

The forgotten genus *Pseudoderbesia* (Bryopsidales, Chlorophyta)

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Abstract – The poorly known siphonous green algal genus *Pseudoderbesia* was originally described from the Caribbean coast of Colombia, and the Canary Islands. Here we describe a collection of *Pseudoderbesia* from Rhodes, Greece, representing the first report of the genus since its original description in 1991. Cultured plants of *Pseudoderbesia* were characterized by upright, regularly dichotomously branched siphons, developing from long stolonoid siphons. Molecular phylogenetic analysis based on *rbcl* and *tufA* sequences confirmed the placement of *Pseudoderbesia* in the family Bryopsidaceae, and shows a sister relationship with *Bryopsis*. Although this is the first record of *Pseudoderbesia* from the Mediterranean Sea, it is possible that the genus is more widespread and has previously been confused with morphologically similar, but unrelated taxa, such as *Pseudochlorodesmis furcellata*, or that it has been erroneously attributed to juvenile stages of larger bryopsidalean algae.

Bryopsidineae / marine green algae / molecular systematics / *Pseudoderbesia arbuscula* / Ulvophyceae

INTRODUCTION

The siphonous green algal genus *Pseudoderbesia* was described by Calderon and Schnetter (1991) based on isolates from the Caribbean coast of Colombia, and the Canary Islands. The Colombian samples were formally described as a new species, *P. arbuscula* E.Calderon & Schnetter, while the authors remained indecisive on whether or not the morphologically slightly different samples from the Canary Islands represented a separate species.

Pseudoderbesia is characterized by small, delicate thalli, a few millimetres in height, composed of prostrate siphons that are attached by rhizoids, and give rise to upright, dichotomously branched filaments. The thin siphons contain numerous elongated plastids, each with a single pyrenoid. *Pseudoderbesia* was placed in the family Bryopsidaceae of the order Bryopsidales based on its delicate

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siphonous thallus architecture and the presence of chloroplasts as only type of plastid (homoplastidy) (Calderon & Schnetter, 1991). Only the gametophytic phase has been observed in culture, with gametangia that develop directly from transformed erect siphonous branches (Calderon & Schnetter, 1991).

The original publication of *Pseudoderbesia* was in Spanish, in a local Colombian journal, *Caldasia*, not widely read by phycologists. This may be one of the reasons why the genus has remained largely unnoticed, and has until today not been reported again in the Caribbean Sea, the Canary Islands, or any other region. In this study, we report on a recent collection of a species belonging to the genus *Pseudoderbesia* from Rhodes, Greece. We provide a description based on cultured material, and assess the systematic position of the genus based on molecular data.

MATERIAL AND METHODS

Minute siphonous thalli (<1 cm) were collected by scuba diving on 10 September 2011 in Ladiko, Rhodes (36.318887N, 28.207352E) on a subtidal cliff, ca. 20 m deep. The siphons were grown in sterile 1x modified Provasoli enriched seawater (West, 2005) at 23°C, under a 12 h:12 h light-dark cycle with a photon flux rate of 25-30 $\mu\text{E m}^{-2} \text{s}^{-1}$. Unialgal cultures were established by repeatedly cutting apical parts of the siphons using fine surgical scissors, and transferring them into fresh medium. Cultures were studied with a Leitz-Diaplan bright field microscope (Leica Microsystems, Wetzlar, Germany) and an Olympus SZX10 stereo microscope (Olympus Co., Tokyo, Japan). Photographs were taken with a ColorView (Olympus) digital camera mounted on the microscopes. Drawings were made with a camera lucida on the bright field microscope. A culture isolate is preserved as a dried herbarium specimen and in formalin in the herbarium of Ghent University (GENT) under accession number HV03339.

Molecular phylogenetic analyses were based on *rbcL* and *tufA* sequences (Table 1). DNA of *Pseudoderbesia* was extracted from algal cultures. In addition DNA was extracted from an unidentified siphonous alga collected from the same locality, one specimen of *Pedobesia lamourouxii*, and three specimens belonging to the genus *Derbesia* (Table 1). DNA extraction, PCR amplification and sequencing were performed as described in Verbruggen *et al.* (2009a). Sequences have been deposited in EMBL/GenBank under accession numbers LK022429-LK022452. A dataset of 48 *rbcL* (1293 bp) and 36 *tufA* sequences (888 bp) was assembled, representing the main clades of Bryopsidales (Verbruggen *et al.*, 2009a) (Table 1). Species names or numbers of *Codium* and *Bryopsis* refer to the same taxa as in Verbruggen *et al.* (2007) and Hollants *et al.* (2013), respectively. Sequences of the two genes were first aligned separately based on the corresponding amino-acid sequences in BioEdit (Hall, 1999), and then concatenated for phylogenetic analysis. Maximum likelihood (ML) and rapid bootstrap analysis was performed using RAxML under the GTRCAT model via the RAxML BlackBox web-server (<http://embnet.vital-it.ch/raxml-bb/>) with default settings (Stamatakis *et al.*, 2008).

