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Standard Paper

The lichen genus *Villophora* (*Teloschistaceae*, Ascomycota)

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Abstract

The Southern Hemisphere lichen genus *Villophora* in subfamily *Teloschistoideae* is analyzed based on DNA sequence data. Six species are described, five of which are new to science: *V. darwiniana* and *V. wallaceana* grow on lignum and bark in southern Patagonia and Tierra del Fuego; *V. onas* and *V. patagonica* are lichenicolous or saxicolous on rocks in southern Patagonia; *V. rimicola* is saxicolous in Antarctica. Based on a three-gene DNA analysis, *Tayloriellina* is shown to be closely related to *Villophora*, and *Tayloriellina microphyllina* is established as a new combination. A key is provided to all species of the two genera. *Raesaeneniana maulensis* is combined into *Villophora*.

Key words: Antarctica, *Caloplaca*, Chile, *Raesaeneniana*, South America, *Tayloriellina*

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Introduction

The lichen genus *Villophora* Søchting *et al.* (family *Teloschistaceae*) was described by Arup *et al.* (2013) to accommodate the species *Caloplaca isidioclada* Zahlbr., which was known from South America, Antarctica and a number of subantarctic islands. Based on molecular data, it was known at the time that a number of undescribed species belonged in the genus and their sequences were included in the molecular analysis of Arup *et al.* (2013). Subsequently, *Villophora microphyllina* (Tuck.) S. Y. Kondr. was included in the genus by Kondratyuk *et al.* (2015).

This paper provides a molecular study of the genus *Villophora*. Five new species of *Villophora* (*V. darwiniana*, *V. onas*, *V. patagonica*, *V. rimicola* and *V. wallaceana*) are described and one species (*V. maulensis*) is combined into the genus. The close relationship of the genus *Tayloriellina* to *Villophora* (*Teloschistoideae*) is confirmed, and the new combination *Tayloriellina microphyllina* is proposed.

Material and Methods

Material

The study is based on collections made mainly by the first and second authors in Patagonia, Antarctica, the Falkland Islands, Crozet and Kerguelen Islands. Collections are located in herbarium C (Copenhagen) unless otherwise indicated. Three of the new species are described from old volcanic rocks in southern Chile, at or close to Morro Chico (Fig. 1), which is also the *locus classicus* for *Catenarina desolata* Søchting *et al.* (Søchting *et al.* 2014).

Morphology and anatomy

Macroscopic descriptions are based on observations made with an Olympus SZH dissecting microscope with an Olympus OM-D camera. Sections were made by hand or with a Reichert-Jung Cryostat 2800 Frigocut E microtome and studied with a Leitz Orthoplan microscope. All measurements were made on material mounted in water. Spores were measured outside the asci and measurements are given as the mean ($\bar{x}$) and standard deviation (SD) of *n* measurements with minimum and maximum measurements in parentheses.

Secondary chemistry

Secondary metabolites were identified using HPLC according to Søchting (1997); thallus and apothecia were analyzed separately. The relative composition of the secondary compounds was calculated based on absorbance at 270 nm according to Søchting (1997). All species of *Villophora* and *Tayloriellina* S. Y. Kondr. *et al.* have a similar chemosyndrome, namely A of Søchting (1997), with the following approximate anthraquinone proportions: 1% teloschistin, 2–3% fallacinal, 1–2% parietinic acid, 1–2% emodin, 92–95% parietin. All yellow, orange or reddish-pigmented parts are K+ purple.

Molecular analyses

DNA sequences were produced as in Arup *et al.* (2013) using direct PCR following Arup *et al.* (2015). Amplifications were made of the internal transcribed spacer regions (nrITS) and the large subunit (nrLSU) of the nuclear ribosomal RNA genes, and of

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Fig. 1. Old volcanic rocks at Morro Chico, Región de Magallanes y Antártica Chilena, Chile. Three of the newly described species, *Villophora darwiniana*, *V. onas* and *V. patagonica* were found at or near this location. In colour online.

the small subunit of the mitochondrial ribosomal RNA gene (mrSSU). Primers for amplification were ITS1F (Gardes & Bruns 1993), ITS4 (White *et al.* 1990), AL1R (Döring *et al.* 2000), LR5 or LR6 (Vilgalys & Hester 1990), mrSSU1 (Zoller *et al.* 1999) and mrSSU7 (Zhou & Stanosz 2001). The PCR parameters included an initial hold at 94 °C for 5 min, then denaturing at 94 °C for 1 min, annealing at 50 or 54 °C (mrSSU) or 53–56 °C (nrITS and nrLSU) for 1 min, decreasing by 1 °C per cycle for the first six of the 39 cycles (touchdown), and extension at 72 °C for 3 min. The sequencing was carried out by Macrogen Inc., South Korea using the same primers as for the PCR. The two resulting strands were assembled using CLC Main Workbench 4.1.2 ™ or Geneious 11.1.5. Subsequent alignments were performed in Geneious 11.1.15 using the MAFFT option and adjusted manually. Sequences have been submitted to GenBank as indicated in Table 1.

Two alignments were produced, one combined dataset of the nrITS, nrLSU and mrSSU genes and one of nrITS sequences, resulting in 14 terminals in the combined analysis and 47 terminals in the ITS analysis. Both alignments include mainly sequences of *Villophora* and the closest related genera of the subfamily *Teloschistoideae*. For both the combined analysis and the ITS alignment, *Wetmoreana decipioides* (Arup) Arup *et al.* was used as outgroup. Introns and ambiguous parts were removed from the alignment before analyses.

Phylogenetic analysis

The alignments of the three different genes were first analyzed separately to check for incongruence between genes, but no incongruences were found. A conflict was assumed to be significant if two different relationships were both supported with posterior probabilities ≥ 0.95. A suitable likelihood model for each of the genes was selected, using BIC as implemented in the software jModelTest v.2.1.4 (Guindon & Gascuel 2003; Darriba *et al.* 2012), evaluating only the 24 models available in MrBayes v.3.2 (Ronquist *et al.* 2012). For the concatenated data set, the SYM + G model was found to be optimal for the nrITS data set, HLKY + I for the nrLSU data set, and SYM + I + G for the mrSSU data set. An extended ITS alignment was also analyzed separately using MrBayes and the evolutionary model GTR + G + I. The parameters used in the analyses followed those of Arup *et al.* (2013) except for the branch length prior that was set to an exponential with mean 1/10. No molecular clock was assumed. Three parallel runs were executed with 2 000 000 generations starting with a random tree and employing six simultaneous chains, five of which were heated in increments of 0.1 °C. Analyses were diagnosed every 1000 generations in the last 50% of the tree sample and automatically halted when convergence was reached. Convergence was defined as a standard deviation of splits (of frequency 0.1) between runs below 0.01. Every 1000th tree was sampled. A majority-rule consensus tree was constructed from the post-burn-in tree samples. The consensus trees were visualized using FigTree v.1.4.4 and redrawn in Adobe Illustrator.

Taxonomy

Villophora Søchting, Frödén & Arup

In Arup *et al.*, *Nord. J. Bot.* **31**(1), 66 (2013); type: *Villophora isidioclada* (Zahlbr.) Søchting, Frödén & Arup.

