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Dictyota falklandica sp. nov. (Dictyotales, Phaeophyceae) from the Falkland Islands and southernmost South America

FRITHJOF C. KÜPPER ^{1,2}, AKIRA F. PETERS ^{1,3}, ELENI KYTINOY^{2,4,5}, ALDO O. ASENSI⁶, CHRISTOPHE VIEIRA ⁷, ERASMO C. MACAYA ^{8,9,10}, AND OLIVIER DE CLERCK ⁷

¹School of Biological Sciences, University of Aberdeen, Cruickshank Building, St. Machar Drive, Aberdeen AB24 3UU, Scotland, UK

²Marine Biodiscovery Centre, Department of Chemistry, University of Aberdeen, Aberdeen AB24 3UE, Scotland, UK

³Bezhin Rosko, F-29250 Santec, Brittany, France

⁴University of the Aegean, Department of Marine Sciences, University Hill, Mytilene, Lesvos Island 81100, Greece

⁵Hellenic Centre for Marine Research, Institute of Oceanography, Athinou - Souniou Ave (46.7th km), Anavyssos 19013, Greece

⁶Independent Scholar

⁷Phycology Research Group and Centre for Molecular Phylogenetics and Evolution, Ghent University, Krijgslaan 281 S8, Ghent 9000, Belgium

⁸Departamento de Oceanografía, Universidad de Concepción, Casilla 160-C, Concepción, Chile

⁹Centro FONDAP de Investigaciones en Dinámica de Ecosistemas Marinos de Altas Latitudes (IDEAL), Independencia 631, Valdivia, Chile

¹⁰Millennium Nucleus Ecology and Sustainable Management of Oceanic Island (ESMOI), Larrondo 1281, Coquimbo, Chile

ABSTRACT

Surveys of the seaweed flora of the Falkland Islands and of Tierra del Fuego revealed the presence of a new species of brown alga. *Dictyota falklandica* sp. nov. inhabits the shallow rocky infralittoral in sheltered localities and the lower intertidal in more exposed sites. *Dictyota falklandica* has a regular to irregular habit of dichotomously branched blades, forming erect thalli composed of a single-layered cortex and medulla, with margins in the apical parts dotted with dormant apical cells. Sporangia occur in irregular groups or longitudinal lines on the thallus surface. Molecular phylogenies based on chloroplast *psbA* and *rbcl* and mitochondrial *cox1* sequences showed that the species from the Falkland Islands is sister to a clade formed by *D. korowai*, recently described from New Zealand and *D. kunthii* known from both the Pacific coast of South America and New Zealand. Temperature tolerance experiments, showing mortality at 25 °C but survival at 20 °C, confirm the cold-temperate affinity of this taxon. Its relationship to other cold-temperate Southern Hemisphere species is discussed, with its closest relatives living in regions with sea surface temperatures of at least 7–10 °C higher.

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INTRODUCTION

Dictyota species are common members of the benthic communities in warm-temperate and tropical seas, and the genus is widely considered to have warm-water affinities (Tronholm *et al.* 2010). Among the 97 *Dictyota* species currently recognized, 87 are described from warm-temperate and tropical seas (Guiry & Guiry 2019). Their effective chemical defense against grazing based on diterpenes (Hay *et al.* 1987; Wiesemeier *et al.* 2007) and high constitutive hydrogen peroxide release, likely for the control of bacterial biofilms (Küpper *et al.* 2002), as well as their ability to propagate through fragmentation (Herren *et al.* 2006), enables them to form sizeable populations even in localities under high grazing pressure such as Ascension Island (Tsiamis *et al.* 2017). Significantly, defense against amphipods is inducible in Chilean *Dictyota kunthii* (C. Agardh) Greville (Macaya & Thiel 2008), which may be a more widespread feature in this genus.

In contrast to the ubiquity of *Dictyota* in warm seas, few reports exist of *Dictyota* species in cold-temperate seas of the southern Hemisphere (Fig. S1). Asensi & Küpper (2012)

