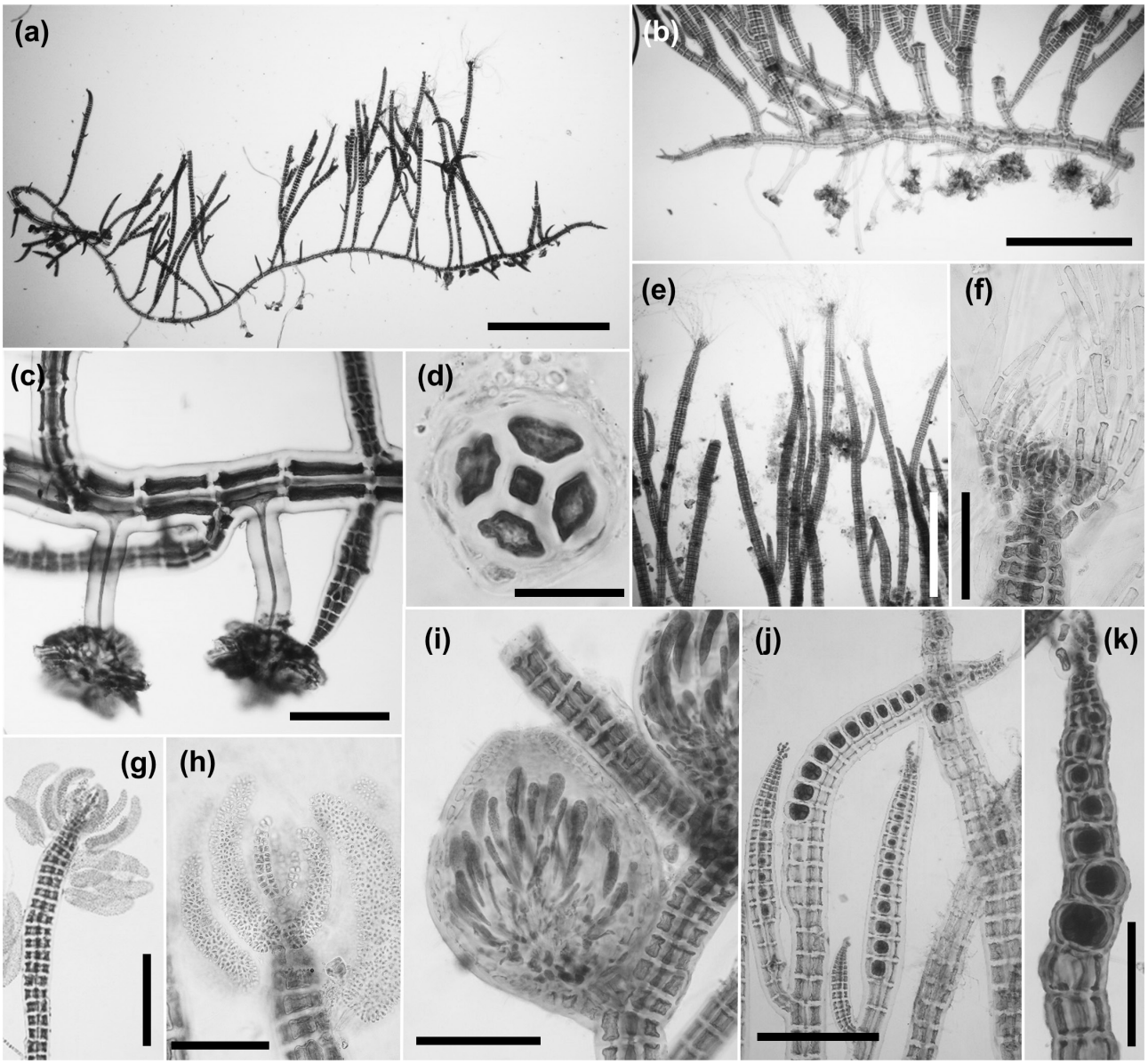

FIGURE 8 *Bryocladia bidwelliorum* Díaz-Tapia sp. nov. (a) Habit. (b) Prostrate axes bearing rhizoids ventrally and erect axes dorsally. (c) Rhizoids in open connection with the pericentral cells. (d) Cross-section of an axis with a central axial cell and four pericentral cells (e) Erect axes scarcely branched endogenously. (f) Apex of an erect axis with trichoblasts on every segment spirally arranged. (g) Apex of an erect axis with spermatangial branches. (h) Spermatangial branches lacking sterile apical cells. (i) Cystocarp. (j–k) Apex of erect axes bearing tetrasporangia arranged in straight (j) or slightly spiral series (k). Scale bars: (a) = 2 mm; (b, e) = 800 μm; (c, g) = 200 μm; (d) = 35 μm; (f, h) = 100 μm; (i, k) = 180 μm; (j) = 350 μm.

HABITAT AND DISTRIBUTION: Subtidal turfs and pontoon of a marina. Western Australia and Queensland.

Bryocladia yuatiorum Díaz-Tapia sp. nov. (Figure 13)

DIAGNOSIS: Distinguished from other species in the complex only by DNA data, with sequences of the holotype MT676279 (*rbc*L) and MT676061 (*cox*1) as reference for the species.

HOLOTYPE (designated here): Turf with tetrasporophytes collected on 20.iii.2015; leg. Pilar Díaz-Tapia & Joana F. Costa, PD1712; MELUA 132372a.

TYPE LOCALITY: Grey, Western Australia, Australia.

HABITAT AND DISTRIBUTION: Intertidal sand-covered rocks. Only known in two sites in Western Australia, the type locality and Rottnest Island.

ETYMOLOGY: "*yuatiorum*" refers to the Yuat, the traditional owners of the land that includes type locality of this species.

