



Juvenile morphology of the large Antarctic canopy-forming brown alga, *Desmarestia menziesii* J. Agardh

Frithjof C. Küpper¹ · Charles D. Amsler² · Simon Morley³ · Bruno de Reviers⁴ · Aurelia Reichardt³ · Lloyd S. Peck³ · Akira F. Peters^{1,5}

Received: 22 May 2019 / Revised: 31 August 2019 / Accepted: 4 September 2019
© The Author(s) 2019

Abstract

For many types of seaweeds in Polar Regions, open questions remain about how their life cycle contributes to their overall adaptation to the extreme abiotic environment. This applies in particular to the major canopy-forming brown algae in much of the Antarctic Peninsula of the genus *Desmarestia*, which was investigated here. Diving surveys around Rothera Research Station (Adelaide Island, Antarctica) during December 2017–February 2018 revealed the widespread presence of a hitherto-unknown life form of *Desmarestia* sp. of a tender, feather-like morphology. Further studies explored whether this could be (1) a new, hitherto undescribed *Desmarestia* species (2) a new record for the region of a known *Desmarestia* species previously recorded elsewhere or (3) a so-far unknown life form of a species recorded for the region. Collections enabled the extraction of PCR-friendly DNA and sequencing of ITS1, which unambiguously showed that the samples belonged to *Desmarestia menziesii*, the only *Desmarestia* species presently recorded for the Adelaide Island/Marguerite Bay region. The presence of the juvenile morphology was subsequently confirmed throughout much of the natural range of *D. menziesii* during cruise-based diving surveys along the Western Antarctic Peninsula in 2019 and from collections at Anvers Island in 1989. Our collections thus constitute its juvenile morphology, which is not previously documented in the literature. The wider significance for the Polar seaweeds is discussed in the context of Taxonomy and Ecology.

Keywords Adelaide Island · Antarctic Peninsula · *Desmarestia chordalis* · *Desmarestia menziesii* · *Desmarestia rossii* · ITS · Southern Ocean

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00300-019-02584-3>) contains supplementary material, which is available to authorized users.

✉ Frithjof C. Küpper
fkuepper@abdn.ac.uk

- ¹ School of Biological Sciences, University of Aberdeen, Cruickshank Building, St. Machar Drive, Aberdeen AB24 3UU, Scotland, UK
- ² Department of Biology, University of Alabama at Birmingham, Birmingham, AL 35233-1405, USA
- ³ British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK
- ⁴ Institut Systématique Evolution Biodiversité (ISYEB), Muséum national d'histoire naturelle, CNRS, Sorbonne Université, EPHE, UA, 57 rue Cuvier, CP 39, 75005 Paris, France
- ⁵ Bezhin Rosko, 40 rue des pêcheurs, 29250 Santec, Brittany, France

Introduction

The Antarctic has some of the most extreme environments on planet Earth. Its marine environment is characterized by low temperatures rarely exceeding the range of -1.8 – 2 °C (Barnes et al. 2006). Compared to the sub-Antarctic region, the Antarctic is generally considered depauperate in terms of seaweed species diversity (Wiencke and Clayton 2002). Pioneering studies of Antarctic seaweed biodiversity, taxonomy and biogeography were conducted over a century ago by Skottsberg (Skottsberg 1907), with a recent synopsis provided by Wiencke and Clayton (2002). Adaptations of polar seaweeds enable them to survive at temperatures around freezing, and during months of darkness in winter (Wiencke et al. 2009). Contrasting with tropical and temperate bioregions, Polar Regions typically show an intertidal zone which is almost devoid of macroalgae. The reason for this are the extreme environmental conditions in the intertidal zone—where temperature extremes range from -50

to +5 °C (Peck et al. 2006; Waller et al. 2006), compounded by strong impacts of sea ice abrasion (Barnes and Souster 2011; Barnes et al. 2014), and the encasing of the intertidal by fast ice in the winter in all continental localities and year round in over 80% of the continent (Peck 2018). It is remarkable that the Antarctic phytobenthos has no representatives of the kelps (Laminariales), which occur in the Arctic and all cold-temperate bioregions worldwide. Their ecological niche and role, as providers of canopy, are mostly replaced by members of the Desmarestiales (Moe and Silva 1977), which were found to originate from cold waters of the southern hemisphere (Peters et al. 1997).