Table 1. List of samples used in this study with collection numbers and EMBL/Genbank accession numbers. Sequences newly generated for this study are in bold

	<i>rbcL</i>	<i>tufA</i>
<i>Avrainvillea lacerata</i> (HV599)	FJ432635	FJ432651
<i>Avrainvillea nigricans</i> (HV891)	FJ432636	FJ432652
<i>Bryopsisidella neglecta</i> (Kobara, s.n.)	AY004766	
<i>Bryopsis corymbosa</i> (HEC4772)	HF583296	LK022441
<i>Bryopsis foliosa</i> (F.0001)	HF583297	LK022442
<i>Bryopsis muscosa</i> (HV1238)	HF583299	LK022443
<i>Bryopsis myosuroides</i> (F.0174)	HF583307	LK022444
<i>Bryopsis</i> sp. 2 (WE2)	HF549165	LK022439
<i>Bryopsis</i> sp. 20 (KE1)	LK022435	LK022452
<i>Bryopsis</i> sp. 21 (TZ0170)	HF549174	LK022440
<i>Bryopsis</i> sp. 24 (HEC12698)	HF583359	LK022445
<i>Bryopsis</i> sp. 28 (ODC1747)	HF583404	LK022446
<i>Bryopsis</i> sp. 9 (JH021)	HF583416	LK022447
<i>Caulerpa flexilis</i> (Fama nr.1 / CA049)	AJ512485	DQ652532
<i>Caulerpa taxifolia</i> (Hanyuda s.n. / Fama s.n.)	AB054016	AJ417939
<i>Caulerpella ambigua</i> (TS78)	FJ432638	FJ432655
<i>Chlorodesmis fastigiata</i> (HV102 / TS24)	FJ432639	
<i>Codium coralloides</i> (KRK003)	EF107977	LK022436
<i>Codium duthieae</i> .1 (KZN2K4.1)	EF107983	JX463040
<i>Codium lucasii</i> .cap.1 (KZN2K4.22)	EF108054	BoLD
<i>Codium pernambucensis</i> (LL0361)	EF108096	JQ966947
<i>Codium platylobium</i> (KZN2K4.10)	EF108067	FJ535856
<i>Codium setchellii</i> .1 (HV01075)	EF108073	LK022437
<i>Codium taylorii</i> (HV01062)	EF108084	LK022438
<i>Derbesia marina</i> (Woolcott)	AF212142	
<i>Derbesia</i> sp. 1 (HV01448)	LK022431	LK022449
<i>Derbesia</i> sp. 2 (HV01298)	LK022430	LK022448
<i>Derbesia</i> sp. 3 (HV01600)	LK022432	
<i>Derbesia tenuissima</i> (H.0755)	FJ535852	FJ535857
<i>Dichotomosiphon tuberosus</i> (Hanyuda s.n.)	AB038487	
<i>Flabellia petiolata</i> (HV1202)	FJ432640	
<i>Halimeda discoidea</i> (Hanyuda s.n. / SOC299)	AB038488	AY826360
<i>Halimeda opuntia</i> (Hanyuda s.n. / HV61)	AB038489	AM049967
<i>Ostreobium</i> sp. (H0753)	FJ535853	FJ535859
<i>Pedobesia lamourouxii</i> (HV01252)	LK022429	
<i>Pedobesia ryukyuensis</i> (Woolcott)	AY004768	
<i>Penicillus dumetosus</i> (Lam)	AY942175	
<i>Pseudochlorodesmis furcellata</i> (HV1250)	FJ432642	
<i>Pseudochlorodesmis</i> sp. (HV1204)	FJ432643	FJ432656
<i>Pseudocodium floridanum</i> (NSF.I23)	AM909692	AM909697
<i>Pseudocodium natalense</i> (KZNB2241)	AM909693	AM049969
<i>Pseudoderbesia</i> sp. (HV3339)	LK022434	LK022451
<i>Rhipilia crassa</i> (H0748)	FJ432645	FJ432657
<i>Rhipiliopsis profunda</i> (DML51973)	FJ432647	FJ432659
<i>Tydemania expeditionis</i> (Lam & Zechman s.n. / HV873)	AY942161	FJ432661
<i>Udotea flabellum</i> (Lam & Zechman s.n.)	AY942166	
<i>Udotea glaucescens</i> (H0862)	FJ432650	
unidentified siphon (HV3164b)	LK022433	LK022450