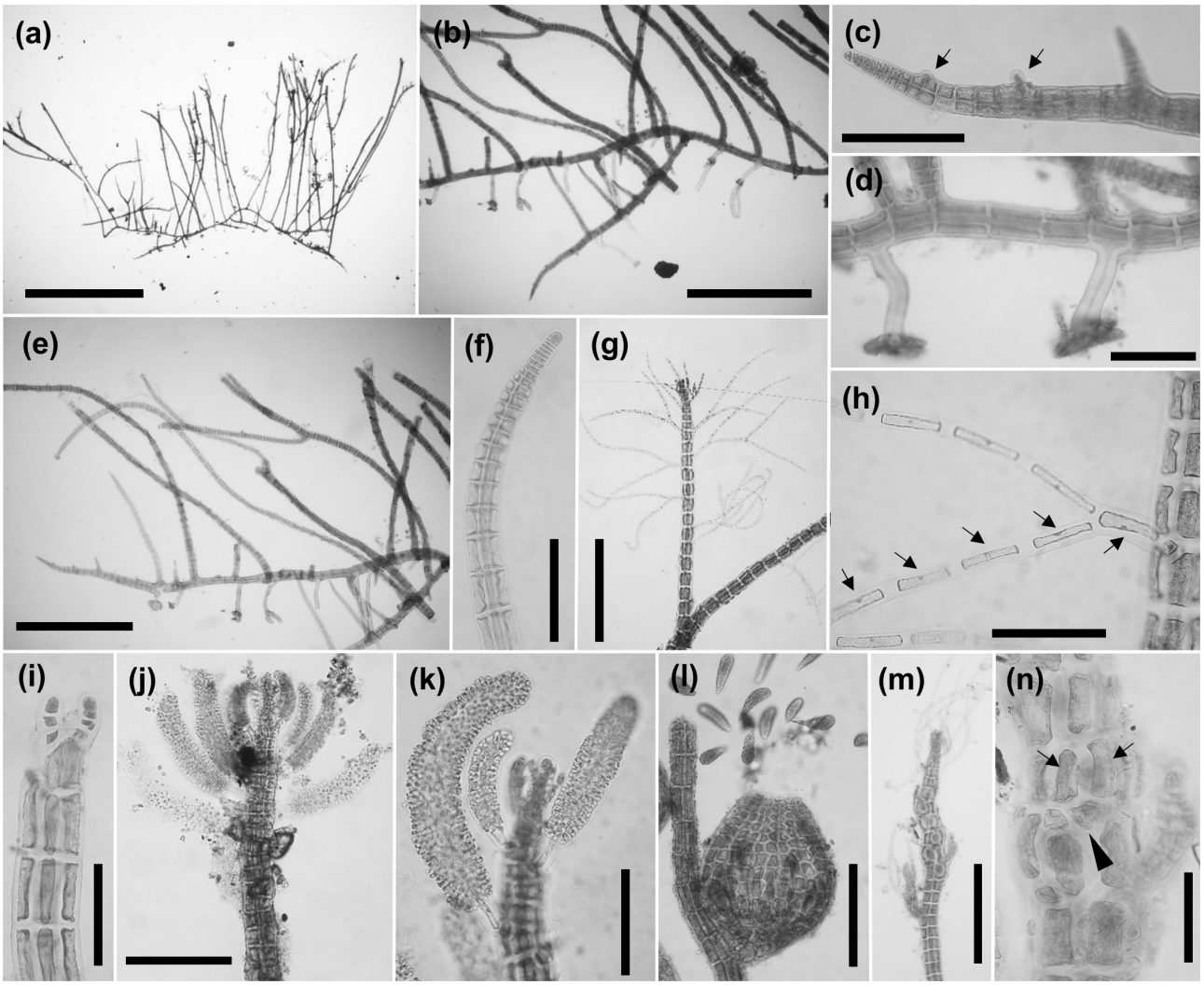

FIGURE 9 *Bryocladia canariensis* Díaz-Tapia sp. nov. (a) Habit. (b) Prostrate axes bearing erect axes dorsally and rhizoids ventrally. (c) Apex of a prostrate axis with young endogenous branches (arrows) formed after the division of the pericentral cells. (d) Prostrate axes with rhizoids in open connection with the pericentral cells. (e) Prostrate axes bearing dorsally unbranched or irregularly branched erect axes. (f) Apex of an erect axis without trichoblasts. (g) Apex of an erect axis with trichoblasts on every segment spirally arranged. (h) Trichoblasts with uninucleate (arrows show nuclei) cells. (i) Apex of a damaged erect axis resuming growth. (j) Apex of an erect axis with spermatangial branches on every segment spirally arranged. (k) Spermatangial branches without sterile apical cells. (l) Cystocarp. (m) Apex of an erect axis with tetrasporangia. (n) Tetrasporangial segment with two presporangial (arrows) and one postsporangial (arrowhead) cover cells. Scale bars: (a) = 3 mm; (b) = 1 mm; (c, l) = 200 μm; (d) = 150 μm; (e) = 850 μm; (f, h, i) = 100 μm; (g) = 400 μm; (j) = 150 μm; (k) = 90 μm; (m) = 300 μm; (n) = 60 μm.

DISCUSSION

In this study, we resolved the taxonomy of nine of the species delineated in the "*Polysiphonia*" *scopulorum* complex (Díaz-Tapia, Ly, & Verbruggen, 2020), clarifying the generic assignment of the lineage in which the complex is placed together with another seven species that were transferred to *Bryocladia*. We designated an epitype for *Polysiphonia scopulorum*, proposed *Bryocladia scopulorum* comb. nov., reinstated *Bryocladia caespitosa* comb. nov. for the only observed species of the complex found in its type locality in South Africa, and described seven new species. Three species of the complex (*P. scopulorum* 2, 10, and 12 in Figure 1) were not formally described in this study because they were collected only once, were sterile, and were only sequenced with one molecular marker (*rbc*L gene). Additional efforts to obtain new collections of these three species are required to advance our knowledge of these species and formally describe them.

