Molecular analyses reveal a new species of Palmariaceae from Subantarctic Chile: *Devaleraea yagan sp. nov*. (Palmariales, Rhodophyta)

Danilo E. Bustamante, Martha S. Calderon, and Andrés Mansilla

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Molecular analyses reveal a new species of Palmariaceae from Subantarctic Chile: *Devaleraea yagan sp. nov*. (Palmariales, Rhodophyta)

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ABSTRACT

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The red algal family Palmariaceae is distributed in the northern and southern hemispheres and currently includes four genera and 25 species. Recent studies based on transcriptome and organellar genome data strongly support a monophyletic family; however, this condition was not confirmed among its constituent genera. Additionally, no reliable morphological diagnostic features have been identified for delimiting *Devaleraea* and *Palmaria*. During expeditions to Subantarctic Chile along isolated channels and fjords to explore macroalgae diversity, we collected samples of specimens from the intertidal and assessed them using morphology and molecular markers (*cox*1, *rbc*L, nuclear-encoded ITS rDNA). Here we describe the new species *Devaleraea yagan* based on multilocus phylogeny and confirm the low genetic divergences in palmariaceaean species using principal coordinate analysis (PCoA). This new species is diagnosed by having its diminutive thalli attached to the substratum by a reduced holdfast and by the presence of rhizoidal cells in the medulla. Further analyses including genomic data of members of *Devaleraea*, *Halosaccion* and *Neohalosacciocolax* lineages are expected to support the taxonomic restructuring of the family.

INTRODUCTION

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The red algal family Palmariaceae is currently composed of the following four genera: *Devaleraea* Guiry, *Halosaccion* Kützing, *Neohalosacciocolax* I.K. Lee & Kurogi and *Palmaria* Stackhouse (Guiry & Guiry 2021). Although the Palmariaceae was strongly supported as monophyletic in transcriptome (Saunders *et al.* 2018) and organellar genomic data (Bustamante *et al.* 2020), this condition was not confirmed among its constituent genera (Saunders *et al.* 2018). The lack of monophyly in the genus *Palmaria*, as currently circumscribed, was commonly observed when using molecular data (Lindstrom & South 1989; Lindstrom *et al.* 1996; Evans & Saunders 2017). Recently, Saunders *et al.* (2018) considered two taxonomic perspectives to resolve this issue: (i) to merge all species of Palmariaceae into a single genus *Palmaria*, which has priority, or (ii) to transfer several species to *Devaleraea* and leave the genus *Halosaccion*, *P. hecatensis* M.W. Hawkes and *P. palmata* (Linnaeus) F. Weber & D. Mohr unaltered. Guiry (1982) distinguished *Devaleraea* from *Halosaccion*, the genus in which the species had been placed, on the basis of vegetative anatomical structure. However, including some but not all species of *Palmaria* in *Devaleraea* will require the transfer of *P. hecatensis* to a new, separate genus, thus making *Palmaria* monotypic. Although not recognized by Guiry (1982), there are some slight morphological differences between *Devaleraea* and other Palmariaceae. For instance,

the number of cortical cell layers seems to be smaller in *Devaleraea* (1–2), and the medulla, when intact, is often made up of two layers (rather than a single, large medullary cell extending from cortex to cortex), which enables the medulla to become hollow by the separation of the two layers, as is the case in *D. ramentacea* (Linnaeus) Guiry and some populations of *D. callophylloides* (M.W. Hawkes & Scagel) G. W. Saunders, C.J. Jackson & Salomaki (Lindeberg & Lindstrom 2010).

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Although morphological observations delimiting these genera have not been confirmed as diagnostic features, several species were assigned erroneously to different genera in the Palmariaceae. For instance, *H. tilesii* Kjellman highly resembles *D. callophylloides* (Setchell & Gardner 1903; Hawkes & Scagel 1986); the former, however, is reported to be hollow in part, whereas Hawkes & Scagel (1986) did not observe hollow specimens of *D. callophylloides*. Additionally, *P. decipiens* (Reinsch) R.W. Ricker from Antarctica, which is phylogenetically embedded in a clade containing *Devaleraea* (Bustamante *et al.* 2020), was also reported to have hollow thalli (Becker *et al.* 2011). Although the morphological feature that differentiates *Devaleraea* and *Palmaria* seems not to be diagnostic, it was considered plesiomorphic (Lindstrom *et al.* 1996). Some species of these genera are hollow, some species are solid and some species can be hollow part of the time and solid at other times (Lindstrom *et al.* 1996; Lindeberg &

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Lindstrom 2010; Skriptsova & Kalita 2020). Moreover, pores on the thallus surface, female germlings composed of a vegetative cell and a carpogonium, and unequal division in the embryo have been reported only in one of the eight species of *Halosaccion*, suggesting that these morphological details need to be analysed in a higher number of species to determine whether they may be considered diagnostic (Mitman & Phinney 1985; van der Meer & Bird 1985).