reported a *Dictyota* sp. from Puerto Deseado (Patagonia, Argentina), where it was present year-round, growing on calcareous algae. There is a high chance that this report corresponds to the entity from Argentina identified as *D. dichotoma* (Hudson) J. V. Lamouroux by Lopes-Filho *et al.* (2017) using DNA sequence information. *Dictyota dichotoma* is primarily known from Europe, but is also present in South Africa and the temperate Atlantic coast of Brazil and Argentina (Tronholm *et al.* 2010; O. De Clerck, pers. obs.). *Dictyota kunthii* occurs in cold to warm-temperate regions along the South American Pacific coast from Peru to Chile, the Juan Fernandez Islands (Ramírez & Osorio 2000; Rodríguez-Ruiz *et al.* 2017), and in New Zealand (Hoffmann & Santelices 1997; Nelson 2013; Ramírez & Santelices 1991). The most southern *Dictyota* described so far is *D. decumbens* (Ricker) Hörnig, Schnetter *et Prud'homme* van Reine from Macquarie Island (54 °S, Ricker 1987). The species was originally described as *Dilophus decumbens* Ricker, because the medulla comprised 2–3, irregularly organized layers of cells near the margins. *Dilophus decumbens* was subsequently transferred to *Dictyota* (Hörnig *et al.* 1992b, 1992a).

CONTACT Frithjof Küpper  fkuepper@abdn.ac.uk

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Recent work (Mystikou *et al.* 2016) reported a hitherto undescribed *Dictyota* sp. from the eastern tip of Tierra del Fuego (Argentina) and from two localities in the Falkland Islands. In a *psbA* phylogeny, this unknown taxon was sister to *D. binghamiae* J.Agardh from Mexico and California (Mystikou *et al.* 2016). However, more research was needed before it could be formally described as a separate species, especially its relationships with Southern Hemisphere taxa (Chile, Juan Fernandez) such as *D. phlyctaenodes* Montagne and *D. kunthii*, which was the rationale for the present study. In this paper, we report on our recent observations and collections of *Dictyota* from the Falkland Islands, including a formal description as a new species, underpinned by temperature tolerance experiments with cultured isolates.

MATERIALS & METHODS

Specimens of *Dictyota* were collected in the shallow subtidal zone at two localities in East Falkland (Fig. 1; Table 1): Blue Beach, San Carlos (51° 34.2676' S, 59° 2.1236' W), on 24 January 2017, at 1 m depth, and the south of North Arm (52° 8.4014' S, 59° 22.174' W) on 26 January 2017, at 2 m depth (Figs. 2–5). Herbarium specimens were prepared in parallel to subsamples which were fixed in 4% formalin-seawater (for microscopy), CTAB buffer and silica gel (both for DNA extraction). Samples in Chile were collected in the Juan Fernandez Archipelago (Robinson Crusoe Island), in the low intertidal (*D. kunthii*) and the shallow subtidal at 1 m depth (*D. phlyctaenodes*) from El Palillo (33°38.3177' S, 78° 49.2879' W) on 12–13 February 2014, respectively. Additional samples of *D. kunthii* were collected from northern Chile in the low intertidal at Caleta Errazuriz (23°26.689' S, 70° 35.3039' W) on 12 November 2012 and from central Chile

in the low intertidal at Cocholgüe (36°36.3011' S, 72°58.4962' W) from August to November 2015.

Underwater photographs were taken with an Olympus Tg4 camera, while micrographs were taken with an Olympus DP50 digital camera (Melville, NY, USA) mounted on a Leitz Diaplan compound microscope or Leica Wild M10 (Wetzlar, Germany) stereo microscope.

Total genomic DNA was extracted from silica gel-dried samples using a modified CTAB-extraction method (Steen *et al.* 2017). Sequences were generated for the plastid-encoded PSII reaction centre protein D1 (*psbA*) and the mitochondrial-encoded cytochrome oxidase subunit 1 (*cox1*) gene. PCR primers and conditions are described in Tronholm *et al.* (2010). Sequences were aligned by eye using MEGA 7 (Kumar *et al.* 2016) and added to a reference species-level alignment of *Dictyota* and related genera (*Canistrocarpus*, *Dictyotopsis*, *Dilophus*, *Scoresbyella* and *Rugulopteryx*). The matrix, a multi-locus alignment of mitochondrial *cox1* and *cox3* genes, and chloroplast *psaA*, *psbA* and *rbcL* genes, consisted of 64 taxa and 5446 positions. The matrix was 81% filled at the gene level (Table S1).