Taxonomic position and circumscription of *Bryocladia*

Our phylogenetic analyses showed that the most recent circumscription of *Polysiphonia* included two main

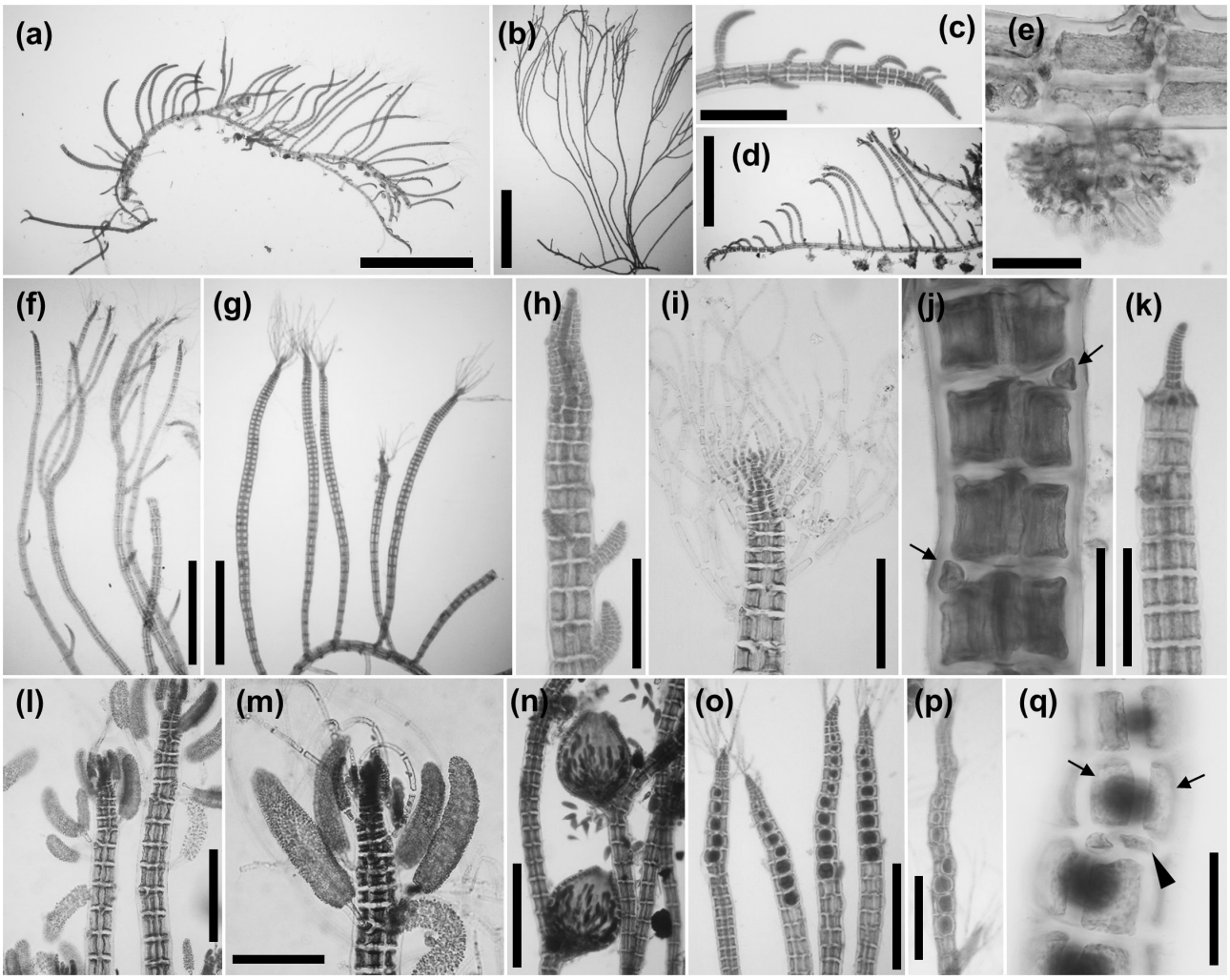

FIGURE 10 *Bryocladia croajingolongensis* Díaz-Tapia sp. nov. (a) Habit of the holotype (MEL 2457778), with unbranched erect axes. (b) Habit of a specimen with erect axes profusely branched in the apical parts. (c) Apex a prostrate axis with young endogenous branches. (d) Prostrate axis bearing rhizoids ventrally and erect axes dorsally. (e) Rhizoid in open connection with the pericentral cell. (f) Apical parts of erect axes with endogenous branches irregularly arranged. (g) Unbranched erect axes. (h) Apex of an erect axis bearing young endogenous branches. (i) Apex of an erect axis with profusely developed trichoblasts. (j) Scar cells of trichoblasts (arrows). (k) Apex of a damaged erect axis resuming growth. (l) Apical parts of erect axes bearing spermatangial branches. (m) Spermatangial branches without sterile apical cells. (n) Cystocarps. (o, p) Series of tetrasporangia. (q) Tetrasporangia with two presporangial (arrows) and one postsporangial (arrowhead) cover cells. Scale bars: (a) = 2 mm; (b) = 3 mm; (c, p) = 350 μm; (d) = 1 mm; (e) = 80 μm; (f, g) = 800 μm; (h, i) = 180 μm; (j) = 60 μm; (k, m) = 150 μm; (l) = 200 μm; (n) = 450 μm; (o) = 400 μm; (q) = 70 μm.

lineages (Díaz-Tapia, Tüney-Kizilkaya, & Taşkin, 2022; Savoie & Saunders, 2019), indicated as *Polysiphonia* and *Bryocladia* in Figure 1. These lineages were not placed as sister in our tree, but their phylogenetic relationships remained unresolved. Previous studies using different taxon selection placed these two clades either as sister lineages or paraphyletic with respect to the tribe Streblocladieae, as is the case in our Figure 1 (Bustamante et al., 2015; Díaz-Tapia, Pasella, & Verbruggen, 2018; Díaz-Tapia, Tüney-Kizilkaya, & Taşkin, 2022; Huisman et al., 2017; Savoie & Saunders, 2019). Moreover, the relationships of a representative species of each of these clades were resolved as monophyletic using a phylogenomic approach (Díaz-Tapia, Maggs, West, & Verbruggen, 2017). Even if these two clades are actually sister lineages, they are very divergent from one another, and we propose that they represent two genera, *Bryocladia* and *Polysiphonia*.