The northernmost parts of Antarctica—in particular, the South Shetland Islands, Anvers Island and the tip of the Antarctic Peninsula—are home to six Desmarestiales species, namely, *D. anceps* Montagne, *D. antarctica* R.L. Moe & P.C. Silva, *D. confervoides* (Bory) M. Ramirez & A.F. Peters and *D. menziesii* J. Agardh, as well as *Himantothallus grandifolius* (A. & E. Gepp) Zinova and *Phaeurus antarcticus* Skottsberg. In contrast, the region of Adelaide Island and Marguerite Bay, about 500 km further south along the Antarctic Peninsula, is impoverished in many aspects of its marine flora. Poorly surveyed in this regard until recently, an inventory of its seaweed diversity was published only a few years ago (Mystikou et al. 2014). In this region, *D. menziesii* is the major canopy-forming species in the depth range of around 5–20 m, and the only *Desmarestia* species recorded.

The present study was triggered when a sample collected in late December 2017 appeared to be a hitherto-unrecorded *Desmarestia* species for this area, which had not been captured by the survey 7 years earlier (Mystikou et al. 2014). Given that it could not be identified morphologically with the existing literature for Antarctic seaweeds (Wiencke and Clayton 2002), the following hypotheses were tested within the framework of this study: (1) Is this a native, novel species, for some reason missed by the previous survey (Mystikou et al. 2014)? (2) Could it be a new arrival for the area, e.g. either due to climate change-linked poleward migration, or an alien species? and (3) Could it be another life form of a known species for the area?

Materials and methods

Algae were collected by SCUBA diving in the vicinity of Rothera Research Station, Adelaide Island, between Dec. 2017 and February 2018. Dive sites surveyed and details of the dives are displayed in Fig. 1a and listed in Supplementary Table 1, respectively.

Immediately following each day of diving, herbarium specimens were prepared by mounting seaweed thalli on Bristol paper. They were deposited in the herbarium of the British Museum – Natural History (BM), British Antarctic Survey (BAS, Cambridge, UK) and Muséum National