RESULTS

The field collected specimen consisted of a minute erect and regularly dichotomously branched siphon, about 5 mm high. Cultured plants (Figs 1-18) formed creeping stolon-like siphons, firmly attached to the culture dish by short rhizoids that were formed in opposite pairs at regular intervals along the siphons (Figs 10-12). At the position of the holdfasts, the stolon-like siphons gave rise to upright, regularly dichotomously branched siphons (Figs 4-10, 12). In full grown cultures, the width of the upright siphons gradually attenuated toward the apices, from 70-130 μm near the base to 15-30 μm below the apices. Diameter of the stolon-like siphons was 30-45 μm . Apical growth was observed in the creeping and upright siphons (Fig. 15). The only plastids observed were chloroplasts (homoplastidy), which were elongated, 5-12 μm long and 2-5 μm wide (Figs 16-18). Each chloroplast contained one or sometimes two pyrenoids, about 1 μm in diameter. The siphons showed vigorous cytoplasmic streaming. Only vegetative growth was observed. Older cultures lacked differentiation in creeping and upright siphons and showed irregular branching.

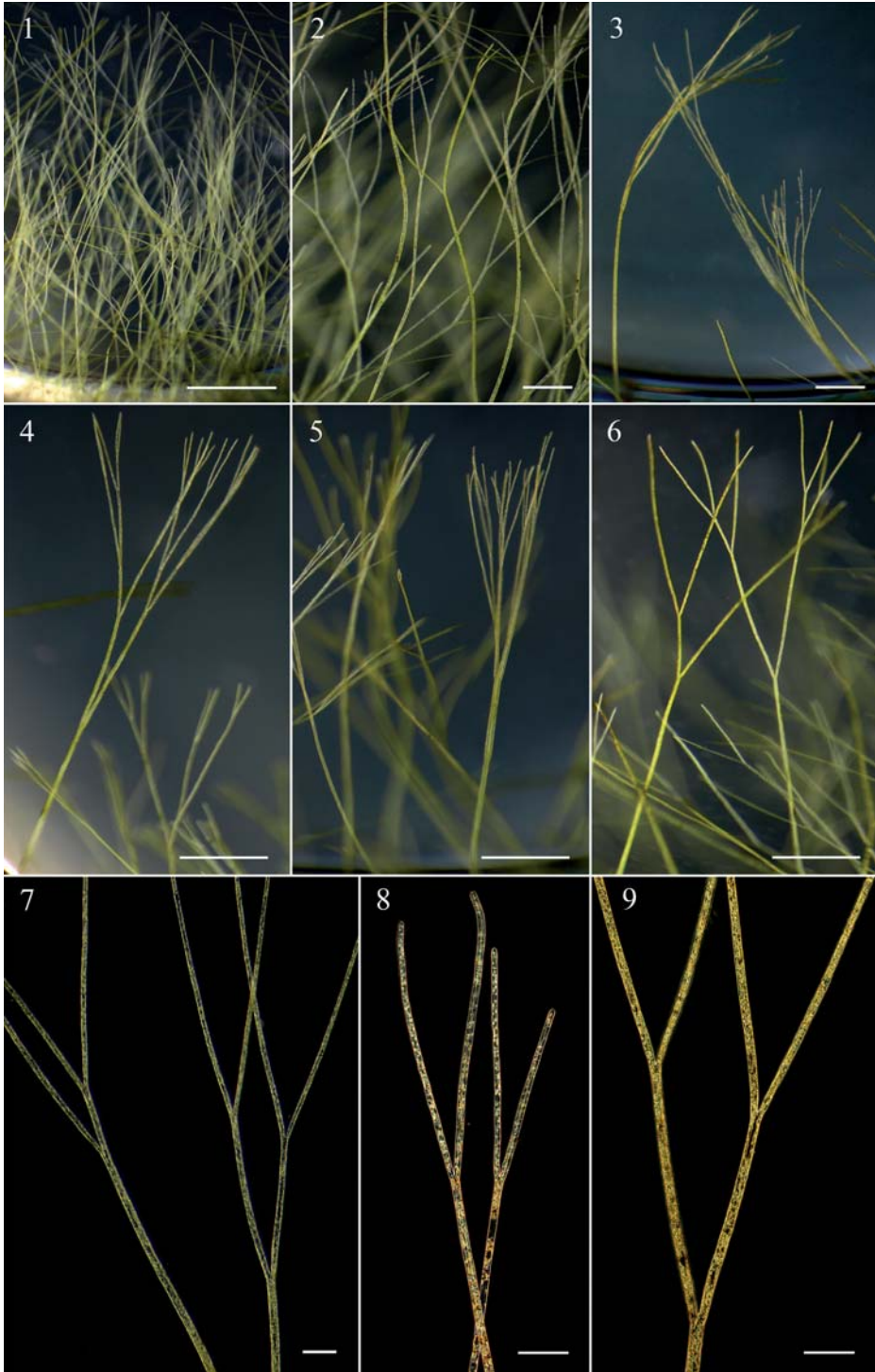
The maximum likelihood phylogeny of the *rbcL-tufA* alignment was congruent with published phylogenies of the Bryopsidales (Verbruggen *et al.*, 2009a, b), showing two main clades corresponding to the suborders Halimedineae and Bryopsidineae. The Bryopsidineae included three clades corresponding to the families Bryopsidaceae, Codiaceae and Derbesiaceae. *Pseudoderbesia* was inferred as sister to the genus *Bryopsis*, within the Bryopsidaceae, with high bootstrap support (Fig. 19).