The main characters of the generitype *Bryocladia cervicornis* include having 9–10 pericentral cells (Kützing, 1847, 1864) and having rhizoids in open connection with the pericentral cells as revealed by our observations of topotype material. Among the family Rhodomelaceae, this combination of characters has been exclusively found in other species of the *Bryocladia* clade (i.e., *B. adamsiae*, *B. cuspidata*, and *B. thyrsigera*), as well as in *Lophosiphonia*. *Lophosiphonia* species are morphologically distinctive, with thin axes (<140 μm) sparsely branched (Díaz-Tapia & Bárbara, 2013; Díaz-Tapia, Tüney-Kizilkaya, & Taşkin, 2022), which contrasts with the thick axes of

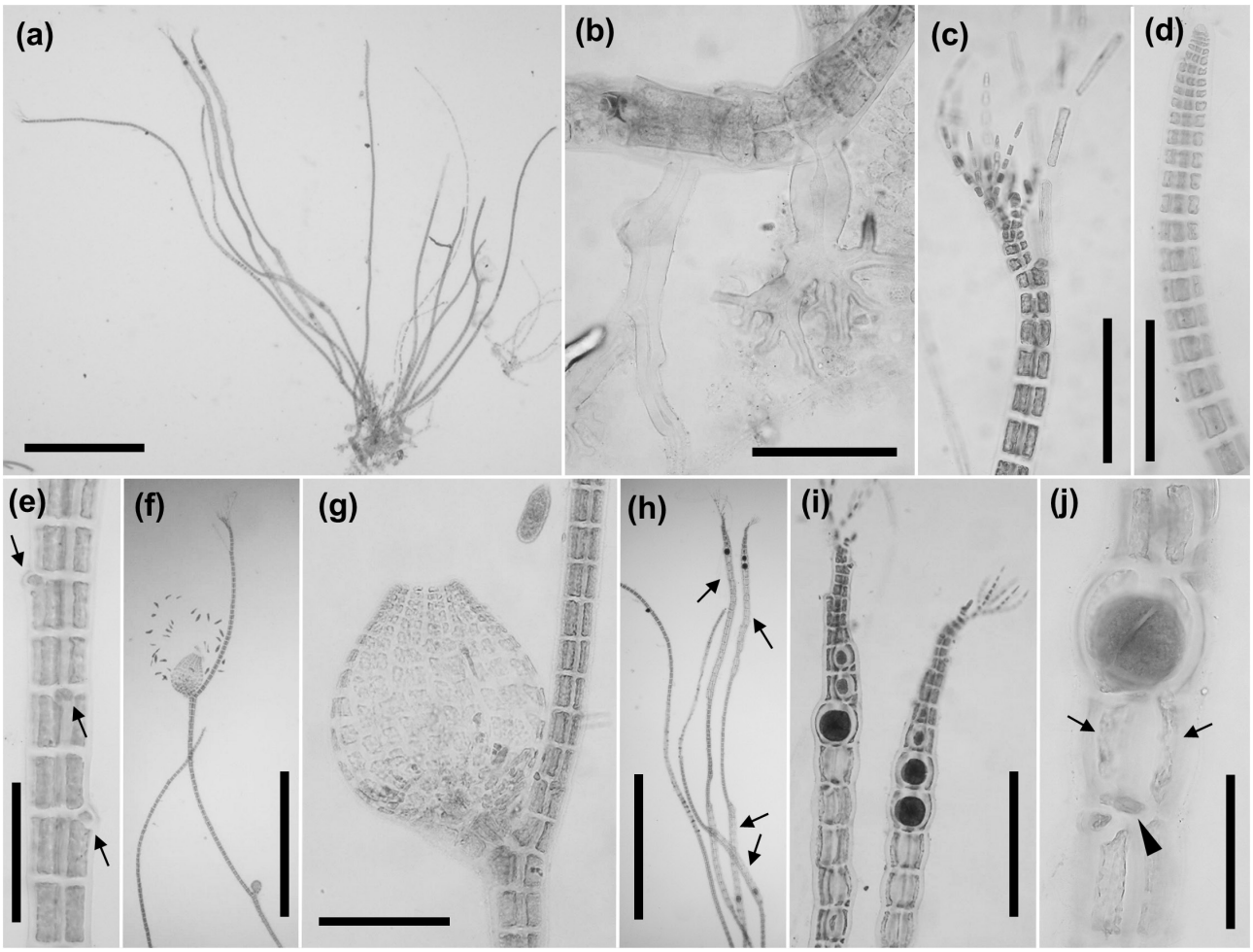

FIGURE 11 *Bryocladia kanamalukana* Díaz-Tapia sp. nov. (a) Habit. (b) Prostrate axis with rhizoids in open connection with the pericentral cells. (c) Apex of an erect axis with trichoblasts on every segment spirally arranged. (d) Apex of an erect axis lacking trichoblasts. (e) Erect axis with trichoblast scar cells (arrows). (f–g) Cystocarp. (h) Erect axes with series (arrows) of tetrasporangia at mid and apical parts. (i) Apex of erect axes with tetrasporangia. (j) Tetrasporangial segment with two presporangial (arrows) and one postsporangial (arrowhead) cover cells. Scale bars: (a, f, h) = 1 mm; (b, c) = 100 μm; (d, e) = 80 μm; (g) = 120 μm; (i) = 200 μm; (j) = 30 μm.

the *Bryocladia* with more than four pericentral cells (>160 μm) clothed by determinate lateral branches spirally arranged (Díaz-Tapia, Pasella, & Verbruggen, 2018; Kützing, 1864; Schneider & Searles, 1991). Thus, morphological characters indicate a close affinity between *B. cervicornis* and other species of the *Bryocladia* clade with more than four pericentral cells.