A maximum-likelihood (ML) tree was generated from the concatenated alignment, partitioned by organelle and codon position. The partition scheme and substitution models were estimated using PartitionFinder 2 (Lanfear *et al.* 2017). ML analyses were conducted using RAxML v8.1 under a GTR + GAMMA model (Stamatakis 2014). The robustness of the resulting phylogenies was tested using 1000 replicates of a rapid bootstrap heuristic (Stamatakis 2006). In addition, a Bayesian tree was estimated using MrBayes 3.2. (Ronquist *et al.* 2012), applying a GTR + GAMMA model applied to every partition. Two runs, consisting of four chains each, were run for 10 million generations. Stationarity and convergence of runs was assessed visually using

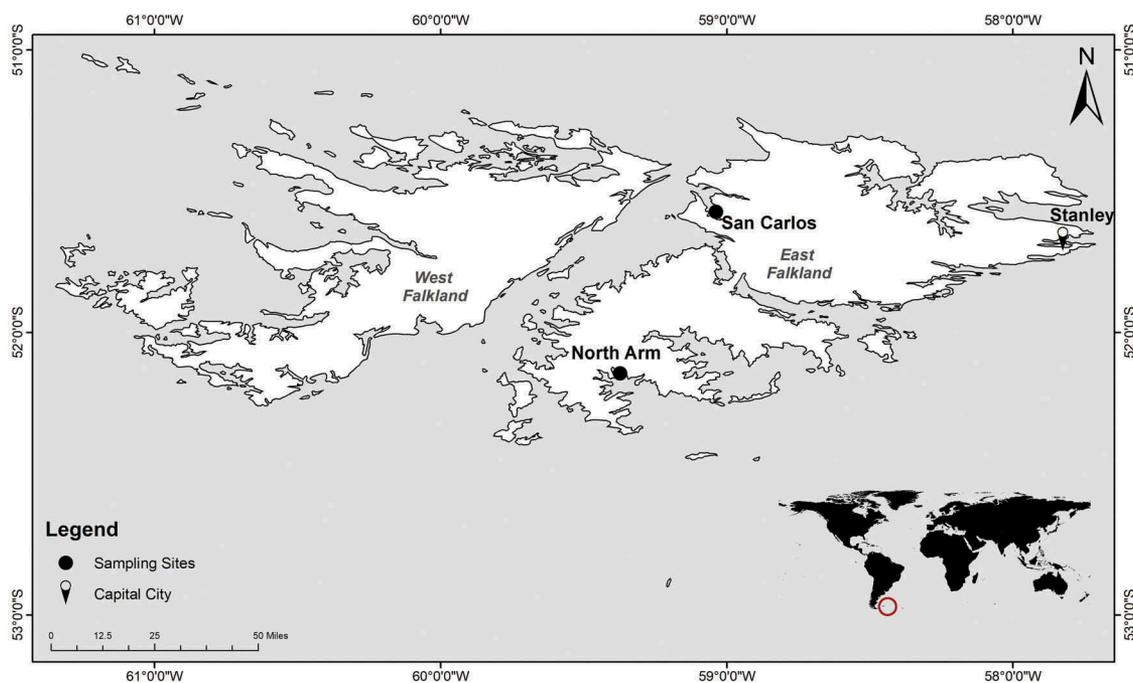


Fig. 1. Localities in the Falkland Islands where *Dictyota falklandica* sp. nov. was found: San Carlos and North Arm.

Table 1. Comparison of key features of *Dictyota decumbens* and *Dictyota falklandica* sp. nov.

	<i>Dictyota decumbens</i>	<i>Dictyota falklandica</i>
Habitat and substratum	Subtidal on rocks, mats several cm thick on boulders or other macroalgae	Subtidal, erect and was always epilithic
Anatomy	Double-layered medulla	Single-layered cortex and medulla
Distribution	Macquarie Island	Eastern Tierra del Fuego and Falkland Islands

Tracer v1.6 (Rambaut *et al.* 2018) and a majority rule consensus tree was calculated after removal of a burn-in of 15%.

For all specimens, we collected mean sea surface temperature (SST mean) based on locality information and environmental layers present in Bio-Oracle v2.0 (Assis *et al.* 2018). Averaged mean surface temperatures correlate equally well or better with marine species distribution ranges compared to average minimum or maximum temperatures as demonstrated by Bosch *et al.* (2018). Ancestral states of SST affinities were reconstructed and visualised on the phylogeny using the fastAnc and contMap functions of the R package *phytools* (Revell 2012).

Three unialgal isolates (coded FI 17–182 and FI 17–186 from San Carlos, and FI 17–203 from North Arm) were obtained from thallus apices. The culture medium was autoclaved, half-strength Provasoli-enriched sea water (Coelho *et al.* 2012), which for the first weeks contained 4 mg l⁻¹ GeO₂ to inhibit diatom growth. During isolation, the algae received natural daylight near a north-facing window, and the temperature ranged between 12–14 °C.