Thallus crustose to microfruticose, consisting of squamules or granules that can be appressed and flattened, but are often

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Table 1. Specimens of *Villophora* and related species used in the phylogenetic analyses (Figs 2 & 3) with voucher information and GenBank Accession numbers. New sequences are in bold.

Species	Voucher information	nrITS	nrLSU	mrSSU
Josefpoeltia parva	Argentina, *Frödén* 1671, LD	KC179296	KC179204	KC179539
J. sorediosa	Chile, *Frödén* 1593, LD	KC179297	KC179205	KC179540
Tassiloa digitaurea	Chile, *Oh* et al. 130214, KoLRI	KP096222		KP096224
T. magellanica 1	Chile, *Søchting* 12265, C	**MW397534**	**MW397530**	**MW397526**
T. magellanica 2	Chile, *Søchting* 11276, C	JF910105		
Tayloriellina erythrosticta 1	Western Australia, *Kärnefelt* 20042803, LD	**MW397535**	**MW397531**	**MW397527**
T. erythrosticta 2	Western Australia, *Kondratyuk* 20435, KW	KT456223		
T. microphyllina 1	USA, *Knudsen* 8970, LD (ITS); USA, *Morse* 11754, LD (LSU); USA, *Thornberg* 382A, UCR (mrSSU)	**MW397536**	**MW397532**	**MW397528**
T. microphyllina 2	USA, *Gaya* 02.27.10-24 & *Lutzoni*, DUKE	KT291462		
Teloschistes flavicans	Chile, *Frödén* 1624, LD	KC179317	KC179255	KC179594
T. hypoglaucus	Kenya, *Frisch* 94/38a, Frisch, priv. hb.	KC179319	KC179256	KC179595
Villophora darwiniana 1	Chile, *Frödén* 1546, LD (*Villophora* sp. 46 in Arup *et al.* (2013))	KC179326	**MW397533**	
V. darwiniana 2	Chile, *Søchting* 10439, C	**MW397537**		
V. darwiniana 3	Chile, *Søchting* 12329, C	**MW397538**		
V. darwiniana 4	Chile, *Søgaard* 40, C	**MW397539**		
V. darwiniana 5	Chile, *Søgaard* 34, C	**MW397540**		
V. darwiniana 6	Chile, *Søgaard* 30, C	**MW397541**		
V. darwiniana 7	Chile, *Søgaard* 14, C	**MW397542**		
V. darwiniana 8	Chile, *Søgaard* 49, C	**MW397543**		
V. darwiniana 9	Chile, *Søchting* 12368, C	**MW397544**		
V. darwiniana 10	Argentina, *Svensson* 1718, UPS	**MW397545**		
V. darwiniana 11	Chile, *Etayo* 24462, C	**MW397546**		
V. darwiniana 12	Argentina, *Svensson* 1727, UPS	**MW397547**		
V. darwiniana 13	Chile, *Søchting* 10412, C	**MW397548**		
V. isidioclada 1	France, Kerguelen Isl., *Søchting* 9411, C (*Villophora* sp. 51 in Arup *et al.* (2013))	KC179331		
V. isidioclada 2	Chile, *Søchting* 9365, C	**MW397549**		
V. isidioclada 3	Chile, *Søchting* 10339, C	**MW397550**		
V. isidioclada 4	Livingston Island, *Søchting* 7592, C	**MW397551**		
V. isidioclada 5	Falkland Islands, *Søchting* 12625, C	**MW397552**		
V. isidioclada 6	Chile, *Søgaard* 109, C	**MW397553**		
V. isidioclada 7	Chile, *Søchting* 10185, C	KC179325	KC179266	KC179606
V. maulensis	Chile, *Wang* et al. 2012, KoLRI			KT456248
V. onas 1	Chile, *Frödén* 1563, LD (ITS, LSU); Chile, *Søchting* 10403, C (mrSSU) (*Villophora* sp. 50 in Arup *et al.* (2013))	KC179330	KC179268	**MW397529**
V. onas 2	Chile, *Søchting* 10441b, C	**MW397554**		
V. onas 3	Chile, *Søchting* 10430, C	**MW397555**		
V. onas 4	Chile, *Søchting* 12379, C	**MW397556**		
V. onas 5	Chile, *Frödén* 1564, LD	**MW397557**		
V. patagonica 1	Chile, *Elvebakk* 99_772, TROM (*Villophora* sp. 47 in Arup *et al.* (2013))	KC179329		
V. patagonica 2	Chile, *Søgaard* 9, C	**MW397558**		
V. patagonica 3	Chile, *Søgaard* 8, C	**MW397559**		

(*Continued*)

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Table 1. (*Continued*)

Species	Voucher information	nrITS	nrLSU	mrSSU
V. patagonica 4	Chile, *Søchting* 12676, C	**MW397560**		
V. patagonica 5	Chile, *Søchting* 12369, C	**MW397561**		
V. rimicola 1	Antarctica, *Søchting* 11425, C	**MW397562**		
V. rimicola 2	Antarctica, *Søchting* 11518, C	**MW397563**		
V. wallaceana 1	Chile, *Søchting* 10399, C (*Villophora* sp. 48 in Arup *et al.* (2013))	KC179328	KC179267	KC179607
V. wallaceana 2	Chile, *Søgaard* 68, C	**MW397564**		
V. wallaceana 3	Chile, *Søchting* 10354, C	**MW397565**		
Wetmoreana decipioides	South Korea, *Thor* 20768, UPS holotype	KC179333	KC179269	KC179608

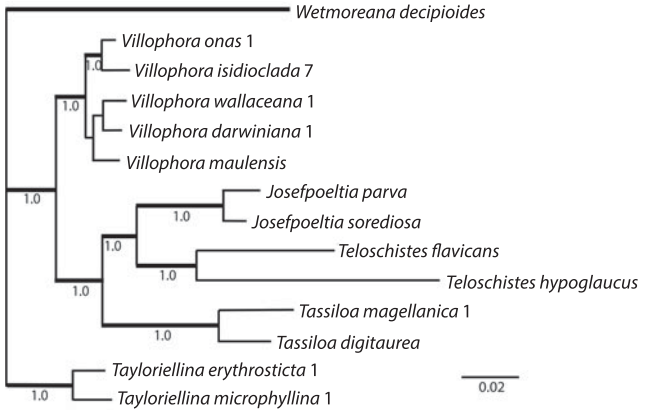

Fig. 2. Phylogenetic analysis of *Villophora* and the closest related genera of the subfamily *Teloschistoideae* based on three genes: nrITS, nrLSU and mrSSU. *Wetmoreana decipioides* was used as the outgroup. The mrSSU gene was available only for *V. maulensis* but it has nevertheless been included in the analysis, and it is clearly not sister to *V. onas* in this tree.

more or less vertical, isidioid with blastidia or soredia. Apothecia often rare, zeorine, occasionally with an isidiate thalline margin. All exposed parts are orange due to anthraquinones belonging to chemosyndrome A of Søchting (1997) and are K + purple. Asci of *Teloschistes*-type; ascospores 8 per ascus, polarilocular. Pycnidia not seen. Photobiont chlorococcoid. On rock, dry bark or wood, occasionally lichenicolous, with highest diversity in the Southern Hemisphere. The genus belongs to the subfamily *Teloschistoideae* (Arup *et al.* 2013; Bungartz *et al.* 2020).