Unfortunately, DNA sequences of *Bryocladia cervicornis* are not available, and destructive sampling of the type or topotype specimens is not permitted. Interestingly, *B. thyrsigera* has been recently reported in China (Tan et al., 2021) and India (Kundu, 2022) based on molecular information (*rbc*L gene). These findings, together with the high morphological resemblance between *B. cervicornis* and *B. thyrsigera* suggest that both species might be closely related or even taxonomic synonyms, and further studies are required in this regard. Therefore, even in the absence of molecular data of specimens of *B. cervicornis* from its type locality, the particular combination of morphological characters of this species indicates that its placement in the *Bryocladia* clade is highly likely. Accordingly, we conclude that species of this clade can be assigned to *Bryocladia*, and our taxonomic proposals followed this. Certainty about this solution could only be definitively achieved through the determination of molecular information from topotype material from Java. This was not possible, and we preferred to adopt this solution rather than continue to perpetuate the unresolved taxonomy of one of the major clades in the tribe Polysiphonieae.

The genus *Bryocladia* was originally erected to include a species characterized by having ecorticate axes with 6–8 pericentral cells and spirally arranged short branches (Falkenberg, 1901; Schmitz & Falkenberg, 1897). Our taxonomic proposals require expanding the concept of this genus. A main feature is having rhizoids in open connection with the pericentral cells, shared with all species of the tribe Polysiphonieae (Díaz-Tapia, Maggs, McIvor, et al., 2017; Díaz-Tapia, Maggs, West, &