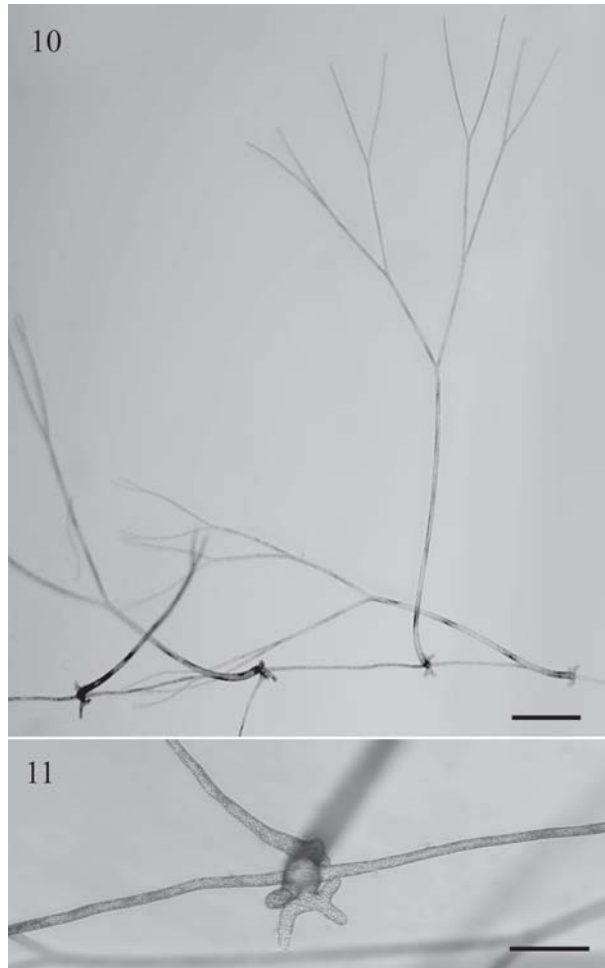
DISCUSSION

The scarcity of records and the apparently scattered geographical distribution of *Pseudoderbesia* is likely a result of undersampling. Because of its diminutive size, *Pseudoderbesia* is easily overlooked or may have been erroneously attributed to morphologically similar green algae, such as *Pseudochlorodesmis furcellata* (see below), or juvenile stages of larger bryopsidalean algae. With this paper, we want to bring the genus back to the attention, and expect that this will result in additional records in the Atlantic Ocean and Mediterranean Sea, and a better view of its geographical distribution.

Although *Pseudoderbesia* is morphologically distinct from other members of the Bryopsidales by its regularly branched upright siphons developing from an extensive stolonoid branching system, it may be confused with some other siphonous green algae with which it bears superficial resemblance, such as *Bryopsidella*, *Pseudochlorodesmis*, *Chlorodesmis* and *Derbesia*. The gametophytic thallus of *Bryopsidella* resembles *Pseudoderbesia* in having branched prostrate siphons and upright siphons, but differs from it by the upright siphons being either unbranched or pinnately branched, and the lack of pyrenoids (Rietema, 1975; Calderón-Sáenz & Schnetter, 1989).

Figs 1-9. Culture of *Pseudoderbesia* sp. (HV03339) from Rhodes, Greece, showing regularly dichotomously branched erect siphons developing from creeping stolon-like siphons (the stolonoid siphons are not visible on the photographs). Scale bars = 5 mm (Fig. 1), 1 mm (Figs 2-6), 100 μm (Figs 7-9). ▶





Figs 10-11. Culture of *Pseudoderbesia* sp. (HV03339). **10.** Stolon-like siphon, attached by short rhizoids formed in opposite pairs at regular intervals along the siphon, giving rise to erect, regularly dichotomously branched siphons. Scale bar = 1 mm. **11.** Details of rhizoid. Scale bar = 200 μ m.