In a laboratory-based experiment, the gross temperature tolerance was determined with cultures pre-cultivated at 15 °C. On day 1, a dish (10 ml) of each of the three isolates (FI 17–182, FI 17–186, FI 17–203) was placed at 15 °C, 20 °C and 25 °C under white light of 30 μmol m⁻¹ sec⁻¹. On day 11, the medium was changed in all cultures, and those which had been incubated at 20 and 25 °C were transferred to 15 °C (where all cultures were kept). On days 24 and 38, the medium was changed in all dishes, and all cultures were continued at 15 °C until final examination two months after start of the experiment.

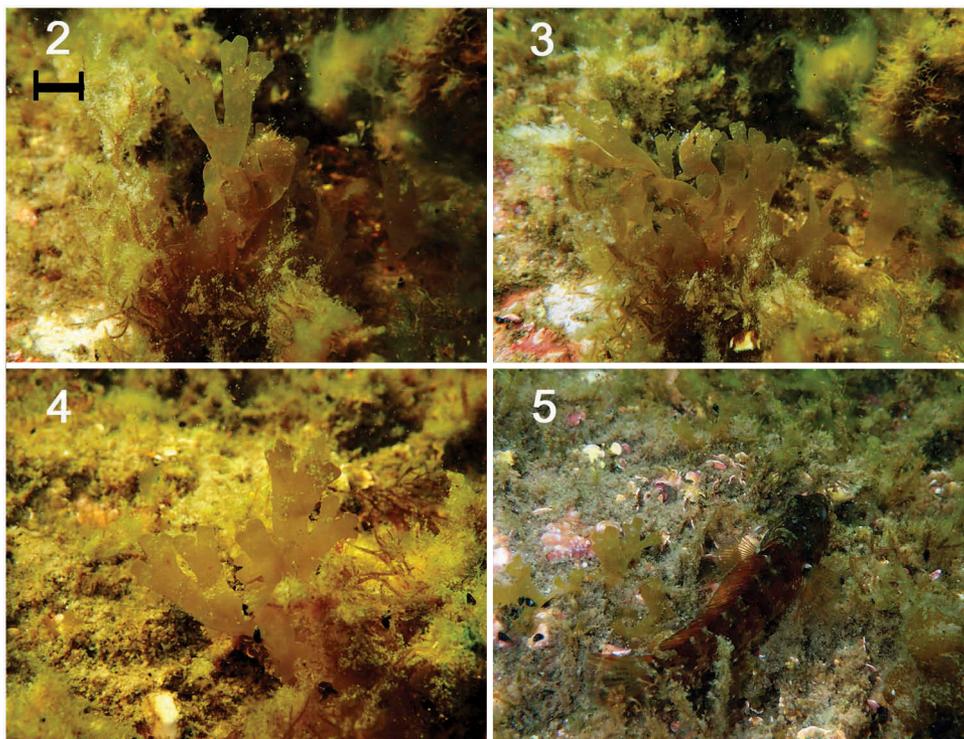
RESULTS

In situ observations

At both San Carlos and North Arm, *Dictyota falklandica* grew on rocky substrata at 1–3 m beneath low tide level, typically under a canopy of *Macrocystis pyrifera* (Linnaeus) C.Agardh (Figs. 2–5). Synchronous with our subtidal collections on the Falkland Islands we examined the rocky intertidal zone close to the two sites. We did not find the species on the rocks or in shallow tide pools.

Phylogeny

The maximum-likelihood and Bayesian phylogenies (Fig. 6) were in good agreement, differing only in parts of the tree that received low support. *Dictyota falklandica* sp. nov. was resolved sister to a clade formed by *D. korowai*, a species recently described from northern New Zealand (Nelson *et al.* 2019) and *D. kunthii* from the Pacific coast of South America and New Zealand. Another closely related species is *D. binghamiae* from the northeastern



Figs 2–5. *Dictyota falklandica* sp. nov. in its natural habitat at North Arm on 26 January 2017, with epiphytes on its thallus and surrounding vegetation. Scale bar = 5 mm.