Ecology and distribution. The genus *Villophora* includes species that are either lichenicolous on saxicolous lichens or grow on rock, wood or tree bark. Six species are currently known from the Southern Hemisphere, five from southern South America and two from Antarctica. Two related genera, *Josefpoeltia* and *Tassiloa*, are native to South America, whereas the more closely related species *Tayloriellina erythrosticta* (Taylor) S. Y. Kondr. *et al.* is known from Australia and *Caloplaca* (*Tayloriellina*) *microphyllina* (Tuck.) Hasse is known from North America. Records of the latter from Europe have not been validated (Wetmore 2004; Arup 2006).

Generic taxonomy. The initial description of the genus *Villophora* was based on molecular data (Arup *et al.* 2013). The five new species described in this paper are closely related to the type species, *V. isidioclada*, in the well-supported *Villophora* clade (Fig. 3).

The genus *Tayloriellina*, hosting the two species *T. erythrosticta* from Australia and the former *V. microphyllina* (Tuck.) S. Y. Kondr. from North America, has a sister position to *Villophora* on the nrITS tree (Fig. 3) but is more distantly located in the three-gene phylogeny, where *Tassiloa* S. Y. Kondr. *et al.*, *Josefpoeltia* S. Y. Kondr. & Kärnefelt and *Teloschistes* appear as closely related genera (Fig. 2).

The genus *Tayloriella* was described by Kondratyuk *et al.* (2015) to accommodate *Caloplaca erythrosticta* but since it turned out that the genus name was already in valid use for an algal genus, they subsequently transferred the species to a new genus *Tayloriellina* (Kondratyuk *et al.* 2016). From Figs 2 and 3 it is clear that *T. erythrosticta* and *V. microphyllina* are sister species that must be hosted in the same genus, either *Villophora* or *Tayloriellina*. Based on the three-gene analysis, we combine *V. microphyllina* into *Tayloriellina* as *T. microphyllina* (Tuck.) Søchting & Arup comb. nov. (MycoBank No.: MB 838280. Basionym: *Placodium microphyllinum* Tuck., *N. Amer. Lich.* (Boston) **1**, 174 (1882)) (Fig. 4A). However, studies based on more than three genes might prove that *Tayloriellina* is part of *Villophora*, as was recently proposed by Wilk *et al.* (2021).

A published mrSSU sequence (GenBank number KT456248) of the holotype of *Raesaeneniana maulensis* (S. Y. Kondr. & Hur) S. Y. Kondr *et al.* (SK 993) indicates that this species belongs in the genus *Villophora*, even though the other sequences (nrITS and nrLSU) of the holotype published in Kondratyuk *et al.* (2015) belong to various remote taxa, including *Umbilicaria*. *Marchantiana maulensis* S. Y. Kondr. & Hur, which was later transferred to *Raesaeneniana maulensis*, was collected in central Chile, and its morphological and anatomical description in Kondratyuk *et al.* (2014) fits well with *Villophora*, particularly the species *V. onas*. Assuming that the mrSSU sequence is correct, we therefore combine it into *Villophora* as *V. maulensis* (S. Y. Kondr. & Hur) Søchting comb. nov. (MycoBank No.: MB 838281. Basionym: *Marchantiana maulensis* S. Y. Kondr. & Hur, *Acta Bot. Hung.* **56**, 108 (2014)) leaving it to extended molecular studies to determine its validity as a species separate from other species in the genus.

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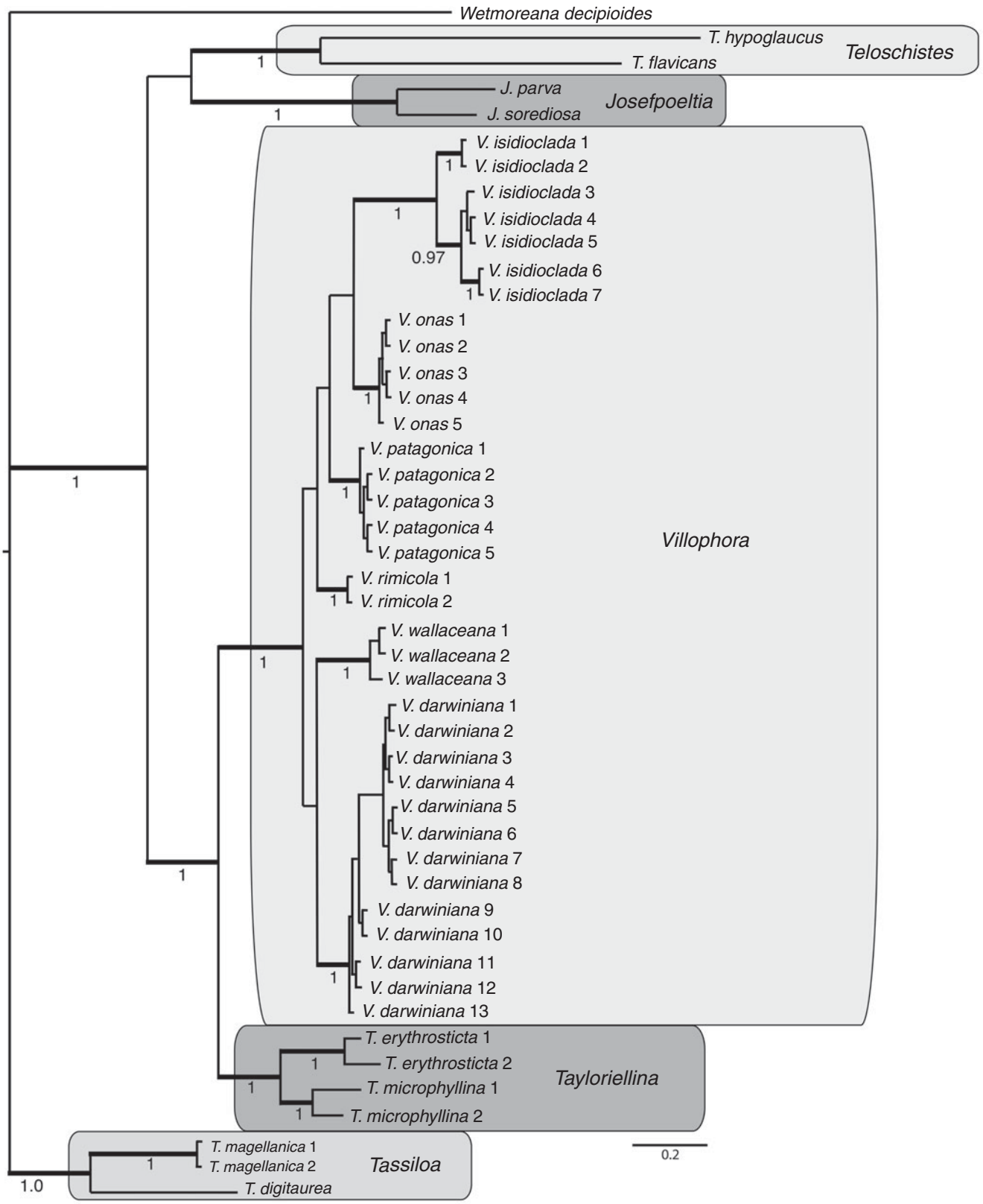

Fig. 3. Phylogenetic analysis of *Villophora* and the closest related genera of the subfamily *Teloschistoideae* based on nrITS alone. *Wetmoreana decipioides* was used as the outgroup.