Two species of Palmariaceae have been reported from high latitudes of the southern hemisphere: *P. decipiens* and *P. georgica* (Reinsch) R.W. Ricker. The former is a dominant marine red algal species that provides habitat, nourishment and shelter for many marine organisms along Antarctic and Subantarctic Island ecosystems (Becker *et al.* 2011), whereas the latter is a small gregarious plant reported from South Georgia, and Heard and Macquarie Islands (Ricker 1987). Recent genomic analyses have confirmed the presence of *P. decipiens* in eastern Antarctica (Bustamante *et al.* 2020). However, there are probably more than two high-latitude southern hemisphere Palmariaceae. For a group that seems to have limited dispersal capabilities, specimens as distant as Macquarie Island and South Georgia are probably distinct species.

During expeditions to southern Chile along remote and isolated channels and fjords to explore macroalgal diversity, specimens of a diminutive entity were collected from the intertidal and subtidal zones, and assessed based on morphology and three molecular markers: nuclear-encoded internal transcribed spacer (ITS), barcode region of the cytochrome c1 region (*cox*1) and ribulose 1-5-biphosphate carboxylase/oxygenase (*rbc*L). This study discovered an undescribed taxon from collections from Subantarctic Chile, which is closely allied to the genus *Devaleraea* on the basis of principal coordinates and phylogenetic analyses.

MATERIAL AND METHODS

Collection of specimens

Specimens of Palmariaceae from the intertidal and subtidal zones were collected during expeditions to southern Chile along the Beagle Channel, London Island (54°38.8740′S, 71°59.2230′W) and the Cormoranes Archipelago (54°47.9865′S, 68°38.0000′W). The collections were air-dried for morphological and molecular analyses, and then preserved in silica gel. Quantitative characters represent range (min–max values) from 30 measurements. Photographs were taken using the Leica MC170 camera attached to an EZ4 Leica stereomicroscope (Leica Microsystem, Wetzlar, Germany). Voucher specimens were deposited at the herbarium of the Laboratorio de Ecosistemas Marinos Antárticos y Sub-antárticos (LEMAS), Universidad de Magallanes, Punta Arenas, Chile, and Herbarium of the Universidad Nacional Toribio Rodriguez de Mendoza (KUELAP).

DNA sequencing and alignment preparation

Genomic DNA was extracted from *c*. 5 mg of dried thallus, which was ground in liquid nitrogen, using a NucleoSpin Plant II Kit (Macherey-Nagel, Düren, Germany) according to the manufacturer's protocol. For PCR and sequencing the following primer pairs were used: ITS (ITS1/ITS2; Lindstrom *et al.* 1996), *cox*1 (F43/R880; Yang *et al.* 2008) and *rbc*L (F57/R753, F645/Rrbcst; Saunders & Moore 2013). For amplification, we used the GoTaq® Green Master Mix (Promega, Wisconsin, USA), preparing 25 µl volumes. The mixture included 3 µl of total DNA solution, 0.5 µl of each forward and reverse primer (10 pmol), 12.5 µl of master mix and 8.5 µl MilliQ water. Reactions for the three markers were cycled in a T100™ Thermal Cycler (Bio-Rad, California, USA) using the following parameters: 94°C for 2 min, followed by 40 cycles of 94°C for 30s, 47°C for 60s and 72°C for 60s, and a final extension of 72°C for 10 min. PCR products were electrophoresed on 1% agarose gels, purified using the NucleoSpin Gel and PCR clean-up kit (Macherey-Nagel, Düren, Germany) following the manufacturer's instructions, and then sequenced commercially (Macrogen, Seoul, Korea). Full-length forward and reverse strands were determined for all taxa, and the electropherograms were edited using the Chromas v1.45 software (McCarthy 1998). The newly generated sequences were deposited in GenBank (Table 1).

Molecular analyses

Saturation of substitution tests were performed using the DAMBE7 software (Xia 2018) to evaluate *cox*1 and *rbc*L data by plotting numbers of transitions and transversions against Kimura-2-parameter distances (K2P). Additionally, the PCoA based on pairwise genetic distances and 1,000 bootstrap replicates for *cox*1 and *rbc*L was performed in GenAlEx v6.502 (Peakall & Smouse 2012) to explore similarities in genetic divergences within the Palmariales. Multivariate analyses were conducted with 686 base pairs (bp) for *cox*1 and for 1368 bp for *rbc*L. The phylogeny was based on the concatenated data combining ITS (1047 bp), *cox*1 (686 bp) and *rbc*L (1368 bp) data using RAxML HPC-PTHREADS-AVX2 (Stamatakis 2014) and MrBayes v3.2.5 (Ronquist *et al.* 2012) softwares for Maximum likelihood (ML) and Bayesian inference (BI), respectively. Genera classified in the Rhodothamniellaceae (i.e. *Camontagnea* Pujals, *Rhodothamniella* Feldmann) were designated as outgroups.

The best-fitting nucleotide substitution model was selected using the program PartitionFinder2 (Lanfear *et al.* 2017) with three partitions. The best partition strategy and model of sequence evolution was selected based on the corrected Akaike Information Criterion (AICc; Sugiura 1978). The general time reversible nucleotide substitution model with a gamma distribution and a proportion of invariable sites (GTR+Γ+I) was selected for the multilocus analysis. Maximum likelihood (ML) analyses were implemented in the raxmlGUI 2.0-beta.6 interface (Edler *et al.* 2019) using the GTR+Γ+I model and with support assessed with 1,000 rapid bootstraps. Bayesian inference was performed with MrBayes v3.2.5 software (Ronquist *et al.* 2012) using Metropolis coupled MCMC. The likelihood vs generation data was plotted using the Tracer v1.6 program (Rambaut *et al.* 2014) to reach a likelihood plateau and set the burn-in value. The convergence of both runs was evaluated using

Table 1. GenBank accession numbers for *rbc*L, *cox*1 and ITS for the specimens and their sequences used in this study.