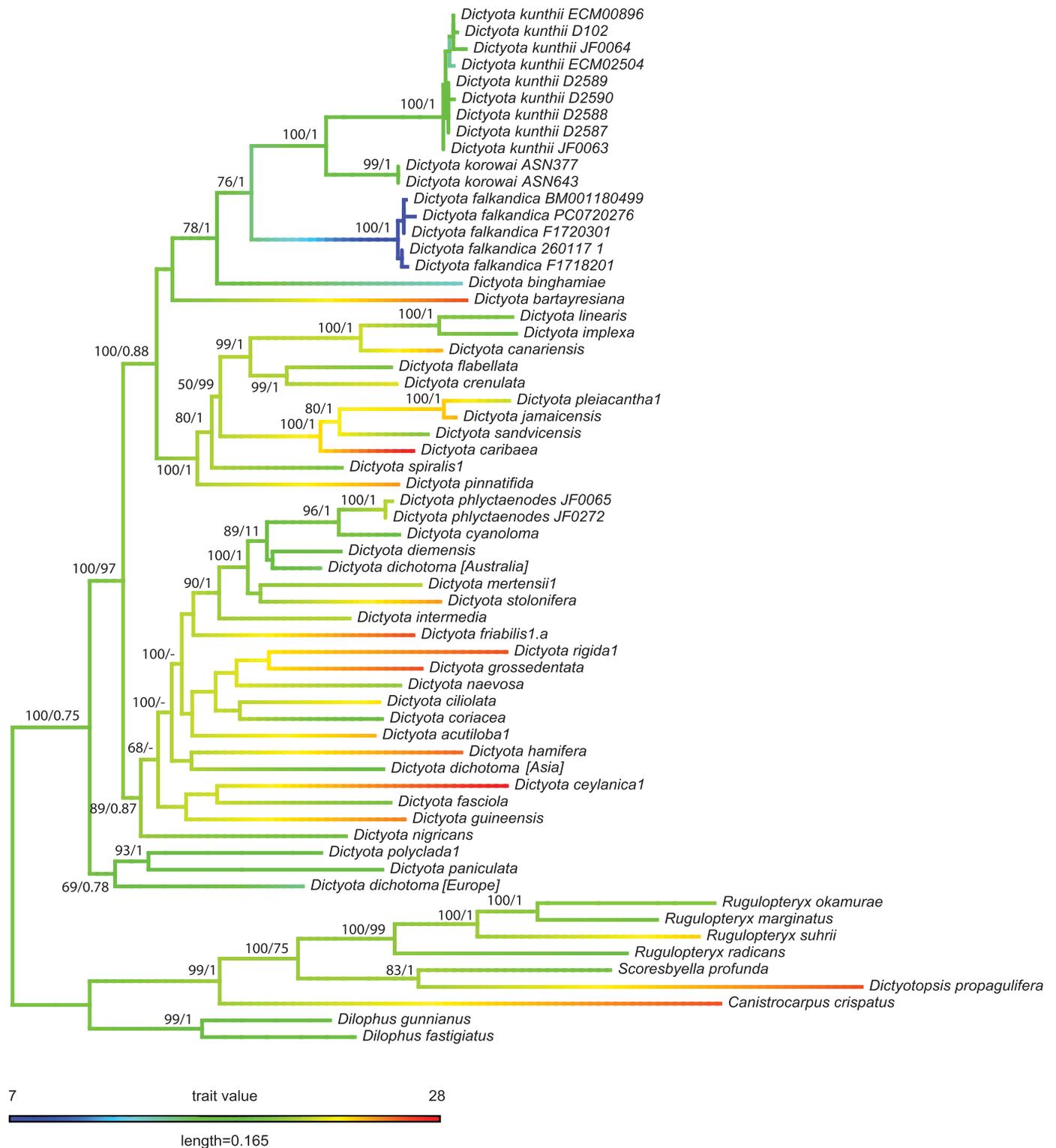


Fig. 6. Maximum-likelihood tree of the concatenated alignment (-Ln = 45270.45) with rapid bootstrap (left) and posterior probabilities (right) values shown on branches. Branch colours are the maximum-likelihood estimates of the ancestral states of mean sea surface temperature.

Pacific. *D. phlyctaenodes*, described from, and possibly endemic to, the Juan Fernandez Islands, appears only distantly related to *D. binghamiae*, *D. falkandica*, *D. korowai* and *D. kunthii*. *D. phlyctaenodes* is resolved in a clade with predominantly Australian species. Likewise, *D. coriacea*, occurring on both sides

of the northern Pacific Ocean, and eastern Pacific species with tropical affinities (*D. crenulata*, *D. flabellata*) are all distantly related to *D. falkandica*.