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Key to *Villophora* (and allied) species

1	On bark or wood	2
	On rock, or lichenicolous on saxicolous lichens	5
2(1)	In North America	**Tayloriellina microphyllina**
	In Southern Hemisphere	3
3(2)	On wood; in Australia	**Tayloriellina erythrosticta**
	On dry bark; in South America	4
4(3)	Thallus micro-squamulose with mainly marginal soralia, but sometimes soralia/blastidia covering most of the squamules	**V. darwiniana**
	Thallus covered by globose granules/isidia	**V. wallaceana**
5(1)	Thallus mostly absent or insignificant	**V. patagonica**
	Thallus prominent	6
6(5)	Thallus well delimited, with crowded, more or less vertical, slim isidia	**V. isidioclada**
	Not with vertical, slim isidia	7
7(6)	Thallus effuse, with elongated, mostly horizontal areoles; exposed rocks in Patagonia	**V. onas**
	Thallus dense cushions of vertical coralloid lobes; in rock crevices in Antarctica	**V. rimicola**

Villophora darwiniana Søchting, Søgaard & Arup sp. nov.

MycoBank No.: MB 838275

Similar to *Tayloriellina microphyllina* but squamules smaller, 0.1–0.3 mm versus 2 mm, occurring in South America versus North America.

Type: Chile, Región de Magallanes y Antártica Chilena, Morro Chico, 52.0576°S, 71.4221°W, 200 m, dead wood of *Nothofagus*, 13 February 2018, *U. Søchting* 12678 (C—holotype).

(Fig. 4B & C)

Thallus indeterminate, 0.5–10 cm, squamulose; *squamules* flat to concave, vivid orange-yellow to vivid orange, rarely whitish in the centre, irregular, 0.1–0.3 mm wide, entirely sorediate/blastidiate at the edge and underside.

Apothecia rare, few to numerous, when present, zeorine, sessile, dispersed to aggregated, regular, up to 0.8 mm diam.; *disc* initially slightly concave, later flat, vivid orange; proper margin ±distinct and persistent, level and concolorous with disc; thalline margin sorediate or blastidiate, soon excluded; *true exciple* prosoplectenchymatous, fan-shaped, 20–50 µm; *hymenium* 60–70 µm; *paraphyses* 1.5–2 µm at base, end cells only slightly enlarged, up to 3 µm thick, apically branched; *asci* with 8 spores; *ascospores* ellipsoid, (9.8–)11.3 ± 1.0(–13.4) × (4.8–)6.2 ± 0.9(–5.8) µm, length/width ratio 1.9 ± 0.3; septum (2.5–)4.2 ± 0.9(–5.8) µm, length/septum width ratio 2.8 ± 0.6 (n = 15).

Molecular results. The species has very uniform nrITS sequences. It occupies a sister position to *V. wallaceana* (Figs 2 & 3). The species was included as '*Villophora* sp. 46' in Arup *et al.* (2013).

Etymology. Villophora darwiniana is named in honour of Charles Darwin, who studied the Magellan Archipelago for many months in 1833 during his voyage on HMS Beagle.

Ecology and distribution. Lignicolous or corticolous on rough bark, mainly of *Nothofagus* spp. at forest edge and in shrub vegetation, 20–620 m alt. Recorded from Province de Santa Cruz, Argentina and Región de Magallanes y de la Antártica Chilena, Chile.

Notes. When squamules are present, *V. darwiniana* is easily recognized by its lignicolous and corticolous habit combined with its vivid orange soredia/blastidia. When it is totally blastidiate or sorediate and no squamules are visible, it may be difficult to distinguish from *V. wallaceana*. The latter is more isidiate, with globose isidia of different sizes, while *V. darwiniana* has soredia/blastidia of ±equal size.

Due to the sorediate squamules and vivid orange colour, it is morphologically rather similar to *Tayloriellina* (*Villophora*) *microphyllina* from North America (Nash *et al.* 2007). *Tayloriellina microphyllina*, however, has larger squamules (Fig. 4A), is molecularly distinct, and has not been confirmed as occurring in South America.

Additional specimens examined. **Argentina:** *Province de Río Negro*: Bariloche Dept., 1.8 km NNE of Lake Juncos, forest-steppe ecotone, 41.000°S, 71.002°W, 900 m, on decaying bark of *Berberis microphylla*, 2009, *M. Svensson* 1727 (UPS); W of Lake Juncos, 41.064°S, 71.016°W, 900 m, on old wooden fence, 2009, *M. Svensson* 1718 (UPS). *Province de Santa Cruz*: Rio Turbida at borderpost NE of Puerto Natales, 51.5633°S, 72.3483°W, 620 m, bark of old *Nothofagus pumilio*, 2005, *U. Søchting* 10418.—**Chile:** *Región de Magallanes y de la Antártica Chilena*, 30 km N of Punta Delgada, Parque Nacíonal Pali Aike, 52.1075° S, 69.7064°W, 186 m, twig on the ground, 2008, *M. Z. Søgaard* 14; NW of Puerto Natales, 50–100 m from fjord, 51.5411°S, 72.8400°W, 5–50 m, fence pole and base of *Nothofagus*, 2008, *M. Z. Søgaard* 30; Parque Nacíonal Torres del Paine, 169 m, 51.0494°S, 72.9367°W, bush, 2008, *MZS* 34 and 40; walk from Lago Grey, 51.1222°S, 73.1242°W, root of fallen *Nothofagus*, 2008, *M. Z. Søgaard* 45, 49; 200 m SW of Hostería Las Torres,