Species	Location	Voucher	*rbc*L	cox1	ITS
Camontagnea oxyclada	Victoria, Australia	G0279	KC134348	KC130153	-
Devaleraea callophylloides	British Columbia, Canada	GWS042452 GWS042466	MH277324	MH593135	MH482484
Devaleraea callophylloides	Alaska, USA	GWS042451 GWS042458	MH482497	MH593136	-
Devaleraea callophylloides	Alaska, USA	GWS008352 GWS005092	MF543841	HM918742	-
Devaleraea marginicrassa	Uzhno-Kurilskaya Bay, Russia	37023-43	AB275867	-	MN032334
Devaleraea mollis	Washington, USA	GWS039508 GWS036294	KX281900	KX281898	-
Devaleraea mollis	British Columbia, Canada	GWS035931	KY250830	KY205175	-
Devaleraea ramentacea	New Brunswick, Canada	GWS005484 GWS003565	MH277312	JX572120	MH272871
Devaleraea ramentacea	Newfoundland and Labrador, Canada	GWS005481	MH277216	JX571995	-
Devaleraea ramentacea	Newfoundland and Labrador, Canada	GWS039277	MH277234	MF543930	MH272850
Devaleraea ramentacea	Canada	GWS009335	KT886264	KT886172	
Devaleraea stenogona	Kit Bay, Russia	37021-1 37021-2	MN052633	MT353883	MN032314
Devaleraea stenogona	Kit Bay, Russia	37021-3/37021-4	MN052636	MT353884	MN032317
Devaleraea titlyanoviorum	Kunashir Island, Russia	LE-A0000179	MT353898	MT701560	MT679721
Devaleraea titlyanoviorum	Rudnaya Bay, Russia	LE-A0000182-3/7	MT353885	MT353880	MT328235
Devaleraea titlyanoviorum	Sakhalin Island, Russia	Sukacheva47 Sakhalin5	MT353895	MT353881	MT328239
Devaleraea yagan	**Archipelago Cormoranes, Magallanes**	**LEMAS035 (DEB042)**	**OL347706**	**OL347708**	**OL352390**
Devaleraea yagan	**London Island, Magallanes**	**LEMAS036 (DEB043)**	**OL347707**	**OL347709**	**OL352399**
Halosaccion americanum	Canada	GWS008214	KT886265	KT886173	
Halosaccion glandiforme	Alaska, USA		U04173	-	
Kallymenicola invisibilis	British Columbia, Canada	GWS002209A	KY250831	KY205176	-
Kallymenicola penetrans	British Columbia, Canada	GWS013011A GWS036093A	KY250845	KY205174	-
Kallymenicola superficialis	British Columbia, Canada	GWS012640A GWS002729A	KY370760	KY205178	-
Meiodiscus concrescens	British Columbia, Canada	GWSC029	-	GU224102	-
Meiodiscus spetsbergensis	Nova Scotia, Canada	SLC005 GU224103	KC134351	GU224103	-
Palmaria decipiens	Antarctica		MF543838	NC 046496	-
Palmaria decipiens	Doumer Island, Antarctica	LMS00004	MN967052	MN967053	-
Palmaria decipiens	East Antarctica	CUP Pade	MN099018	MN099016	-
Palmaria hecatensis	Alaska, USA	GWS035930 GWS035847	KY250833	MF543956	
Palmaria palmata	New Brunswick, Canada	GWS003845 GWS014600	KT886266	KT886175	MF543986
Palmaria palmata	New Brunswick, Canada	GWS001790	U04186	KY572816	MF543990
Rhodonematella subimmersa	British Columbia, Canada	GWS035350 GWS002835	KY250821	HM918519	-
Rhodophysema georgei	Nova Scotia, Canada	GWSCRG001	KC134338	KT886176	-
Rhodophysema minus	British Columbia, Canada	GWS019420 GWS003287	KY250840	GU224122	-
Rhodophysemopsis hyperborea	Newfoundland and Labrador, Canada	GWS040281	KY250805	-	-
Rhodothamniella floridula	Wales, UK	GWSC13606 GWS25529	KC134330	KJ179939	-
Rubrointrusa membranacea	British Columbia, Canada	GWS010516 SLC020	KT886267	GU224123	-

Tracer to observe if runs reached an effective sample size greater than 200. To evaluate posterior probabilities, we conducted two runs each with four chains (three hot and one cold) for 10,000,000 generations, sampling trees every 1,000 generations. A burn-in of 25% was used to avoid suboptimal trees in the final consensus tree (Calderon *et al.* 2021).