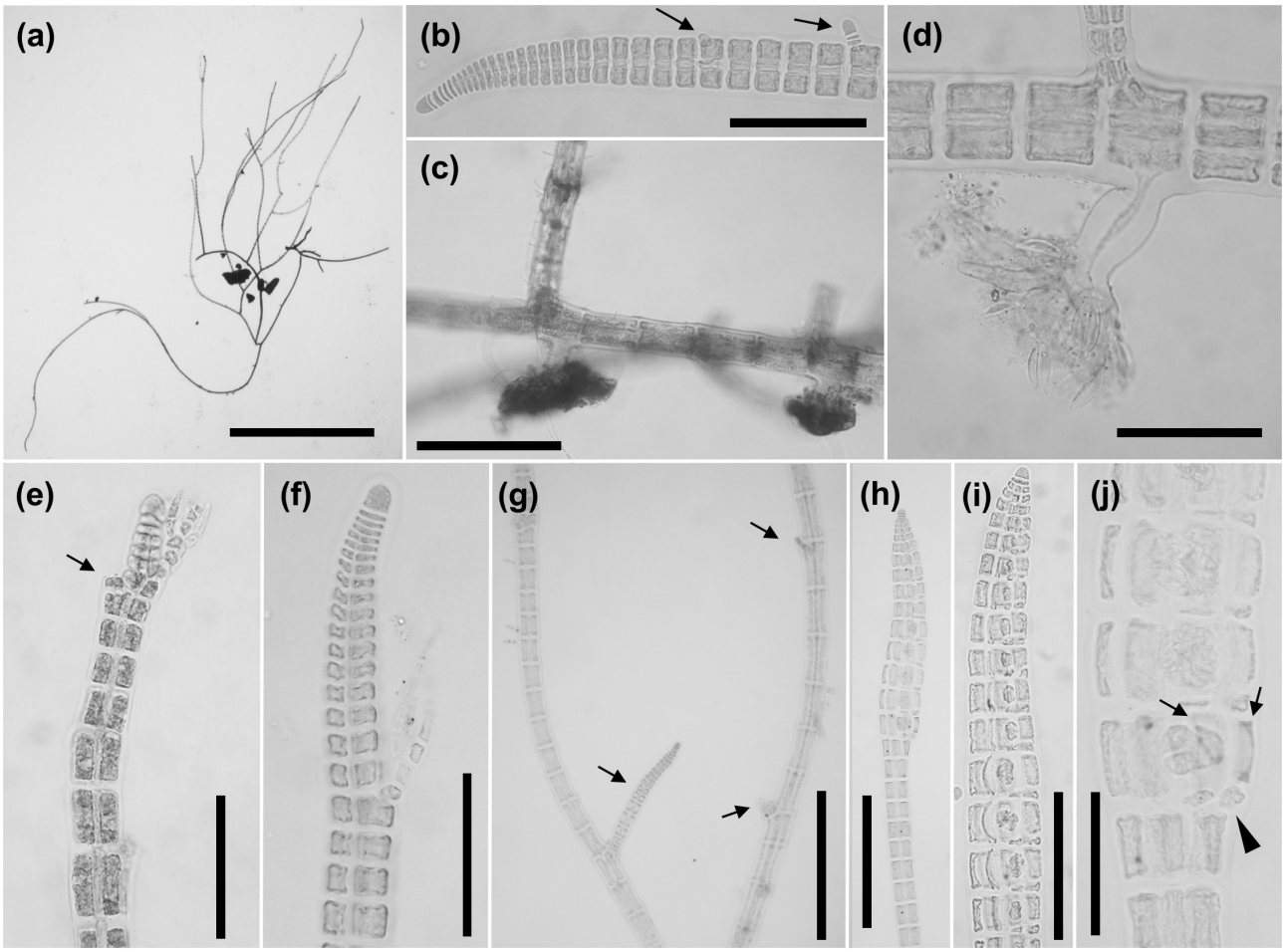

FIGURE 12 *Bryocladia wadjemupensis* Díaz-Tapia sp. nov. (a) Habit. (b) Apex of a prostrate axis bearing young erect axes (arrow). (c) Prostrate axis with rhizoids. (d) Rhizoid in open connection with the pericentral cell. (e) Apex of an erect axis with trichoblasts or their scar cells (arrow) on every segment. (f) Apex of an erect axis with a single trichoblast. (g) Erect axes with young adventitious branches (arrows). (h) Apex of an erect axis with tetrasporangia. (i) Straight series of tetrasporangia. (j) Tetrasporangia with two presporangial (arrows) and one postsporangial (arrowhead) cover cells. Scale bars: (a) = 3 mm; (b) = 80 μm; (c) = 170 μm; (d-f) = 60 μm; (g, h) = 200 μm; (i) = 100 μm; (j) = 50 μm.

Verbruggen, 2017). *Bryocladia* species are also characterized by having axes with four pericentral cells or a number that ranges between 6–8 and 9–12 and most species having only endogenous branches. The number of pericentral cells differs from *Lophosiphonia*, in which the molecularly confirmed species have a fixed number within each species (six or seven), while in *Polysiphonia* all species have four (Díaz-Tapia, Maggs, McIvor, et al., 2017; Díaz-Tapia, Maggs, West, & Verbruggen, 2017). The predominance of species with only endogenous branches in *Bryocladia* differs from *Polysiphonia*, in which all molecularly confirmed species have exogenous branches. However, there are exceptions in *Bryocladia*, and *B. adamsiae*, *B. cuspidata*, *B. thyrsigera*, or *B. villum* also produce exogenous branches. Therefore, the combination of characters proposed for the delineation of *Bryocladia* allow distinguishing most but not all species of the genus, and phylogenetic analyses are needed to confidently determine generic assignments of species in the tribe Polysiphonieae.

Assigning species to previously described taxa

Assigning names to cryptic species is often a tedious task for which decisions need to be made in the face of uncertainty around the molecular identities of type collections. In this work, we chose to designate a molecularly characterized epitype for *Bryocladia scopulorum* from the type locality, Rottnest Island, Western Australia. Several reasons led us to consider the holotype as ambiguous when attempting to assign newly collected specimens to *B. scopulorum*. First, three species of the *B. scopulorum* complex were identified in Rottnest Island, Western Australia (*B. scopulorum*, *B. wadjemupensis*, and *B. yuatiorum*), so molecular characterization of topotype material could not conclusively resolve the identity of *B. scopulorum*. Second, it is highly likely that type material could consist of a mixture of similar species. One of our three collections of *B. scopulorum* in the type locality included two of the species of the complex, *B. scopulorum* and