Taken together, this suggests that this is a species new to science, which is formally described below:

Dictyota falklandica* F.C.Küpper, A.F.Peters, A.O.Asensi & O.DeClerck *sp. nov.

Figs. 2–5, 7–14

DIAGNOSIS: Species characterised by a regular to irregular dichotomously branching habit of erect blades up to 65 mm long and 5 mm wide, each branch growing by division of a meristematic apical cell. Margins of the whole thallus dotted with dormant apical cells. *In situ* colour medium to pale brown, retaining the same colour when dry.

HOLOTYPE: Herbarium specimen from San Carlos (F39) was deposited in the Natural History Museum (BM), London, UK as No. BM013828094, accompanied by vials with CTAB samples (Vial F17-186 BM013792001; Vial F18-203 BM013792002; Vial F17-182 BM013792003).

ISOTYPE: An isotype from North Arm was deposited in the Muséum National d'Histoire Naturelle – Paris, as no. PC 0776066. Material from the 3 live cultures fixed in CTAB buffer was deposited in the Muséum National d'Histoire Naturelle – Paris, accompanying the isotype specimen, as no. PC 0776066.

TYPE LOCALITY: Blue Beach, San Carlos, East Falkland, Falkland Islands, 51° 34.2676' S, 59° 2.1236' W. The type locality of this species at San Carlos is historically significant as the landing site of the forces who liberated the Falkland Islands in 1982.

ETYMOLOGY: The organism is named after the Falkland Islands, where the type material was collected.

REPRESENTATIVE SEQUENCES: MK516759 – MK516759 (*cox1*) and MK516799– MK516800 (*psbA*), and MK516815 (*rbcl*).

ISOTYPE CULTURE: A unialgal culture isolated on 31 January 2017 from the type material collected at San Carlos was deposited in the Culture Collection of Algae and Protozoa (no. CCAP 1335/1).

Vegetative and reproductive morphology

Dictyota falklandica grew upright, but lacked a conspicuous base. The species was attached by patches of rhizoids, present near basal parts of thalli (Fig. 8). Apices were obtuse, with protruding lens-shaped apical cells. Irregular branching in the apical parts of thalli might be related to regained meristematic activity of additional apical cells which dot the margins of the apical parts of the thallus (Figs. 7, 9). Dichotomies were evenly spaced every 13–15 mm. The branching angle was approximately 45–50°. Surface and margins were smooth, and lacked teeth or proliferations (Fig. 11).

The thallus was composed of a single-layered cortex and medulla (Figs. 13–15). Tangential divisions of cortical and medulla cells, resulting in a multi-layered cortex or medulla, were not observed, not even in the most basal regions. Cells contained multiple discoid plastids devoid of pyrenoids. Cortical cells were rectangular to nearly isodiametric in surface view (Fig. 9), (22–) 30 (–38) µm long, (12–) 17 (–22) µm wide and 10–12 µm high (Figs. 12, 14). Medullary cells were (77–) 101 (–129) µm long, (46–) 57 (–77) µm wide (Fig. 9) and 95–120 µm high (Fig. 14).

Male and female gametophytes were not observed. Immature sporangia occurred in irregular groups or longitudinal lines on the thallus surface (Fig. 12). Sporangia were not surrounded by an involucre and were borne on a single stalk cell. Thalli had tufts of hairs randomly scattered on both surfaces (Fig. 13).