RESULTS

Genetic diversity

The saturation test revealed no evidence for saturation of substitution at any codon position. The PCoA showed similarities of genetic divergence within the Meiodiscaceae,
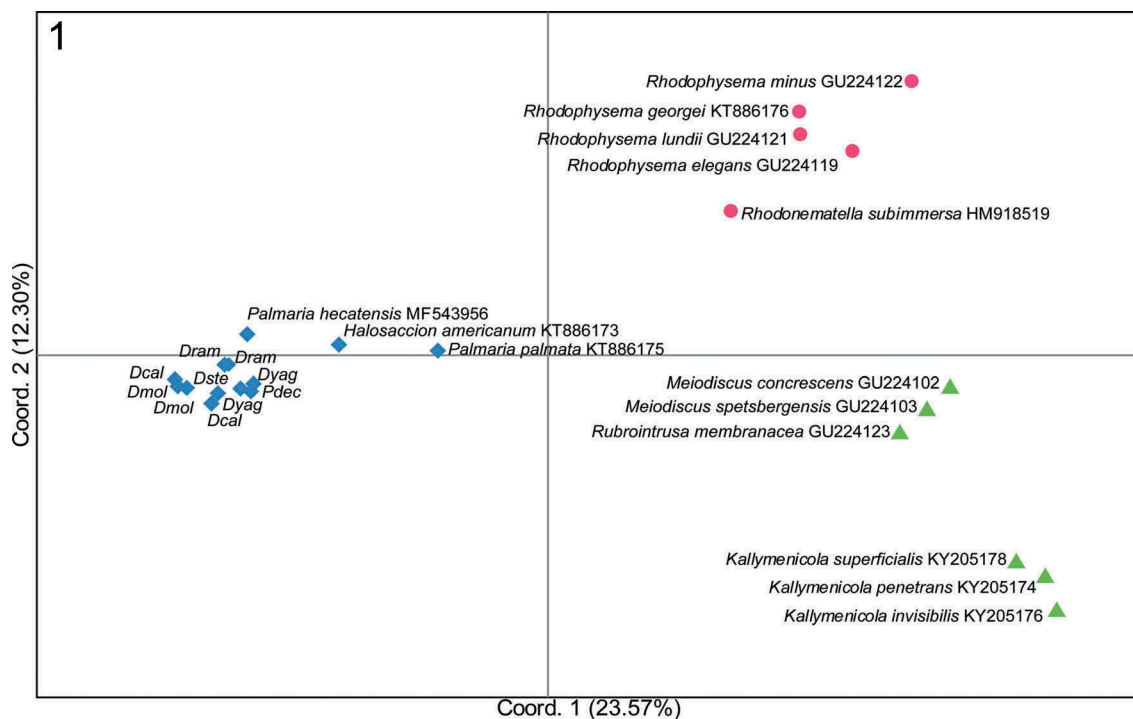
Fig. 1. Principal coordinate plot of *cox*1 accessions of members of Meiodiscaceae (triangle), Palmariaceae (diamond) and Rhodophysemataceae (circle). Dcal, *Devaleraea callophylloides*; Dmar, *D. marginicrassa*; Dmol, *D. mollis*, Dram, *D. ramentacea*; Dste, *D. stenogona*; Dyag, *D. yagan*; and Pdec, *P. decipiens*.

Palmariaceae and Rhodophysemataceae for *cox*1 (Fig. 1) and *rbc*L (Fig. 2). The plane of the first two main axes of the PCoA, which accounted for 35.9% of the total variation expressed for *cox*1, and 52.34% for *rbc*L, showed that species of Palmariaceace were grouped with shorter distances due to their low genetic divergence (Tables 2, 3) compared to species within the Meiodiscaceae and Rhodophysemataceae, which were quite spread out, especially for *rbc*L and along coordinate 2 (Fig. 2).

Phylogenetic analyses

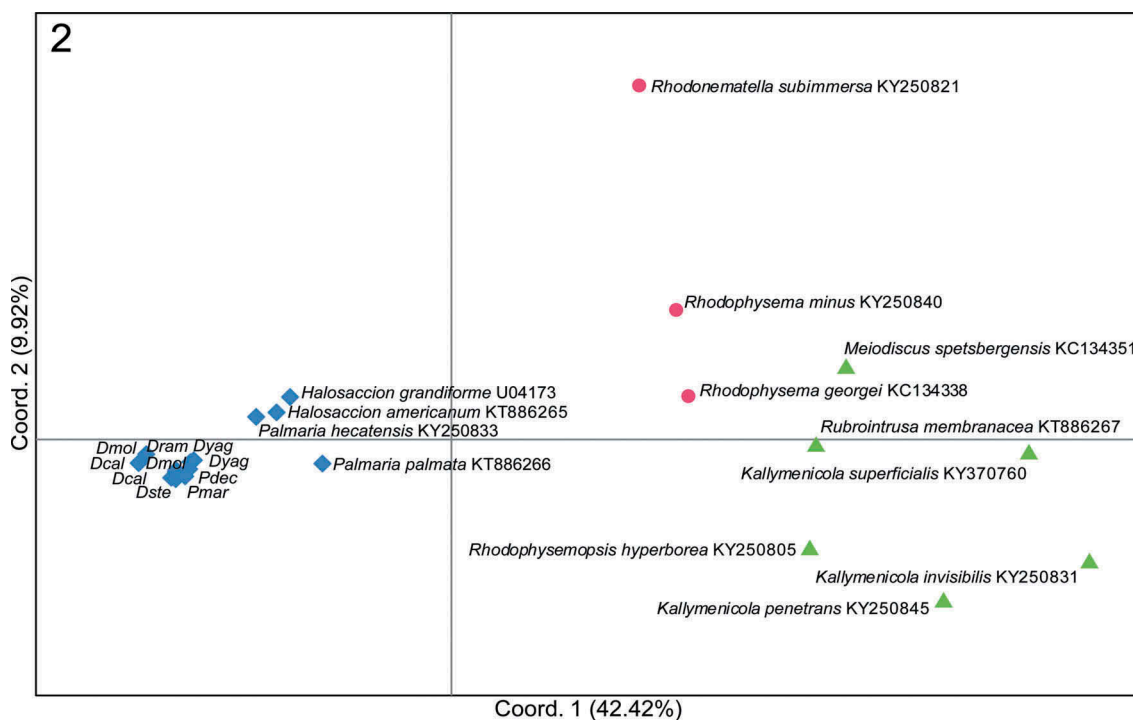Phylogenetic trees obtained from the ML and BI analyses strongly confirmed the monophyly of the Palmariaceae