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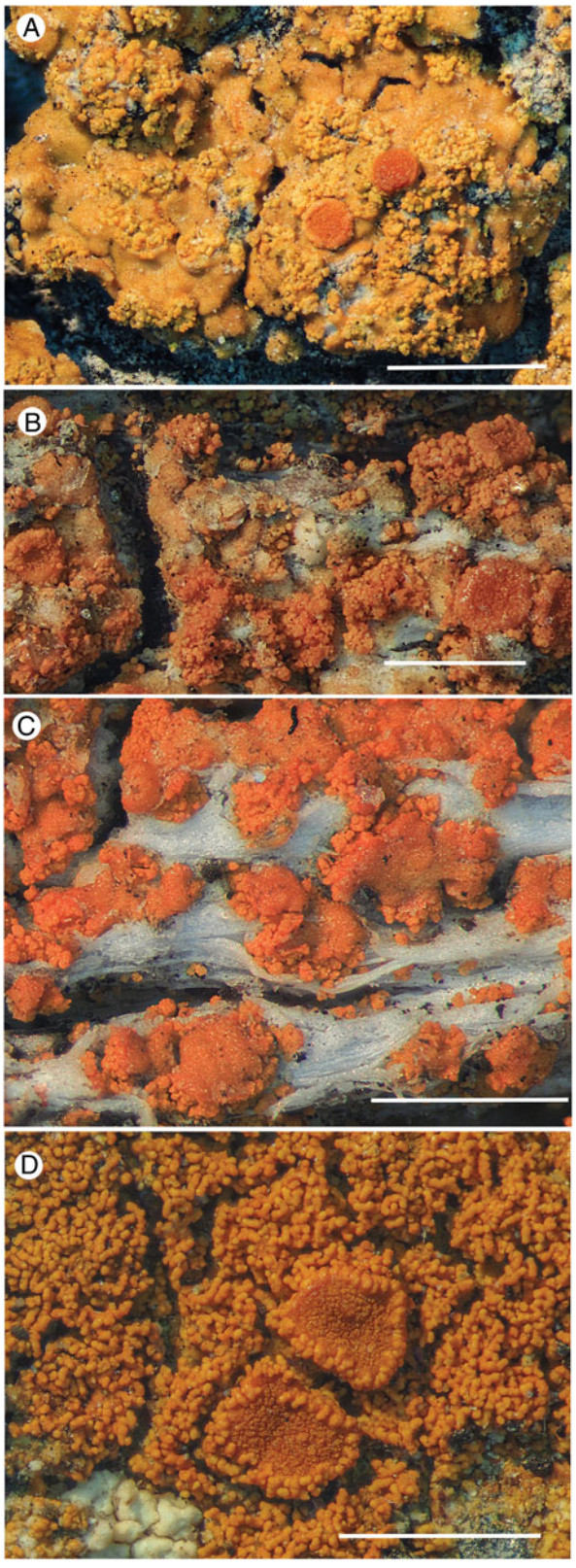

Fig. 4. A, *Tayloriellina microphyllina* (*U. Søchting* 9900). B & C, *Villophora darwiniana* (*M. Z. Søgaard* 14). B, thallus almost dissolved in soredia, and with apothecia. C, thallus squamules persisting, and with marginal soralia. D, *V. isidioclada* (*M. Z. Søgaard* 109). Scales: A & D = 1 mm; B & C = 0.5 mm. In colour online.

50.983°S, 72.866°W, 100 m, on lignum of *Nothofagus antarctica*, 1996, *A. Elvebakk* 96:013 (TROM); Rio Paine valley, 3–4 km SW of Guardería Laguna Amarga, 51.000°S, 72.833°W, 80 m, on *Discaria chacaye*, 1996, *A. Elvebakk* 96:690 (TROM); Miradór Lago Nordenskjold, halfway between Laguna Largo and Laguna Mellizas, 51.050°S, 72.916°W, 200 m, on dry, sun-exposed, dead twigs of *Discaria chacaye*, 1997, *A. Elvebakk* 97:449 (TROM); Morro Chico, 100 km N of Punta Arenas, 52.0575°S, 71.4212°W, 195 m, bark of *Nothofagus antarctica*, 2015, *U. Søchting* 12368, 12367; 52.0576°S, 71.4221°W, 200 m, 2018, *U. Søchting* 122677; Province Antártica Chilena, Isla Navarino, 6 km SW of Puerto Willliams, dead *Nothofagus*, 21 m, 54.9325°S, 67.6489°W, 2008, *M. Z. Søgaard* 70; Isla Navarino, 30 km WNW of Puerto Williams, coastal trail between Wulaia and José, 55.015°S, 68.165°W, 10 m, dead bark of *Nothofagus*, 2005, *U. Søchting* 10354; Canal Beagle, Cabo Hyades, Bahia Yendegaia, Puerto Contreras, 54.8605°S, 68.8146°W, 2 m, 2015, *U. Søchting* 12329.

Villophora isidioclada (Zahlbr.) Søchting, Frödén & Arup

(Fig. 4D)

Thallus crustose to micro-fruticose, vivid orange-yellow to vivid orange, up to 2 cm wide, up to 1 mm thick, rimose-areolate; areoles 0.6–1.4 mm diam., covered by dense coralloid, horizontal, ascending or ±vertical isidia; isidia 20–50 µm thick, slightly moniliform; prothallus rare, very thin, effuse, brighter than thallus. Thallus cortex paraplectenchymatous with globular cells, 3–4 µm diam.

Apothecia very rare, dispersed, regular to angular, up to 0.9 mm diam., zeorine; thalline margin well developed, crenate-isidiate (or smooth at Kerguelen), concolorous with thallus; proper margin thin; *disc* flat to eventually slightly convex, finely fissured, strong reddish brown, episamma coarse; *true exciple* prosoplectenchymatous, fan-shaped, 20–100 µm; *hymenium* 70–80 µm; *paraphyses* 1.5–2 µm at base, end cells only slightly enlarged, up to 3 µm thick, apically branched; asci with 8 spores; *ascospores* ellipsoid, (13.4–)15.7 ± 1.4(–18.6) × (6.8–)8.8 ± 0.9(–10.3) µm, length/width ratio 1.8 ± 0.2; septum (4.0–)5.8 ± 1.0(–8.9) µm; length/septum width ratio 2.8 ± 0.6 (n = 21).

Molecular results. ITS sequences of specimens from the Subantarctic Islands, Kerguelen and Crozet form a separate clade deviating from the Patagonian/Antarctic *V. isidioclada* (*V. isidioclada* 1 and 2 in Fig. 3). Pending a broader sampling they are included here in *V. isidioclada*. Deviating molecular characters in the Subantarctic Islands are also seen in the genus *Austroplaca* (unpublished data) and might indicate a speciation beginning after separation from the parent populations in South America.

The species was included as '*Villophora* sp. 51' in Arup *et al.* (2013).

Ecology and distribution. Maritime rocks and cliffs, normally 2–10 m a.s.l. The species is recorded from Juan Fernandez (type, Zahlbruckner (1924)), southern South America, South Shetland Islands, maritime Antarctica, the Falkland Islands, South Georgia, South Orkney Islands, Crozet Islands and Kerguelen Islands.

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Notes. *Villophora isidioclada* may be somewhat similar to *Tassiloa digitaurea* (Søgaard *et al.*) S. Y. Kondr. *et al.*, but *V. isidioclada* has thinner isidia (30–50 µm) compared to the thicker, more lobulate isidia (60–100 µm thick) of *T. digitaurea*.