Pseudochlorodesmis and *Chlorodesmis* resemble *Pseudoderbesia* in their dichotomously branched siphons. In particular, *Pseudochlorodesmis furcellata*, a species widely reported in the Mediterranean Sea and NE Atlantic Ocean (Guiry & Guiry, 2014; Guiry *et al.*, 2014), may be confused with *Pseudoderbesia* because of the regular dichotomously branched siphons (Zanardini, 1860; Børgesen, 1925; Coppejans, 1983). *Pseudochlorodesmis* and *Chlorodesmis* differ from *Pseudoderbesia* by the constrictions of the siphons at dichotomies (at least at the base of the thallus) and the lack of prostrate stolonoid-like siphons (Womersley, 1984; Kraft, 2007), although it should be noted that this distinction between the genera may become blurred by morphological variability and plasticity. Perhaps a taxonomic more reliable character is the type of plastids: *Pseudochlorodesmis*

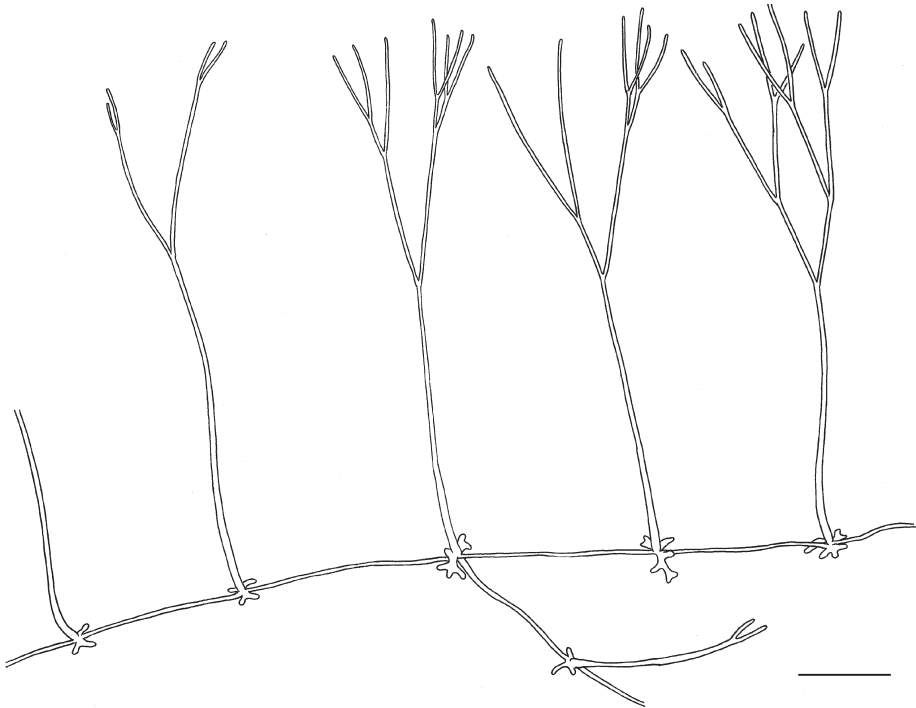
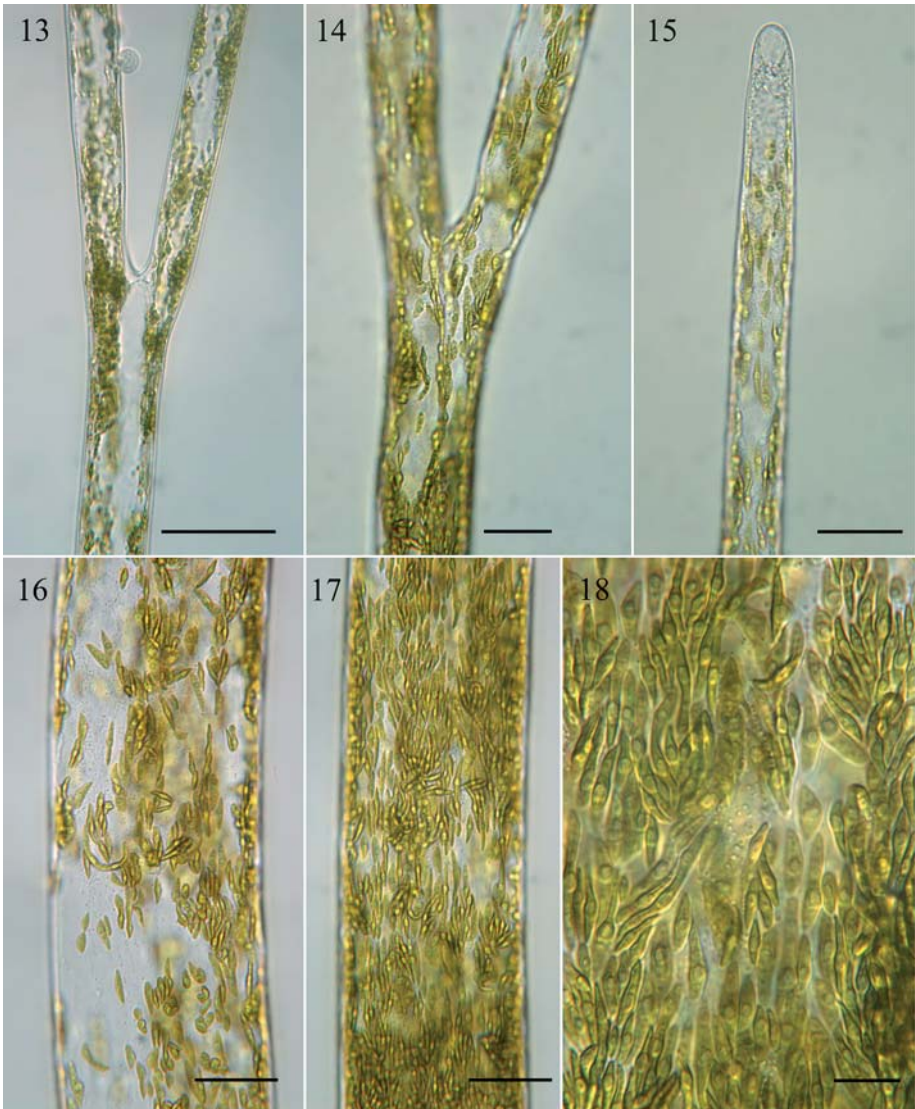