Fig. 2. Principal coordinate plot of *rbc*L accessions of members of Meiodiscaceae (triangle), Palmariaceae (diamond) and Rhodophysemataceae (circle). Dcal, *Devaleraea callophylloides*; Dmar, *D. marginicrassa*; Dmol, *D. mollis*; Dram, *D. ramentacea*; Dste, *D. stenogona*; Dyag, *D. yagan*; and Pdec, *P. decipiens*.

(Fig. 3). The multilocus phylogeny (*cox*1 + *rbc*L + ITS) resolved *Devaleraea*, *Halosaccion* and *Palmaria* as members of the Palmariaceae. The genus *Palmaria* was paraphyletic. Among species of the Palmariaceae, the undescribed entity from southern Chile was embedded in the lineage *Devaleraea* and resolved in a sister position, but with low support, to the clade composed of *Devaleraea* candidates, namely, the Antarctic *Palmaria* sp. (CUP-Pade) and *P. decipiens* (LMS00004). The southern Chilean species differed from *Palmaria* sp. by 7.9%–8.4% for *cox*1 and 0.7%–0.9% for *rbc*L, and from *P. decipiens* by 7.0%–7.5% for *cox*1 and 0.7%–0.9% for *rbc*L.

Taxonomic treatment

Anatomical observations of our material from Chile revealed that the specimens shared 'diagnostic' characters common to the genera *Devaleraea* and *Palmaria*, including the lack of a hollow thallus. PCoA and multilocus phylogeny revealed that the unidentified species of Palmariaceae was strongly supported as a distinct entity in the genus *Devaleraea*. The data support the proposal of this material as a new species:

Devaleraea yagan D.E. Bustamante, M.S. Calderon & A. Mansilla *sp. nov.*
Figs 4–9

DESCRIPTION: Plants diminutive, 0.5–2.5 cm in height (Fig. 4), fronds compressed, thin and not hollow, reddish to reddish-brown with terete stipes attached to a discoid holdfast. Stipe expanded gradually into a blade up to 0.15–0.24 mm thick and 0.31–0.95 mm broad. Blades irregularly dichotomously to subdichotomously branched one to three times with narrow bases of 75–93 µm, rounded or obtuse tips (Figs 5, 6). Branches 0.5–5 mm in length, narrowly lanceolate, dichotomously divided in the upper parts. Blades 75–280 µm thick. At surface view, cells irregularly shaped in younger and older parts (Figs 7, 8). Medulla consisting of two layers of large rounded or oval cells of 82.1–95.3 × 91.5–101.3 µm surrounded by one or two layers of smaller cells of 57.8–65.2 × 43.1–65.6 µm (Figs 9, 10). Rhizoidal cells of 4.4–6.1 × 5.9–6.4 µm developing between large medullary cells. Cortex composed of one to two rows of cells of 5.2–7.3 × 5.6–8.5 µm (Figs 9, 10). In tetrasporophytes (Fig. 11), tetrasporangial sori formed on both surfaces of the blade and covering the lamina except the basal portion (Fig. 12). Tetrasporangia of 13.5–26.3 × 8.9–12.9 µm (Fig. 13), borne on stalk cells. Male and female gametophytes were not observed.

HOLOTYPE: LEMAS036 (Fig. 4), collected 11 August 2013 by A. Mansilla, deposited at the herbarium of the Laboratorio de Ecosistemas Marinos Antárticos y Sub-antárticos (LEMAS), Universidad de Magallanes, Punta Arenas, Chile.

ISOTYPE: KUELAP897, deposited at the Herbarium of the Universidad Nacional Toribio Rodriguez de Mendoza (KUELAP).

TYPE LOCALITY: Chile, Magallanes, London Island, 54°38.8740′S, 71°59.2230′W.

PARATYPE: **Chile**: Magallanes, Archipelago Cormoranes, 54°47.9865′S, 68°38.0000′W, colected 13 August 2013 by A. Mansilla, LEMAS035.