Additional specimens examined. **Antarctica:** *South Shetland Islands*: Livingston Island, South Bay, Punta Polaca, 62.666°S, 60.383°W, 20 m, acid, sedimentary bedrock, eutrophicated rock near sea, 1998, *U. Søchting* 7592; Punta Polaca, 62.6630°S, 60.3939°W, 25 m, 1998 & 2018, *U. Søchting* 7592, *U. Søchting* 12745, 12747 & 12759.—**Chile:** *Región de Magallanes y de la Antártica Chilena*: Isla Navarino, E of Puerto Navarino, 54.9314°S, 68.3578°W, 4–5 m, E-facing maritime cliff, 2008, *M. Z. Søgaard* 109; Isla Navarino, 40 km W of Puerto Williams, 54.9183°S, 68.3178°W, 2 m, maritime rocks, 2005, *U. Søchting* 10165; Isla Navarino, 20 km W of Puerto Williams, Caleta Mejillones, 54.9011°S, 69.1667°W, 10 m, horizontal maritime rocks, 2005, *U. Søchting* 10185; Isla Navarino, 30 km WNW of Puerto Williams, Wulaia, 55.0356°S, 68.1356°W, 7 m, maritime rocks, 2005, *U. Søchting* 10339; Canal Beagle, Seno Holandia, 54.9420°S, 69.1545°W, maritime rocks, 2 m from the sea, top of coastal rock, *U. Søchting* 12296; Seno Espana, 54.7914°S, 69.7569°W, 2 m, W-exposed, maritime rock, 1 m from the sea, 2015, *U. Søchting* 12304; Isla Martinez, 54.9133°S, 68.2719°W, 3 m, 2015, *U. Søchting* 12336.—**Falkland Islands:** *East Island*: Goose Green E of New Haven, Soladero farm, 51.7239°S, 59.0559° W, 2 m, low mudstone rocks at shore, *U. Søchting* 12625.—**Kerguelen Island:** *c.* 2 km SE of Port aux Francais, 49.3533°S, 70.2283°E, 2 m, 1998, *U. Søchting* 9411; Peninsule Rallier du Baty, E-most part of Arete Jérémine by W end of Anse du Gros Ventre, 49.7178°S, 68.9181°E, 20 m, wind-exposed horizontal gabbro rocks *c.* 50 m from sea, 1999, *R. S. Poulsen* 879; Golfe du Morbihan, Ile Mayes, 49.4700°S, 69.9467°E, coastal rocks, basalt, 1998, *U. Søchting* 9450, 9455; Presqu'île Ronarch, Cabane Sourcil Noir, 49.6910°S, 70.2700°E, 20 m, sheltered canyon with shaded, vertical sides, basalt, 1998, *U. Søchting* 9443.—**Crozet Island:** Base Alfred-Faure at Bay du Marin, 46.433°S, 51.858°E, 123 m, disturbed *Azorella*-grass vegetation, basalt, 1998, *U. Søchting* 9365.

Villophora onas Søchting, Søgaard & Arup sp. nov.

MycoBank No.: MB 838276

Thallus lichenicolous or saxicolous, crustose with horizontal or ascending areoles. Similar to the European *Flavoplaca coronata* but differing in its often lichenicolous habit and longer spore septum. Apothecia numerous, zeorine. Spores polarilocular, 13–17 × 6.5–8 µm.

Type: Chile, Región de Magallanes y de la Antártica Chilena, 100 km SE of Puerto Natales, 15 km NW of Morro Chico, 52.128°S, 71.173°W, 300 m, erratic acid stone, 2 February 2005, *U. Søchting* 10430a (C—holotype).

(Fig. 5A)

Thallus crustose, consisting of moniliform to coralloid, spherical to elongated, horizontal or ascending areoles, 0.05–0.15 mm diam., vivid orange-yellow to strongly reddish orange; lichenicolous on crustose lichens and then partly immersed in grey matrix, or epilithic with well-developed thallus.

Apothecia mostly present, numerous, dispersed to aggregated, zeorine, sessile, to 0.8 mm diam., ±regular to angular; margin up to 0.07 mm broad; thalline margin concolorous with the thallus, crenulate and soon excluded; proper margin level with and slightly paler than the disc, smooth; *disc* flat to eventually slightly convex, episamma fine; *thalline exciple* with paraplectenchymatous cortex with globular lumina, *c.* 10 µm diam.; *true exciple* prosoplectenchymatous, fan-shaped, narrow, 20–30 µm; *hymenium* 70–80 µm; *paraphyses* 1.5–2 µm at base, end cells only slightly enlarged, up to 4 µm thick, apically branched; *asci* with 8 spores; *ascospores* ellipsoid, (12.8–)14.4 ± 1.4(–18.4) × (6.1–)7.3 ± 0.8(–9.25) µm, length/width ratio 2.0 ± 0.3; septum (4–)5.5 ± 0.9(–7.9) µm, length/septum width ratio 2.7 ± 0.4 (n = 32).

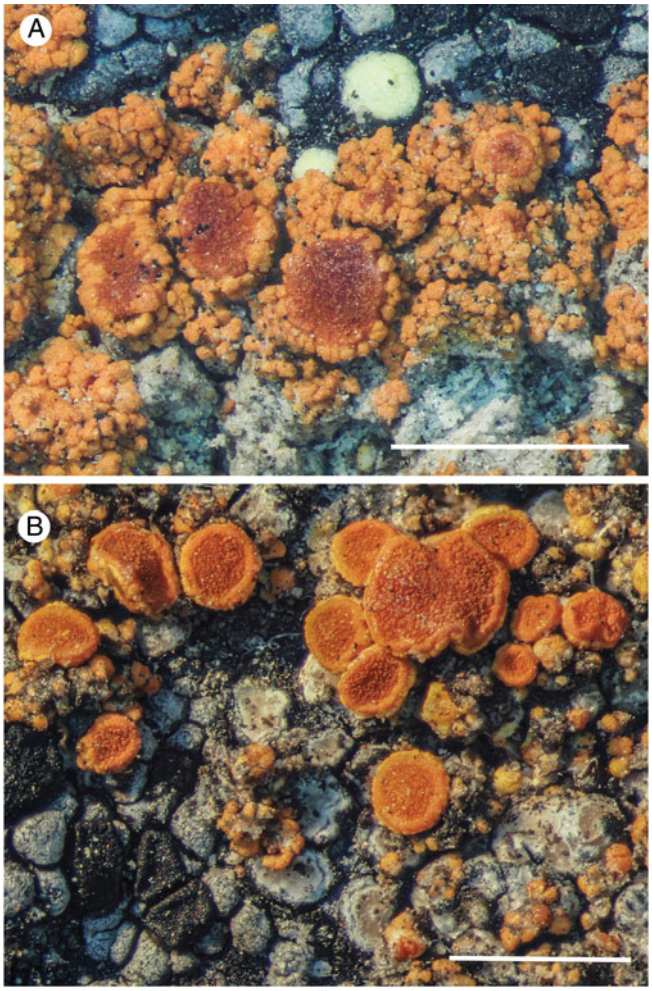

Fig. 5. A, *Villophora onas*, holotype. B, *V. patagonica*, holotype. Scale = 1 mm. In colour online.

Molecular results. The nrITS-sequences of *V. onas* are very uniform and make up a sister clade to *V. isidioclada*.

The species was included as '*Villophora* sp. 50' in Arup *et al.* (2013).

Etymology. The name *Villophora onas* commemorates the native Onas tribe inhabiting the steppes of Tierra del Fuego prior to the advent of European settlers.

Ecology and distribution. Lichenicolous on crustose, saxicolous lichens, such as *Rhizocarpon* sp., or saxicolous on stone in steppe, but also among shrubs in alpine heathland, 40–300 m a.s.l. Recorded from Chile, Tierra del Fuego north to 50°S.

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Notes. *Villophora onas* is characterized by an often lichenicolous life habit, combined with the yellow to vivid orange, always granular to isidiate thallus with numerous apothecia. It is similar to the European species *Flavoplaca coronata* in its granular appearance but differs in not being truly isidiate, in its often lichenicolous habit, having a longer spore septum, and in occurring in South America. Further molecular studies may show it to be closely related to *V. maulensis*.