Fig. 12. Culture of *Pseudoderbesia* sp. (HV03339), showing stolon-like siphon, attached by short rhizoids formed in opposite pairs at regular intervals along the siphon, giving rise to erect, regularly dichotomously branched siphons. Scale bar = 1 mm.

and *Chlorodesmis* exhibit heteroplastidy (containing both chloroplasts and amyloplasts), while *Pseudoderbesia* contains chloroplasts only. This feature, however, has, to our knowledge, not been thoroughly investigated in Mediterranean *P. furcellata*. The distinction between *Pseudoderbesia* and *Pseudochlorodesmis* has been confirmed by molecular phylogenetic data: *Pseudoderbesia* is placed within the suborder Bryopsidineae (Fig. 19), while *Pseudochlorodesmis* falls within the Halimedineae (Verbruggen *et al.*, 2009b).

Fertile thalli of *Derbesia* can be distinguished from fertile thalli of *Pseudoderbesia*: *Derbesia* has a vesicular gametophytic phase and a filamentous sporophytic phase producing specialized lateral sporangia. *Pseudoderbesia*, on the other hand, has a gametophytic phase with unspecialized gametangia, which develop directly from siphonous branches (Calderon & Schnetter, 1991). Sterile sporophytes of some *Derbesia* species, however, are much more difficult to distinguish from sterile gametophytes of *Pseudoderbesia*. The sporophytic stage of *Pseudoderbesia* is unknown and may also have been misidentified. As discussed by Calderon & Schnetter (1991), some species of *Derbesia* that have been described based on sterile material closely resemble *Pseudoderbesia* and may indeed belong to the latter genus. These include *Derbesia fastigiata* W.R.Taylor (1928), *Derbesia attenuata* Dawson (1954) and *D. padinae* Trono (1972 '1971').

Derbesia fastigiata forms small thalli up to 2 cm high, composed of regularly dichotomously branched upright siphons, up to 100 μm at the base,



Figs 13-18. Culture of *Pseudoderbesia* sp. (HV03339). **13-14.** Details of dichotomies. **15.** Detail of apex. **16-18.** Details of siphon with numerous elongated chloroplasts, each containing one or sometimes two pyrenoids. Scale bars = 50 µm (Fig. 13), 20 µm (Figs 14-17), 10 µm (Fig. 18).