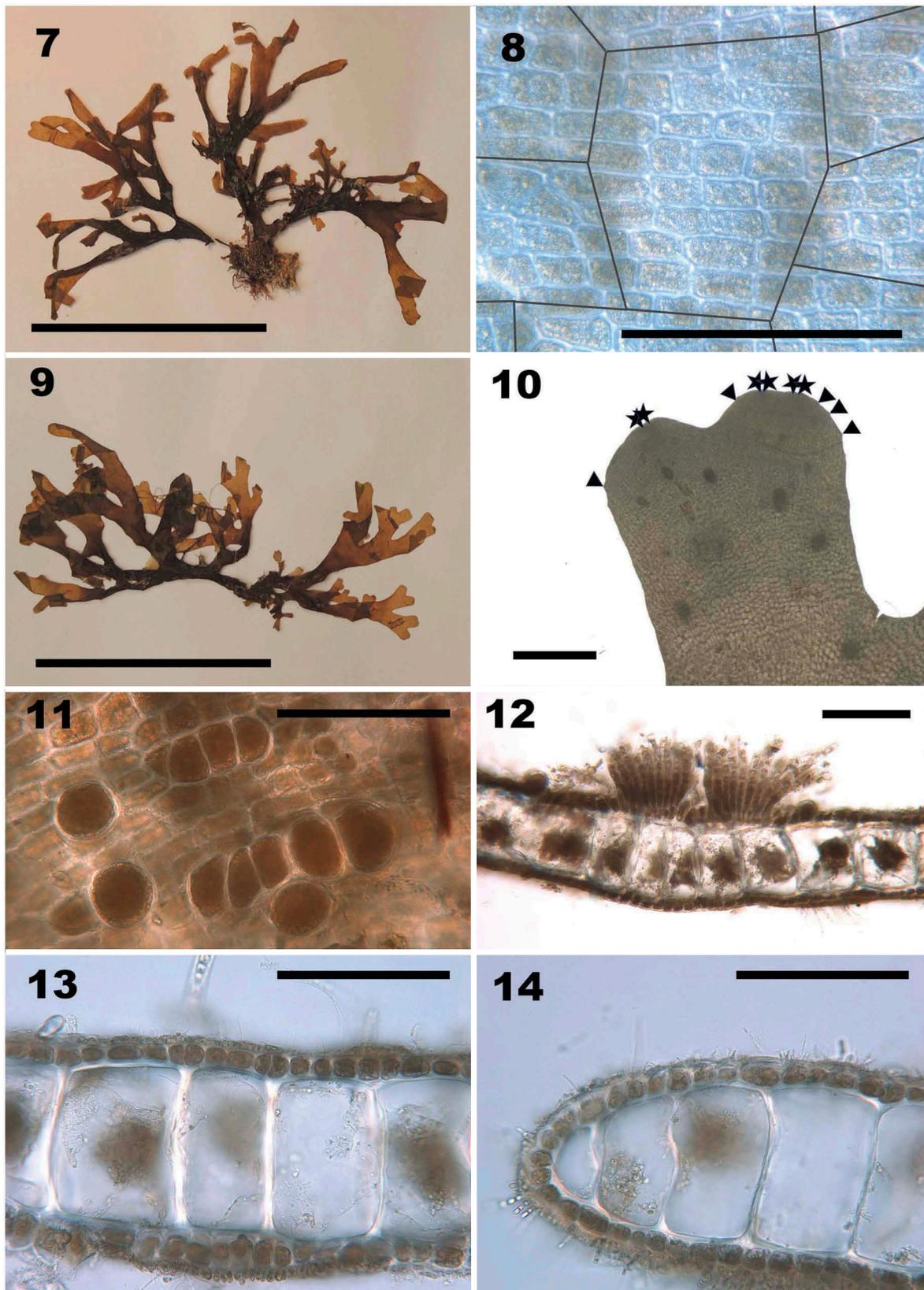
Temperature tolerance

Two months after the start of the experiment, cultures of the three isolates exposed to 25 °C for 11 days showed clear signs of stress – two were dead, and one culture was mostly bleached with only small tissue parts remaining pigmented. In contrast, the cultures at 20 or 15 °C for the same duration had healthy (brown – dark brown) pigmentation and growth.

DISCUSSION

The order Dictyotales is frequent in temperate to tropical seas, and particularly diverse in Australia and New Zealand (Guiry & Guiry 2019; Nelson *et al.* 2019; Phillips 2001). However, the nearby subantarctic region is largely devoid of this order, and it is missing in Antarctica (Papenfuss 1964; Wiencke & Clayton 2002; Wiencke *et al.* 2014). This study highlights that the overall diverse seaweed flora of the Falkland Islands still has significant potential for new discoveries, warranting further surveys and taxonomic studies (Küpper & Kamenos 2018). *Dictyota falklandica sp. nov.* from the Falkland Islands and southernmost South America is one of the few species able to grow in cold-temperate waters, and it appears to be geographically confined to this cold-temperate region. Its closest relatives, *D. korowai*, *D. binghamiae* and *D. kunthii*, live in regions with sea surface temperatures at least 7–10 °C higher. In the Falkland Islands, surface water temperatures oscillate between 5 and 9 °C (Arkhipkin *et al.* 2013), similar to temperatures present in eastern Tierra del Fuego (Rivas & Pisoni 2010). One of the collecting sites, North Arm, lies in the SE part of the Falkland Islands, which is strongly influenced by cold subantarctic waters. In high-temperature tolerance experiments, our cultures of *D. falklandica* survived 20 °C but not 25 °C for an 11-day duration. It resembles other subantarctic species from South America, which have upper survival temperatures between 19.9 and 24.5 but not 25 °C (Peters & Breeman 1993). Such species, albeit adapted to the cold-temperate subantarctic environment, have a large 'safety margin' which may allow occurrence in milder habitats such as shallow pools or the intertidal. At Bahía Thetis (Tierra del Fuego; Mystikou *et al.* 2016), *D. falklandica* had been collected in the mid-intertidal zone of a more exposed site, as judged from the presence of *Durvillaea antarctica* (Chamisso) Hariot.