Additional specimens examined. **Chile:** *Región de Aisén*: along the road Coyhaique-Coyhaique alto, 45.5055°S, 71.7132°W, 700 m, exposed cliffs in open pastureland, 2001, *P. Frödén* 1563 (LD). *Región de Magallanes y de la Antártica Chilena*: E end of Lago del Toro, 51.0506°S, 72.5517°W, 40 m, rock, 2005, *U. Søchting* 10441b; Sierra Baguales, 50.8778°S, 72.3850°W, 2–300 m, rocks in steppe landscape, 1999, *A. Elvebakk* 99:1140 (TROMS); Sierra Baguales, 50.7917°S, 72.4119°W, *c.* 300 m, rocks in steppe landscape, 1999, *A. Elvebakk* 99:1171 (TROMS); Isla Navarino, 25 km W of Puerto Williams, Paso Mladineo, 55.0008°S, 68.0858°W, 580 m, W-exposed basaltic overhang, 2005, *U. Søchting* 10382; Morro Chico, 100 km N of Punta Arenas, 52.0570°S, 71.4202°W, 228 m, basaltic rock of old volcano in steppe, horizontal rock on soil, 2015, *U. Søchting* 12379; Tierra del Fuego, along road y-71 *c.* 22 km W of San Sebastian, 80 m, on siliceous schistose boulder in grass steppe, 2001, *U. Arup* L01577 (LD).

Villophora patagonica Søchting & Søgaard sp. nov.

MycoBank No.: MB 838277

Similar to *Athallia inconnexa* in its lichenicolous habit but differing in the generally poorly developed thallus, in not being confined to the genera *Acarospora* and *Aspicilia* s. lat., wider spores and in its distribution in Patagonia.

Type: Chile, Región de Magallanes y de la Antártica Chilena, Morro Chico, 52.0576°S, 71.4221°W, 200 m, bedrock basalt, 13 February 2018, *U. Søchting* 12676 (C—holotype).

(Fig. 5B)

Thallus lichenicolous, insignificant or consisting of minute, pale orange areolae, dispersed around the apothecia, 5–15 mm diam.

Apothecia always present, scattered to crowded, sessile, regular to slightly angular, up to 1 mm diam., deep orange, zeorine; margin 0.04 mm thick; thalline margin thin, soon excluded, orange-yellow; proper margin distinct and persistent, slightly prominent, orange, darker than the thalline margin; *disc* flat to eventually slightly convex, dark orange, with medium coarse episamma; *true exciple* prosoplectenchymatous, fan-shaped, 50–60 µm; *hymenium* 50–70 µm; *paraphyses* 1.5–2 µm at base, end cells only slightly enlarged, up to 3 µm thick, apically branched; *asci* with 8 spores; *ascospores* broadly ellipsoid, (9.4–)12.5 ± 1.3(–16.1) × (5.9–)7.7 ± 0.9(–9.7) µm, length/width ratio 1.6 ± 0.2; septum (3.2–)4.7 ± 0.9(–6.7) µm; length/septum width ratio 2.7 ± 0.3 (n = 35).

Molecular results. *Villophora patagonica* has very uniform nrITS sequences.

The species was included as '*Villophora* sp. 47' in Arup *et al.* (2013).

Etymology. The name refers to the known distribution in the dry regions of southernmost South America.

Ecology and distribution. Lichenicolous on crustose, saxicolous lichens on siliceous and volcanic rocks, possibly eventually independent of host, on old volcanic rocks in steppe vegetation, 190–360 m. Sometimes with *Catenarina desolata* Søchting *et al.* Known from the Región de Magallanes y de la Antártica Chilena, Chile.

Additional specimens examined. **Chile:** *Región de Magallanes y de la Antártica Chilena*: 30 km N of Punta Delgada, Parque Nacíonal Pali Aike, 52.1103°S, 69.7008°W, 186 m, on crustose lichens on lava, 2008, *M. Z. Søgaard* 8, 9; Morro Chico, 52.0500°S, 71.4666°W, 200 m, on rocks in NW-facing boulder slope, 1999, *A. Elvebakk* 99:772 (TROM).

Villophora rimicola Søchting sp. nov.

MycoBank No.: MB 838278

Similar to *Austroplaca erecta* in its cushion-like thallus but differing in the bright orange colour versus yellow, in the larger spores with a longer spore septum and in being confined to Antarctica. Thallus saxicolous, forming tight, vertical, anastomosing, pale lobes producing orange areoles on the surface. Apothecia few, zeorine. Ascospores 15–17 × 8.5–9.5 µm, septum 4–5.5 µm.

Type: Antarctica, Loubet Coast, Adelaide Island, Ryder Bay, Lagoon Island, 67.5927°S, 68.2379°W, 30 m, W-exposed scree, on rock between *Usnea* spp., 20 January 2011, *U. Søchting* 11518 (C—holotype).

(Fig. 6A–C)

Thallus epilithic, crustose to micro-fruticose, consisting of vertical, terete, coralloid, anastomosing, pale lobes, most often forming tight cushions in rock crevices (Fig. 6C); cushion surface formed by the strongly orange-pigmented lobe ends (Fig. 6B), up to 0.25 mm diam.

Apothecia infrequent, aggregated, zeorine, sessile, to 1 mm diam., ±regular; margin up to 0.04 mm broad; thalline margin concolorous with the thallus, crenulate and soon excluded; proper margin level with and slightly lighter than the disc, smooth; *disc* flat to eventually slightly convex, episamma fine; *true exciple* prosoplectenchymatous, fan-shaped, narrow, 20–40 µm; *hymenium* 70–80 µm; *paraphyses* 1.5–2 µm at base, end cells only slightly enlarged, up to 3 µm thick, apically branched; *asci* with 8 spores; *ascospores* ellipsoid, (14.7–)15.8 ± 1.0(–17.4) × (8.0–)9.0 ± 0.6(–9.4) µm, length/width ratio 1.8 ± 0.2; septum (4.0–)4.6 ± 0.7(–5.4) µm; length/septum width ratio 3.5 ± 0.4 (n = 5, ripe apothecia sparse).

Etymology. The species epithet relates to the growth in crevices. Latin: *rima* = crack, cleft and *colere* = to live, to dwell.

Ecology and distribution. Saxicolous in crevices, often eutrophicated by skuas or penguins. From sea level and up to at least 250 m. Recorded from several localities around the British Antarctic Survey base at Rothera Point on Adelaide Island, Antarctica. It is interesting that the species has so far not been recorded from the well-studied maritime Antarctic, such as the South Shetland Islands.