attenuating to about 10 µm at the apices (Taylor, 1928; Littler & Littler, 2000). A stolonoid branch system has not been observed, but this could be a collection artefact. *Derbesia fastigiata* was originally described from Florida and has since then been reported from the Caribbean Sea and Western Atlantic, where it grows epiphytic on other marine plants in the intertidal and shallow subtidal (Littler & Littler, 2000; Wynne, 2011). Records of *D. fastigiata* from other parts of the world, including the Pacific Ocean, will need to be confirmed. For example, *D. fastigiata*

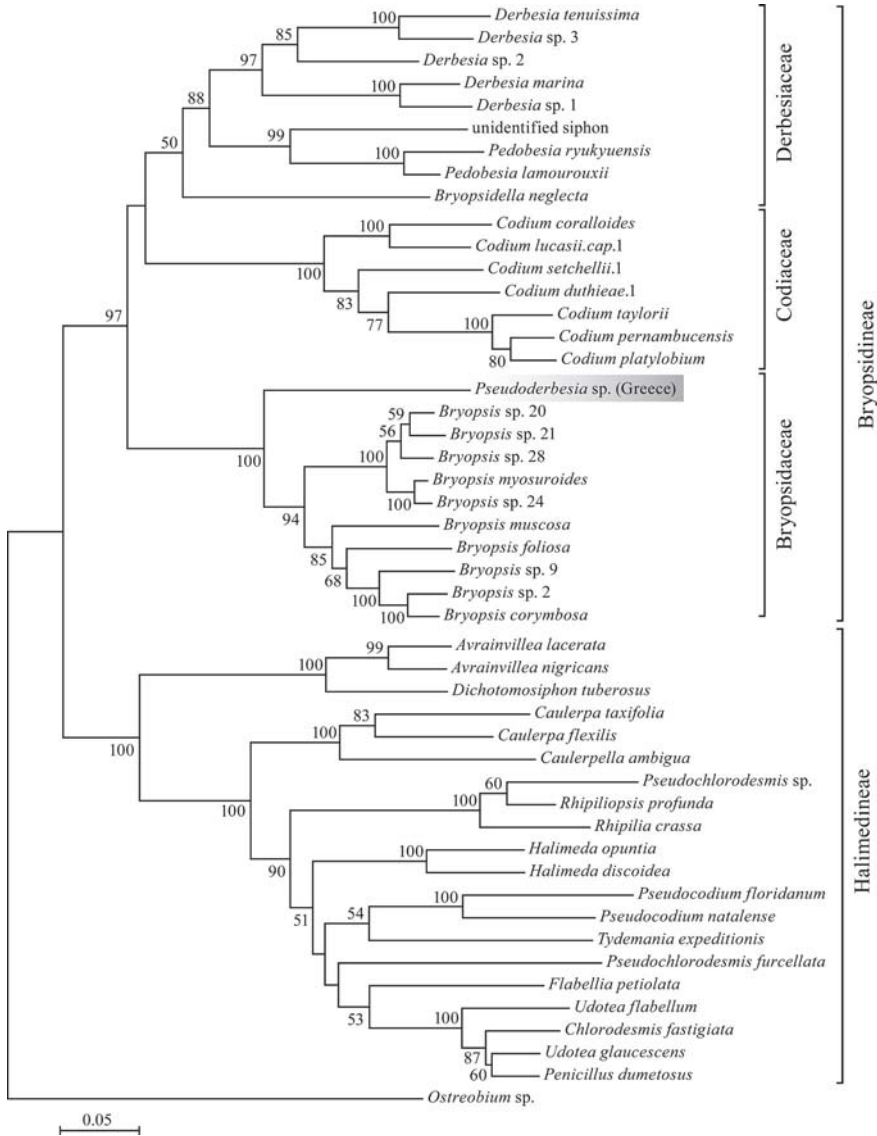


Fig. 19. Maximum likelihood (ML) tree of the Bryopsidales inferred from *rbcL* and *tufA* sequences, showing the phylogenetic position of *Pseudoderbesia*. ML bootstrap values (> 50%) are indicated at branches.

from Hawaii has been described with lateral ellipsoid sporangia (Abbott & Huisman, 2004), indicating that at least the Hawaiian plants are true members of *Derbesia*.

Derbesia attenuata Dawson (1954) also closely resembles *Pseudoderbesia*, forming small epiphytic thalli, up to 5 mm high, with a prostrate siphonous branching system giving rise to erect, dichotomously branched siphons, 40-50 µm

at the base, attenuating to 10-12 μm near the apices, and rounded chloroplasts, about 3 μm in diameter. *Derbesia attenuata* was originally described from Vietnam and has since then been recorded across the Pacific (Guiry & Guiry, 2012).