Mystikou *et al.* (2016) concluded that *D. falklandica sp. nov.* (as *Dictyota sp.*) is morphologically and genetically different from other *Dictyota* species. In the present study, *Dictyota falklandica* was resolved as sister to *D. kunthii* from the Pacific coast of South America, the Juan Fernandez Islands, New Zealand and Australia (Guiry & Guiry 2019) and *D. korowai* from northern New Zealand (Nelson *et al.* 2019). However, the phylogenetic relationship of *D. falklandica* to *D. decumbens* endemic to subantarctic Macquarie Island is unknown, as no sequences are available of *D. decumbens*. The hydrographic conditions at Macquarie Island just north of the Antarctic Convergence resemble those at the Falkland Islands, with even slightly lower sea surface temperatures of 3.0–7.3 °C (Ricker 1987). However, although one can hypothesize that *D. falklandica sp. nov.* may be



Figs 7–14. Herbarium specimens and micrographs of *Dictyota falklandica* sp. nov.

Fig. 7. Isotype (PC accession no. 0776066). Scale bar = 5 cm.

Fig. 8. Surface view, with walls of larger medullar cells indicated by black lines. Scale bar = 50 μ m.

Fig. 9. Holotype specimen (BM accession no. BM013828094). Scale bar = 5 cm.

Fig. 10. Apical region of branching thallus, with actively growing apical cells (asterisks) as well as marginal dormant apical cells (arrowheads). Scale bar = 1 mm.

Fig. 11. Spores on thallus surface in irregular longitudinal groups. Scale bar = 50 μ m.

Fig. 12. Cross section of thallus with two hair tufts. Scale bar = 100 μ m.

Fig. 13. Cross section of central blade area. Scale bar = 100 μ m.

Fig. 14. Cross section of blade margin. Scale bar = 100 μ m.

related to *D. decumbens*, the geographic distance and morphological differences (the latter was initially described as *Dilophus decumbens* due to a double-layered medulla; Ricker 1987) suggests they are not conspecific. A number of recent studies on macroalgae with a circum-Antarctic distribution show that only large species or taxa that are good drifters [*Macrocystis pyrifera*, *Durvillaea antarctica*, *Adenocystis utricularis* (Bory) Skottsberg] and possibly their symbionts and pathogens such as *Maullinia braseltonii* P.Murúa, P.Goecke & S.Neuhauser (Blake *et al.* 2017; Murua *et al.* 2017), *Herpodiscus durvilleae* (Lindauer) G.R.South (Fraser & Waters 2013) and *Laminariocolax aecidioides* (Rosenvinge) Peters (Bernard *et al.* 2018) are genetically similar in the different land masses and islands, whereas less good drifters and smaller algae [e.g. *Lessonia* spp., the cryptic species included in *Bostrychia intricata* (Bory) Montagne] rather form different species in the distant localities (Fraser & Waters 2013; Fraser *et al.* 2013; Martin & Zuccarello 2012; Muangmai *et al.* 2014). Like *D. decumbens*, *D. falklandica* sp. nov. was found in the subtidal zone. However, *D. decumbens* has a prostrate habit. It forms several cm thick mats on boulders or other macroalgae (Ricker 1987), whereas the alga described here was erect and always epilithic. Available herbarium specimens of *D. decumbens* had been fixed in formalin before mounting (Ricker 1987) and are therefore unsuitable for the extraction of DNA. We prefer to describe the Falkland *Dictyota* as a separate species based on morphological differences and geographic separation.

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ORCID

Frithjof C. Küpper  <http://orcid.org/0000-0003-1273-7109>
 Akira F. Peters  <http://orcid.org/0000-0001-5332-199X>
 Christophe Vieira  <http://orcid.org/0000-0002-5035-0426>
 Erasmo C. Macaya  <http://orcid.org/0000-0002-9878-483X>
 Olivier De Clerck  <http://orcid.org/0000-0002-3699-8402>

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