ETYMOLOGY: The species epithet, used as a noun in apposition, was taken from the name of the autochthonous aboriginal Yagan people, who subsist using traditional fishing methods. The cultural centre of these people is close to the type locality.
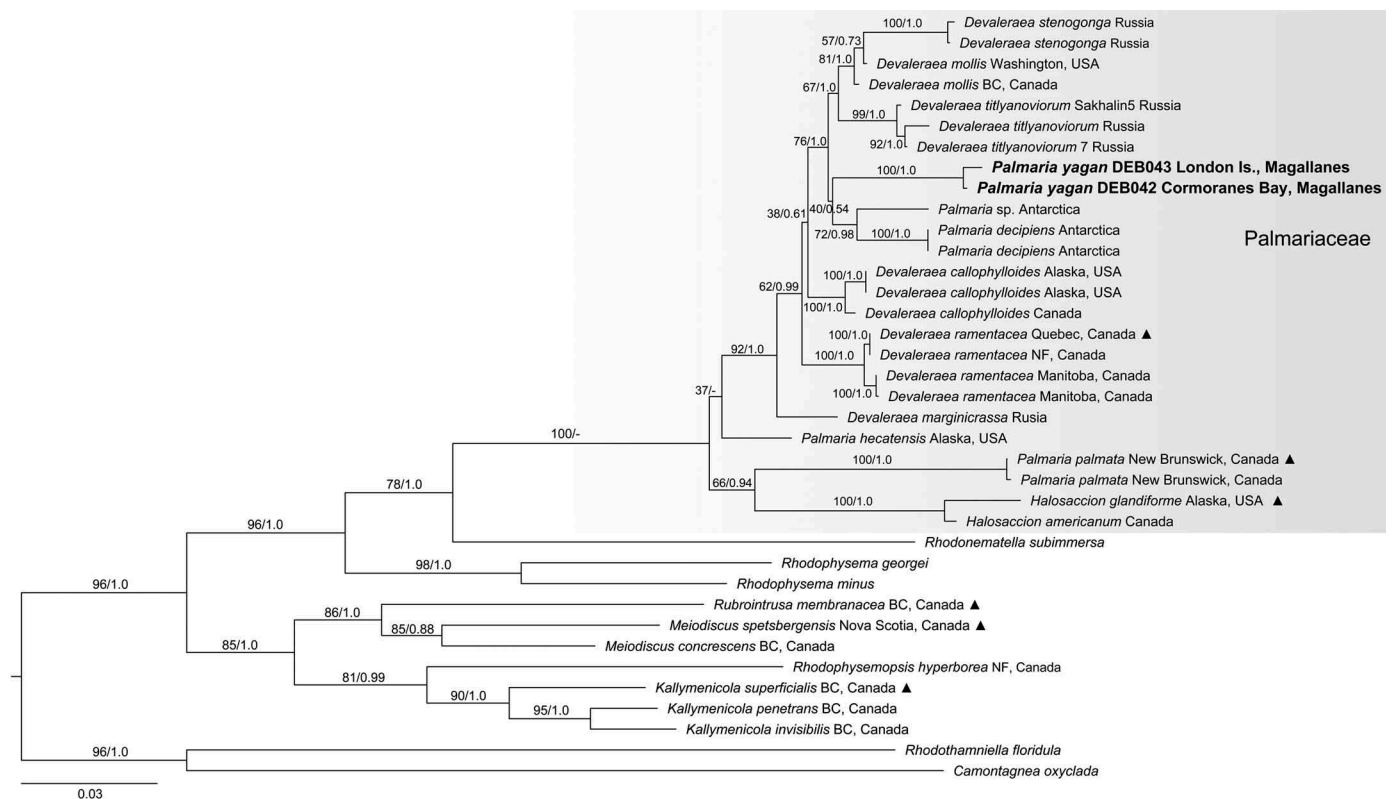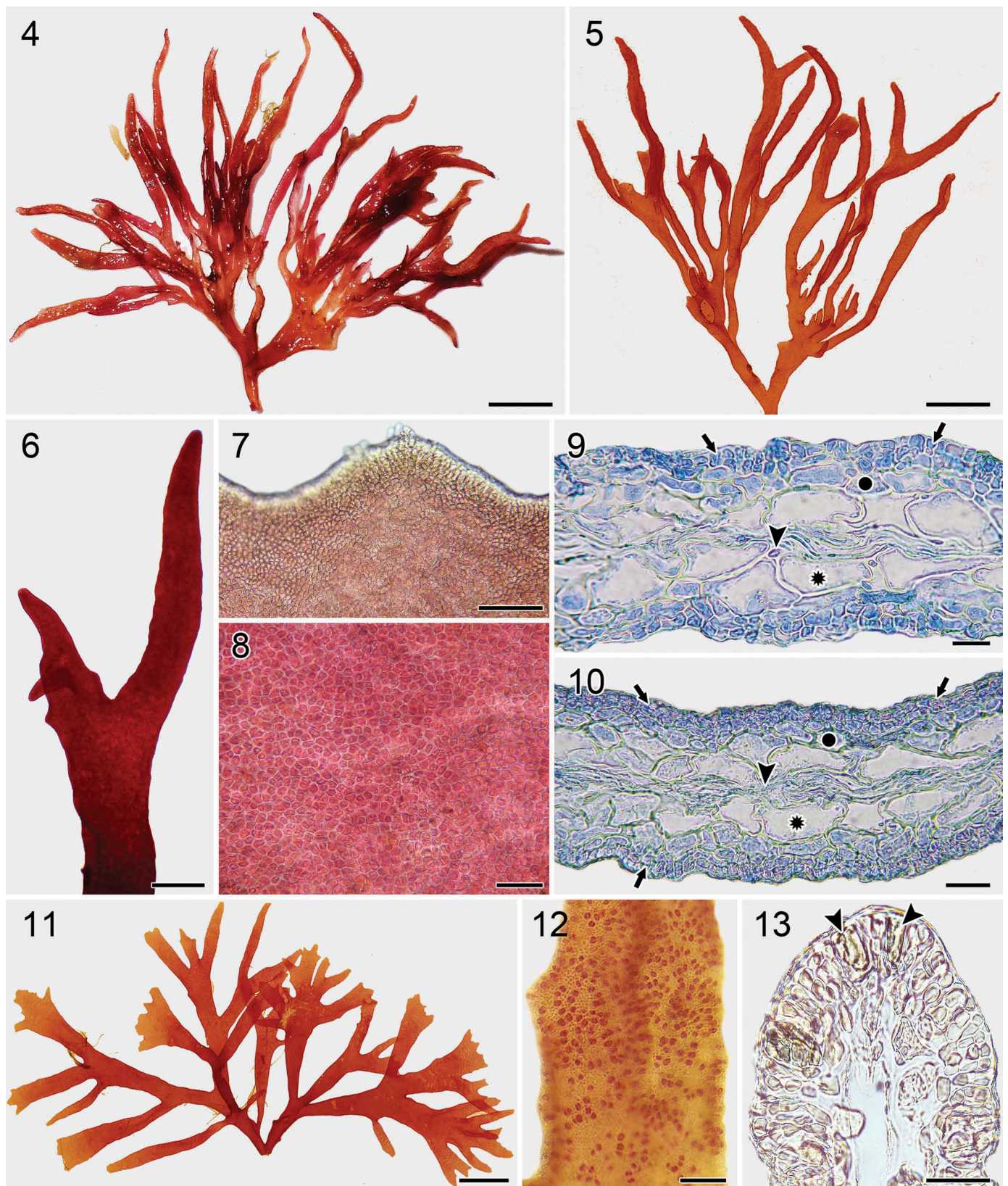