Another *Derbesia* species that is morphologically closely allied to *Pseudoderbesia* is *D. padinae* Trono (1972 '1971'). This species grows epiphytic on *Padina* and forms small erect siphons up to 1.5 cm high produced by prostrate siphons. The erect siphons are 50-60 μm at the base, attenuating to 6-8 μm near the apices. After the original description from Palau, *D. padinae* has only been reported from Guam and Micronesia (Lobban & Tsuda, 2003).

Calderon & Schnetter (1991) only described the Colombian isolates as a new species, *P. arbuscula*, while they remained indecisive about whether or not the isolates from the Canary Islands represented a separate species. The isolate from Greece shows morphological similarities with both the Colombian and Canary island plants (Table 2). In the absence of molecular data for the Colombian and Canary island plants, we refrain from describing the Mediterranean plants as a new species.

Our molecular phylogenetic analysis placed *Pseudoderbesia* sister to *Bryopsis* in the family Bryopsidaceae (Fig. 19). The family, originally erected for the single genus *Bryopsis*, now includes about six genera, of which *Bryopsis*, *Pseudobryopsis* and *Trichosolen* are best known. *Bryopsis*, characterized by a typical feather-like thallus, is the largest and most widespread genus of the family with over 55 described species distributed from tropical to temperate regions (AlgaeBase, Guiry & Guiry, 2014). *Pseudobryopsis* and *Trichosolen* (not included in our phylogenetic analysis) are morphologically allied to *Bryopsis* but differ in reproductive traits, with gametes formed in unmodified pinnules in *Bryopsis*, and in specialized gametangia in *Pseudobryopsis* and *Trichosolen* (Feldmann, 1969; Henne & Schnetter, 1999). Less well-known genera of the family include *Bryopsidella* from the Mediterranean and Canary Islands (Calderón-Sáenz & Schnetter, 1989), and the Antarctic genus *Lambia* (Delépine, 1967). *Derbesia* and *Pedobesia* have traditionally been assigned to a separate family Derbesiaceae, although some authors only recognized a single family, Bryopsidaceae, based on similarities in life histories (Rietema, 1975; Silva, 1982). A sister relationship between the Derbesiaceae and Bryopsidaceae has been suggested based on the shared occurrence of filamentous thalli and sporic meiosis, which separates the two families from the Codiaceae (Vroom *et al.*, 1998).

As well as pointing *Pseudoderbesia* as a member of the family Bryopsidaceae, molecular phylogenetic data has confirmed the presence of three main clades within the suborder Bryopsidineae, corresponding to the three traditionally recognized families: Bryopsidaceae, Codiaceae and Derbesiaceae. However, the relationship between these clades is not well supported (Verbruggen *et al.*, 2009a; this study). Additional sampling of less well-known genera, such as *Pseudobryopsis*, *Bryopsidella* and *Lambia*, however, will be needed to assess family boundaries and relationships.

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Table 2. Comparison of morphological features between *Pseudoderbesia* from Colombia, Canary Islands and Greece, and three *Derbesia* species showing close morphological resemblance to *Pseudoderbesia*

	<i>P. arbuscula</i> (Colombia)	<i>P. sp.</i> (Canary Islands)	<i>P. sp.</i> (Greece)	<i>D. fastigiata</i> (Caribbean Sea and Western Atlantic)	<i>D. attenuata</i> (Vietnam)	<i>D. pacinae</i> (W Pacific Islands)
Thallus height	1.5-4.3 mm	1.6-2.2 mm *	Up to 5 mm	0.5-2 cm	2.5-4.5 mm	1.5-4 mm
Stolonoid siphons, diameter	24-35 µm	40-60 µm	30-45 µm	Not described	30 µm	15-40 µm
Erect siphons, diameter near base	54-84 µm	80-120 µm *	70-130 µm	50-100 µm	40-50 µm	50-60 µm
Erect siphons, diameter below apex	18-24 µm	6-13 µm	15-30 µm	8-11 µm	10-12 µm	6-8 µm
Rhizoids	Short, distally lobed, surrounded by a mucilaginous layer	Long, not lobed, not surrounded by a mucilaginous layer	Short, not lobed, not surrounded by a mucilaginous layer	?	?	Long, not lobed
Chloroplast shape, length / width	Elongate to ovate, 5-15 µm / 4-5 µm	Ovate, 4-5 µm / 2-4 µm	Elongate, 5-12 µm / 2-5 µm	?	?	?
Reference	(Calderon & Schmetter, 1991)	(Calderon & Schmetter, 1991)	This study	(Taylor, 1928; Littler & Littler, 2000)	(Dawson, 1954)	(Trono, 1972 '1971')

* Measurements based on original drawing (Calderon & Schmetter 1991, Fig. 2)

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