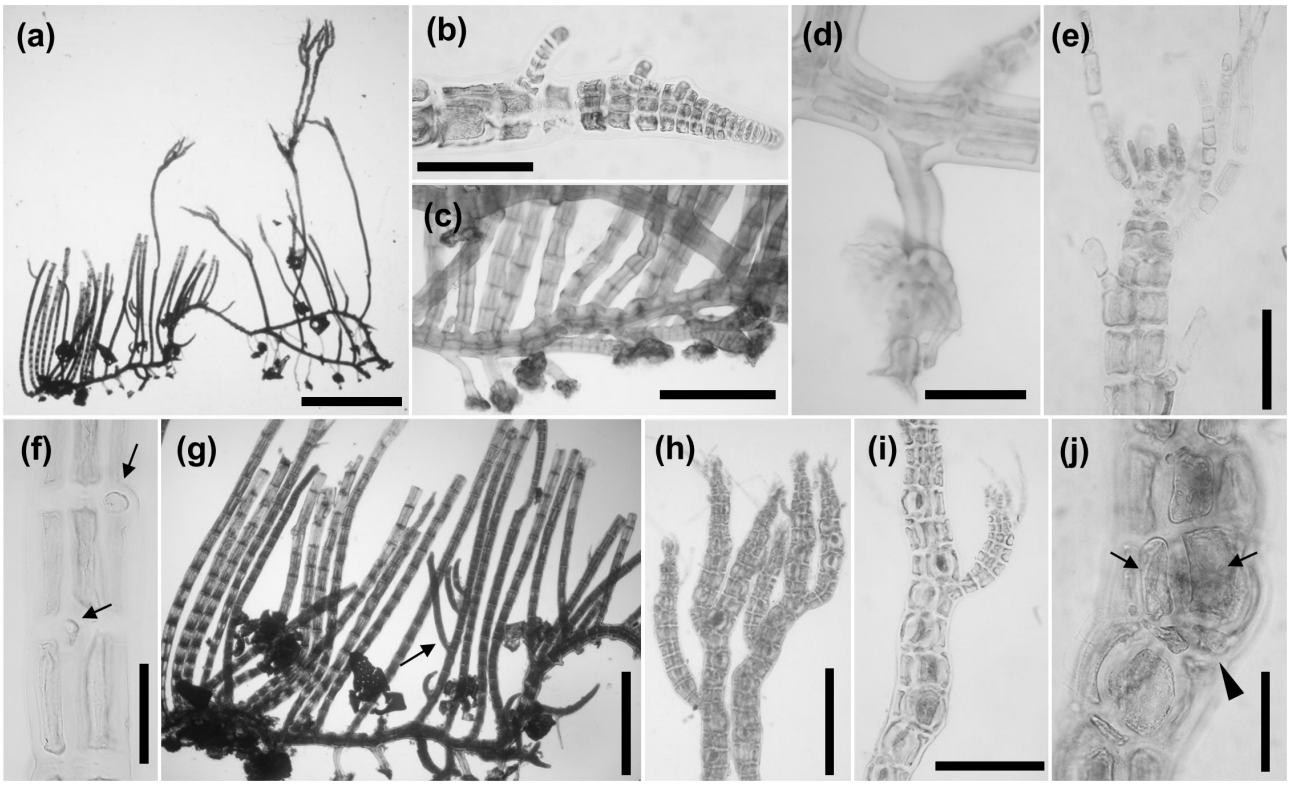

FIGURE 13 *Bryocladia yuatiorum* Díaz-Tapia sp. nov. (a) Habit. (b) Apex of a prostrate axis with young endogenous branches. (c) Prostrate axes bearing rhizoids ventrally and erect axes dorsally. (d) Rhizoid in open connection with the pericentral cell. (e) Apex of an erect axis with trichoblasts on every segment spirally arranged. (f) Erect axis with scar cells of trichoblasts (arrows). (g) Prostrate axes bearing erect axes with young adventitious branches (arrow). (h) Apex of an erect axis irregularly branched, bearing series of tetrasporangia. (i) Series of tetrasporangia. (j) Tetrasporangia with two presporangial (arrows) and one postsporangial (arrowhead) cover cells. Scale bars: (a) = 1.7 mm; (b) = 80 μm; (c) = 400 μm; (d) = 120 μm; (e, f, j) = 70 μm; (g) = 700 μm; (h) = 350 μm; (i) = 200 μm.

B. yuatiorum, growing intermixed in the same turfs. In our collection, these species could be initially separated immediately after collection based on subtle color differences. However, they were morphologically indistinguishable after preservation in formalin.

Obtaining DNA sequences from the type material was another option to resolve the identity of the holotype of *Bryocladia scopulorum*, but several problems prevented us from attempting this approach. The type collection includes the lectotype housed at TCD (Parnell et al., 2010, as *Polysiphonia*) and isotypes at BM and MEL. The lectotype of *B. scopulorum* belongs to Harvey's Travelling Set, housed at Trinity College of Dublin herbarium, and it is unavailable for loan (Parnell et al., 2010). The lectotype and isolectotypes are small, so a significant part of the specimens would have been needed for DNA sequencing, which we considered too wasteful a use of these unique and precious samples. Moreover, in addition to the potential issue of mixed species mentioned earlier, turf-forming species often have a variety of small epiphytes (<2 mm in length; Díaz-Tapia et al., 2013; Littler & Littler, 2013; Wallenstein et al., 2009). These additional species cannot be properly distinguished in pressed specimens and result in a significant likelihood of contamination issues. This problem would be aggravated because the type material of *B. scopulorum* is more than 150 years old, and sequencing small gene fragments of old herbarium specimens is particularly sensitive to contaminations (Saunders & McDevit, 2012). All these considerations led us to choose epitypification as the best solution for *B. scopulorum*.

Among the three species found in Rottnest Island, we selected as epitype the species that we found was most similar to the lectotype in appearance and grew in the most similar habitat. Our collections of *Bryocladia wadjemupensis* were from the shallow subtidal (–3 m), differing from the intertidal habitat described for *B. scopulorum* (Harvey, 1855). The specimens of *B. yuatiorum* were shorter (up to 6 mm in length) than the lectotype (15 mm). *Bryocladia scopulorum* was collected in the intertidal and its length ranges from 7 to 15 mm (this work, Huisman et al., 2017). The selected epitype is the same species that was recently molecularly and morphologically characterized in Rottnest Island (Huisman et al., 2017).

Bryocladia caespitosa is other relevant taxon name available for the species of the *B. scopulorum* complex, and even though it had been synonymized with *B. scopulorum* in the past, the relationships between

these species had not been studied using molecular data (Díaz-Tapia & Bárbara, 2013; Rull Lluch, 2002; Stegenga et al., 1997). The type locality of *B. caespitosa* is Muizenberg, South Africa (Pocock, 1953, as *Falkenbergiella caespitosa*), and our collections from this locality and other two South African sites resulted in the identification of a single species of the complex. *Bryocladia scopulorum* and *B. caespitosa* were resolved as distinct species in our phylogenies and should thus not be regarded taxonomic synonyms. We reinstate *Polysiphonia caespitosa* and transfer it to *Bryocladia* to reflect its phylogenetic position. Our material agrees with the original morphological description of the species (Pocock, 1953).

Bryocladia rudis from New Zealand has also been thought to be related to *B. scopulorum* based on its morphology (Harvey, 1855; Womersley, 1979; as *Polysiphonia*) and unfortunately, molecular data are not available for this species. However, *B. rudis* differs from *B. scopulorum* in having acute apices and a regular branching pattern that contrast with the dome-shaped apices and irregular branching of species in the *B. scopulorum* complex when branches are present (Adams, 1991, 1994; this work).

Other related taxon names are *Bryocladia villum* or *P. scopulorum* var. *villum* whose type locality is in Mexico (Agardh, 1863). Sequences of two different entities assigned to these names are available in GenBank (Díaz-Tapia, Maggs, et al., 2018; Savoie & Saunders, 2019; Stuercke & Freshwater, 2008). One of these entities is apparently restricted to the Pacific Americas (Savoie & Saunders, 2019), while the other has a wider distribution that includes southern Europe, Australia, and the Atlantic Americas (Díaz-Tapia, Maggs, et al., 2018; Stuercke & Freshwater, 2008). The taxonomy of these two entities needs further clarification, but both were resolved as different from all the species we consider as part of the *B. scopulorum* complex (Figure 1). These two species are red in color, and the thalli are slender (Díaz-Tapia, pers. obs. on our own collections and images available at http://www.boldsystems.org/), differing from the dark brown to black color and rigid texture of the species in the *B. scopulorum* complex. Given that phylogenetic positions, genetic divergences (>3.5% and 5.9% in the *rbc*L and *cox*1 gene markers, respectively; see tables S2–S3 in Díaz-Tapia, Ly, & Verbruggen, 2020), and morphology of the two entities assigned to *B. villum* clearly show that this species differs from *B. scopulorum*, *B. villum* should continue to be treated as a species rather than as a variety.