Fig. 3. Phylogenetic tree based on RAxML analysis of the concatenated data (*cox*1 + *rbc*L + ITS). Values on branch nodes are bootstrap supports and Bayesian posterior probabilities. Generitypes are indicated by ▲. The scale bar indicates nucleotide substitutions.

Figs 4–13. Morphology and anatomy of *Palmaria yagan sp. nov.*

Fig. 4. Holotype specimen (LEMAS036). Scale bar = 2 mm.

Figs 5, 6. Irregularly dichotomously to subdichotomously branched blades. Scale bar in Fig. 5 = 2 mm; Scale bar in Fig. 6 = 100 μm.

Fig. 7. Margins of blades. Scale bar = 100 μm.

Fig. 8. Superficial view of blades. Scale bar = 100 μm.

Figs 9, 10. Cross-sectional views of apical (Fig. 9) and middle part (Fig. 10) of blades showing 1- or 2-layered cortex (arrows), medulla with smaller cells (circles) surrounding larger cells (stars), and rhizoidal cells (arrowheads). Scale bar in Fig. 9 = 50 μm; Scale bar in Fig. 10 = 100 μm.

Fig. 11. Blade of tetrasporophyte. Scale bar = 2 mm.

Fig. 12. Superficial view of blades containing tetrasporangia. Scale bar = 100 μm.

Fig. 13. Cross-sectional views of blades with tetrasporangia (arrowhead). Scale bar = 25 μm.

DISTRIBUTION: At present, known only from Magallanes (Subantarctic Chile).

DISCUSSION

The monophyly of the family Palmariaceae has been extensively demonstrated (Lam *et al.* 2016; Saunders *et al.* 2018; Bustamante *et al.* 2020; Skriptsova & Kalita 2020). However, diagnostic features that allow delimitation of the genera *Devaleraea* and *Palmaria* have not been unequivocally confirmed. Congenericity between *Devaleraea* and *Palmaria* was first suggested by Guiry (1982), then again by Lindstrom & South (1989) and Rice *et al.* (1991). The critical feature is the presence of a hollow thallus, which was considered the only distinguishing character. However, a hollow thallus is not a good feature for distinguishing *Devaleraea* or *Palmaria* since species of *Halosaccion* are also hollow. This character was used by Guiry (1982) to separate *Devaleraea* and *Palmaria*, but it clearly does not hold up now since several non-hollow species are congeneric with the type (and at least one species is sometimes hollow and sometimes not). The lack of reliable features to distinguish *Devaleraea* and *Palmaria* is currently overcome by performing phylogenetic analyses since the monophyly of *Devaleraea*, with its present circumscription, was confirmed (Saunders *et al.* 2018; Skriptsova & Kalita 2020).