Additional specimens examined. **Antarctica:** *Loubet Coast*: Adelaide Island, Ryder Bay, Anchorage Island, 67.6046°S,

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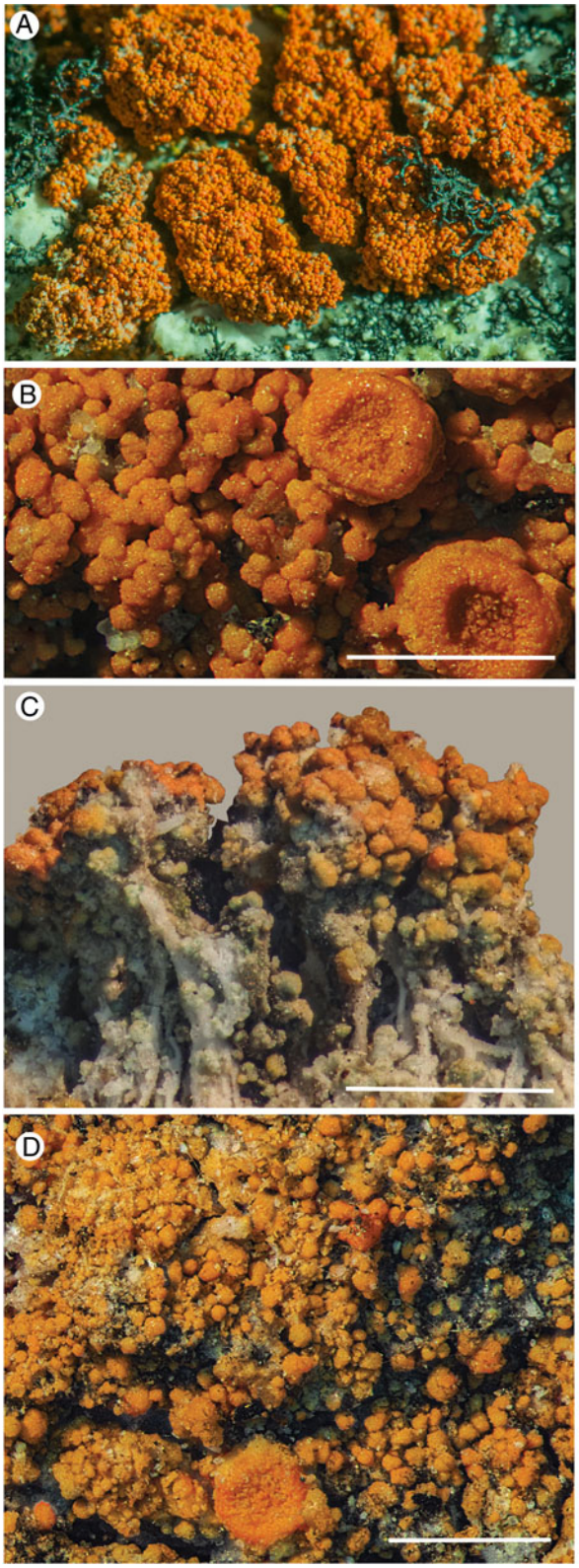

Fig. 6. A–C, *Villophora rimicola*. A, field photograph (*U. Søchting* 11425b). B, thallus viewed from above (*U. Søchting* 11447). C, holotype, vertical section through thallus. D, *V. wallaceana*, holotype. Scales: B & C = 1 mm; D = 0.5 mm. In colour online.

68.2163°W, 10 m, coastal rock with bird influence, vertical, NW-exposed rock, 2011, *U. Søchting* 11425; 67.6016°S, 68.2098°W, 29 m, horizontal pebbles, 2011, *U. Søchting* 11447; Léonie Island, 67.6018°S, 68.3614°W, 29 m, NE-exposed rocks with skuas, among *Usnea* spp., 2011, *U. Søchting* 11384; 67.5939°S, 68.3451°W, 16 m, exposed crevices, 2011, *U. Søchting* 11414; Rothera Point, Cross Hill, 67.5717°S, 68.1265°W, 20 m, eutrophicated rock crevices, 2011, *U. Søchting* 11415; Reptile Ridge, 67.5574°S, 68.1528°W, 250 m, S-exposed mountain ridge of granite diorite, exposed horizontal rock, 2011, *U. Søchting* 11533.

Villophora wallaceana Søchting & Søgaard sp. nov.

MycoBank No.: MB 838279

Similar to *Villophora darwiniana* but differs in that the thallus consists of globose granules instead of producing squamules with soredia/blastidia on the edge, and in having wider spores with a slightly wider septum.

Type: Chile, Región de Magallanes y de la Antártica Chilena, Isla Navarino, *c.* 25 km W of Puerto Willliams, 7 km S of Lum, 54.9583°S, 68.0917°W, 370 m, pristine forest of *Nothofagus pumilio*, dead bark of *N. pumilio*, 26 January 2005, *U. Søchting* 10399 (C—holotype).

(Fig. 6D)

Thallus indeterminate, consisting of scattered or crowded, globose, isidioid, corticate granules of uneven size, 0.04–0.08 mm diam., deep orange-yellow to deep orange; thallus partly crustose and almost smooth with flat, adpressed, minute, 75–155 µm broad, slightly brighter coloured areolae associated with the isidia.

Apothecia rare, dispersed to aggregated, sessile, zeorine, regular, 0.2–0.5 mm diam., vivid yellow to vivid orange; *disc* flat, with medium coarse episamma; proper margin prominent; thalline margin concolorous with thallus, continuous to discontinuous, with occasional isidia; *true exciple* prosoplectenchymatous, fan-shaped, *c.* 85 µm; *hymenium* 60–65 µm; *paraphyses* 1.5–2 µm at base, apically branched, with only slightly inflated terminal cells, up to 3.5 µm; *ascospores* ellipsoid, (12.1–)13.7 ± 1.1(–14.7) × (6.7–)7.7 ± 0.6(–8.0) µm, length/width ratio 1.8 ± 0.2; septum (4–)5.4 ± 1.0(–6.7) µm; length/septum width ratio 2.6 ± 0.6 (n = 4).

Molecular results. *Villophora wallaceana* is sister species to *V. darwiniana*, which is also the species with the most similar morphology.

The species was included as '*Villophora* sp. 48' in Arup *et al.* (2013).

Etymology. Named after the outstanding biologist and biogeographer Alfred Russel Wallace (1823–1913).

Ecology and distribution. Rough bark of *Nothofagus pumilio* in pristine forest. It is so far known only from Isla Navarino in Región de Magallanes y de la Antártica Chilena, Chile.

Notes. *Villophora wallaceana* may be difficult to distinguish from *V. darwiniana*, but the latter has squamules with soredia/blastidia of ±uniform size from the underside and margins. *Villophora wallaceana* has globose isidia of uneven size. *Villophora wallaceana* and *V. darwiniana* are the only known species of *Villophora* on bark and lignum in South America.

Additional specimens examined. **Chile:** *Región de Magallanes y de la Antártica Chilena*: Isla Navarino, 5 km SW of Puerto

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Williams, 54.9528°S, 67.6386°W, 171 m, *Nothofagus*, 2008, *M. Z. Søgaard* 68; Isla Navarino, 2 km SW of Puerto Williams, Cerro Bandera, 54.9500°S, 67.6417°W, 110 m, on *Nothofagus pumilio*, 2005, *U. Søchting* 10251; Isla Navarino, 30 km WNW of Puerto Williams, coastal trail between Wulaia and Caleta José, 55.015°S, 68.165°W, 10 m, dead bark of *Nothofagus*, 2005, *U. Søchting* 10354.

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