Delineation of seven new species

The seven new species described in this work were delineated based on molecular information (two gene markers, *rbc*L and *cox*1, and three methods, PTP, ABGD, and GMYC) but were generally morphologically indistinguishable from one another even after meticulous statistical analyses of morphological characters and morphometric traits (Díaz-Tapia, Ly, & Verbruggen, 2020; this work). The only character that unequivocally differentiates *Bryocladia bidwelliorum* from other species in the complex is that it has tetrasporangia with two presporangial cover cells, while an additional postsporangial cover cell is present in the other eight species of the complex in which this reproductive structure was observed. Most species in the Polysiphonieae have three cover cells (Díaz-Tapia, Maggs, McIvor, et al., 2017), but *B. bidwelliorum* and its close relative *B. adamsiae* are exceptions (Díaz-Tapia, Pasella, & Verbruggen, 2018). In turn, this pair of species differs in the number of pericentral cells (4 vs. 10–12, respectively). However, the utility of tetrasporangial cover cells for species identification is limited, as it requires reproductive tetrasporophytes. In fact, this character could not be determined for the three species of the complex that remain undescribed, for which only sterile material was found. Given that this complex represents several genuinely indistinguishable species, the use of DNA sequences is essential for accurate species identification in Australia or the Mediterranean, where more than one species has been detected.

The cryptic species in the *Bryocladia scopulorum* complex include several close relatives (*B. scopulorum*, *B. canariensis*, *B. caespitosa*, *B. yuatiorum*, and *B. croajingolongensis*) as well as a set of lineages that are not closely related (*B. bidwelliorum*, *B. amanguorum*, *B. wadjemupensis*, and *B. kanamalukana*). It is unclear at this stage whether morphological convergence among distant lineages, morphological stasis, or genetic constraints imposing limits to the evolution of novel morphological forms are responsible for this (Leliaert et al., 2014; Zuccarello et al., 2018). Further studies in the *Bryocladia* clade are required to elucidate the diversification of morphologies. However, this type of work will require better resolution of internal branches, potentially achievable using a phylogenomic approaches similar to those that have successfully resolved challenging phylogenies in the red algae at various taxonomic levels (Costa et al., 2016; Díaz-Tapia et al., 2019; Díaz-Tapia, Maggs, West, & Verbruggen, 2017; Díaz-Tapia, Rodríguez-Buján, et al., 2022; Iha et al., 2018).

CONCLUSIONS

This study improves the higher level classification of the tribe Polysiphonieae, proposing the name *Bryocladia* for one of its main lineages and restricting *Polysiphonia* to the lineage containing its type species. We formally described seven new species in *Bryocladia*, adding to the other species in this

lineage. This work provides an example of how extensive complexes of truly cryptic species can be resolved taxonomically based on molecular information, to carry out nomenclatural reconciliation with validly published species names. However, further work is required, as several species remain formally undescribed (e.g., there are two molecular *B. subtilissima*, a "*Polysiphonia*" sp., and three other species of the *B. scopulorum* complex that require additional collections), and the resolution of our single-gene phylogenies do not permit for detailed insights into evolutionary trends. Most species of this lineage are small and inconspicuous in the field despite often being abundant, and most of them inhabit algal turfs, arguably one of the most understudied macroalgal consortia. Thus, further efforts studying this type of assemblages, particularly in less explored regions, will surely result in the discovery of additional new species.

AUTHOR CONTRIBUTIONS

Pilar Díaz Tapia: Conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (supporting); investigation (equal); methodology (equal); writing – original draft (lead). **Heroen Verbruggen:** Conceptualization (equal); data curation (supporting); formal analysis (supporting); funding acquisition (lead); investigation (equal); methodology (equal); writing – review and editing (lead).

ACKNOWLEDGMENTS

We thank M. Ly, J. Costa, V. Marcelino, M. Brookes, C. Cremen, G. Bribiesca-Contreras, C. Jackson, I. Bárbara, K. Dixon, L. Le Gall, M. Verlaque, L. Muñoz, A. Neto for providing assistance during field and lab work. We also thanks to the Parks Victoria and Bush Blitz teams for assistance in the field. We thank Nicolien Sol for providing images of specimen L.4033460 and arranging for the loan of the *B. cervicornis* specimen L.4033461 from L herbarium, Naturalis Biodiversity Center. We thank J. Birch (MELU), A. Waskowicz (MELU), N. Karunajeewa (MEL) and I. Bárbara (SANT) for managing herbarium specimens. We thank J. Bolton for providing information about the holotype of *B. caespitosa*. We thank C. Schneider and M. Guiry for advice on nomenclatural issues. This research was supported by computational facilities of Centro de Supercomputación de Galicia (CESGA). Funding was provided by the Australian Biological Resources Study (grant 4-G046WSD). Field work in Australia was made possible through funding from the Holsworth Wildlife Research Endowment and Bush Blitz. Sampling in the Mediterranean was made possible through funding from the British Phycological Society.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Maximum-likelihood phylogeny of the tribe Polysiphonieae based on cox1 gene sequences. Branch support values are indicated on branches as non-parametric/ultrafast bootstrap when ≥80% and ≥95%, respectively; asterisks represent full support.

Table S1. Specimens and DNA sequences used in molecular and morphological analyses. GenBank accessions printed in bold indicate sequences used in the phylogeny when several were avaliable.

How to cite this article: Díaz-Tapia, P., & Verbruggen, H. (2024). Resolving the taxonomy of the *Polysiphonia scopulorum* complex and the *Bryocladia* lineage (Rhodomelaceae, Rhodophyta). *Journal of Phycology*, *60*, 49–72. https://doi.org/10.1111/jpy.13402