The genetic divergence between *Devaleraea* and *Palmaria* is lower than the values observed among other genera within sister families, namely Rhodophysemataceae, Meiodiscaceae and Rhodothamniellaceae (Fig. 2; Table 2). The genetic distances for Palmariaceae are lower than between species of *Kallymenicola* J.R. Evans & G.W. Saunders (Meiodiscaceae) or *Rhodophysema* Batters (Rhodophysemataceae) (Table 3). This is confirmed by the *rbc*L PCoA where the total variation explained by the two coordinates exceeded 50%, and Palmariaceae species are closer among themselves than species within the Meiodiscaceae and Rhodophysemataceae. These data added arguments that may favour the merger of all species in the Palmariaceae into a single genus, *Palmaria*. However, further analyses including genomic data of members of *Devaleraea* (which is likely to be replaced by the older generic name *Leptosarca* A. Gepp & E. Gepp, on the basis of the synonymy, established by Saunders *et al.* 2018, between *L. simplex* A. Gepp & E. Gepp and *Palmaria palmata*), *Halosaccion* and *Neohalosacciocolax* may either confirm the monophyly of these genera or suggest their merger into a single genus. This study describes the new species *D. yagan* as a member of the genus *Devaleraea* to avoid

Table 2. Intergeneric genetic distances (*p*-distances) in percentages for *cox*1 and *rbc*L markers among different genera of Palmariales.

Family	Genera	*cox*1	*rbc*L
Palmariaceae	*Devaleraea-Halosaccion-Palmaria*	5.7–11.0	0.9–3.5
Rhodophysemataceae	*Rhodonematella-Rhodophysema*	13.5–14.0	6.7–8.4
Meiodiscaceae	*Kallymenicola-Meiodiscus-Rhodophysemopsis-Rubrointrusa*	10.8–16.0	4.8–6.4
Rhodothamniellaceae	*Camontagnea-Rhodothamniella*	19.7	8

Table 3. Interspecific genetic distances (*p*-distances) in percentages for *cox*1 and *rbc*L markers among species of *Devaleraea*, *Kallymenicola* and *Rhodophysema*.

Family	Genera	*cox*1	*rbc*L
Palmariaceae	*Devaleraea*	4.1–8.4	0.1–1.1
Rhodophysemataceae	*Rhodophysema*	7.9–10.4	5.2
Meiodiscaceae	*Kallymenicola*	4.2–6.1	3.8–4.6

nomenclatural confusion and following the current taxonomic consensus. In summary, despite progress in molecular, phenotypic and cultural studies of the family Palmariaceae, we are obviously still far from fully understanding the phylogeny and systematics of the family.

The new species from Subantarctic Chile, *Devaleraea yagan*, is characterized by having a diminutive thallus attached by a reduced holdfast and rhizoidal cells occurring among large medullary cells. These features distinguish *D. yagan* from other Palmariaceae, especially from phylogenetically related species such as *D. mollis* (Setchell & N.L. Gardner) G.W. Saunders, C. J. Jackson & Salomaki, which reaches up to 35 cm in length (van der Meer & Bird 1985), *D. stenogona* (Perestenko) Skriptsova & T.L. Kalita, reaching up to 25 cm (Skriptsova & Kalita 2020), *D. titlyanoviorum* Skriptsova & T.L. Kalita, being up to 20 cm (Skriptsova *et al.* 2020), and *P. decipiens*, which reaches 70 cm (Becker *et al.* 2011). All these species are further characterized by larger sizes of medullary cells and by not having rhizoidal cells in the medulla. The new species *D. yagan* is restricted to the Magellan Region along the Beagle Channel, which is defined as an estuarine-like environment receiving large volumes of freshwater contributions from the surrounding rivers and glaciers (Isla *et al.* 1999) and having an average temperature of 5 to 6°C and annual rainfall of around 500 mm yr^{-1} (Gordillo *et al.* 2015). These particular conditions may biogeographically separate *D. yagan* from other species in the southern hemisphere, although *D. yagan* and *P. georgica* may overlap in the Subantarctic Islands (Ricker 1987). The latter is morphologically distinguished from *D. yagan* by having cortical hairs (Ricker 1987).

Over 18 species of Palmariaceae have been confirmed molecularly in the northern hemisphere (Lindstrom *et al.* 1996; Lam *et al.* 2016; Saunders *et al.* 2018; Skriptsova & Kalita 2020; Skriptsova *et al.* 2020). Conversely, only three species, including *D. yagan*, have been reported from the southern hemisphere (Bustamante *et al.* 2020). This widespread distribution in cold-temperate and Arctic/Antarctic regions indicates that biogeographic dispersal occurred (Lindstrom *et al.* 1996). Isolation of populations due to environmental changes (e.g. glaciations, sea level and seawater temperature changes) probably provided rare founder events that have driven recent speciation in the Palmariaceae (Breeman 1988, 1990; Avise 1992). A detailed characterization of Palmariaceae from southern waters may perhaps give insights into these hypotheses (Saunders *et al.* 2018). However, the isolated realms where *P. decipiens* and *P. georgica* (from South Georgia) and *D. yagan* (from the Beagle Channel, Magallanes) were found illustrate the sampling difficulty in Antarctic and Subantarctic regions. Therefore, ambitious commitments by institutes and

funding agencies from the national Antarctic Treaty parties are needed to pursue biodiversity surveys, by investing in research, monitoring and exploration programs across Subantarctic and Antarctic regions (Convey & Peck 2019).

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