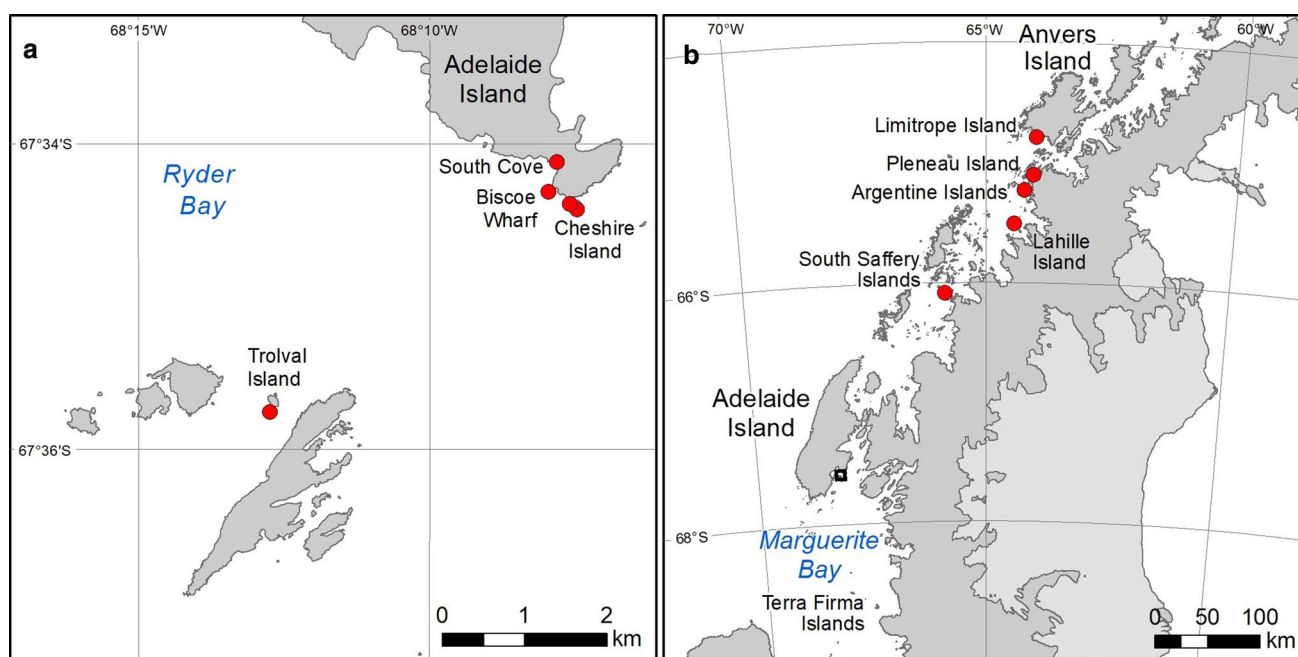


Fig. 1 Map of the study area with the dive sites. **a** The vicinity of Rothera Research Station surveyed in January 2018; **b** The sites along the Western Antarctic Peninsula surveyed in April 2019. The small square on Adelaide Island indicates the location of the map in Fig. 1a.

Red dots are dive sites and the open black square is Rothera Research Station. Source: Map produced by the British Antarctic Survey Mapping and Geographic Information Centre

d'Histoire Naturelle – Cryptogamie (PC). Fragments of all specimens were kept in silica crystals or 96% ethanol, both of which conserve DNA for further molecular studies.

The diving work at Rothera was complemented by cruise-based diving surveys in April and May 2019 at 15 sites along the Western Antarctic Peninsula ranging from the Terra Firma Islands in Marguerite Bay (S 68° 41.5', W 067° 31.6') to the Joubin Islands west of southern Anvers Island (S 64° 46.4', W 064° 22.2'). Subsequently, we examined voucher material collected from several other small islands off southern Anvers Island in 1989 (Amsler et al. 1995). Dive sites surveyed and details of the dives are displayed in Fig. 1b and listed in Supplementary Table 1, respectively.

DNA was extracted on samples # 180118-1.1 and # 180118-1.2 using CTAB buffer as described previously (Gachon et al. 2009). Polymerase chain reactions (PCR) were employed to amplify a fragment of the nuclear ribosomal DNA containing 3'-SSU, ITS1, and partial 5.8S, using the primer pair ITS1/KIR1, ITS1 (5' TCCGTAGGTGAA CCTGCGG 3'; White et al. 1990) and KIR1 (5' TTCAA GTTTTGATGATT 3'; Lane et al. 2006). PCR was carried out with an initial denaturation at 94 °C for 3 min, followed by 35 cycles of amplification consisting of denaturation at 94 °C for 30 s, annealing at 50 °C for 30 s, and then elongation at 72 °C for 1 min. The 35 cycles were followed by a final extension at 72 °C for 5 min. PCR amplification was performed in a total volume of 25 µL, containing 0.25 units µL⁻¹ of *Taq* DNA Polymerase (Promega), 1 × GoTaq Buffer, 5 mM MgCl₂, 0.5 mM dNTPs, 0.3 mM of each primer and 1.7 µL of template DNA. The DNA sequence obtained was aligned manually with Se-AL™ v2.0a11 (Sequencing Alignment Editor Version 2.0 alpha 11; <https://tree.bio.ed.ac.uk/software/seal/>) and meticulously checked for correctness by inspecting the chromatograms.

Identification of herbarium specimens, and live field material was attempted using available keys, in particular that of Wiencke and Clayton (2002). For present-day taxonomic and nomenclatural aspects, AlgaeBase (Guiry and Guiry 2018) was consulted.

Furthermore, the collections of the British Museum-Natural History (BM), of the Muséum National d'Histoire Naturelle – Cryptogamie (PC), and of the University of California, Berkeley (UC) were searched for any specimens from the Antarctic labelled as *Desmarestia menziesii*, or corresponding to the morphology (but possibly labelled under different taxonomic names) described here.

Results

An unknown *Desmarestia* sp., initially found during a dive at the Biscoe Wharf, was subsequently observed at most sites surveyed (Table S1; Figs. 2 and 3). It intrigued the

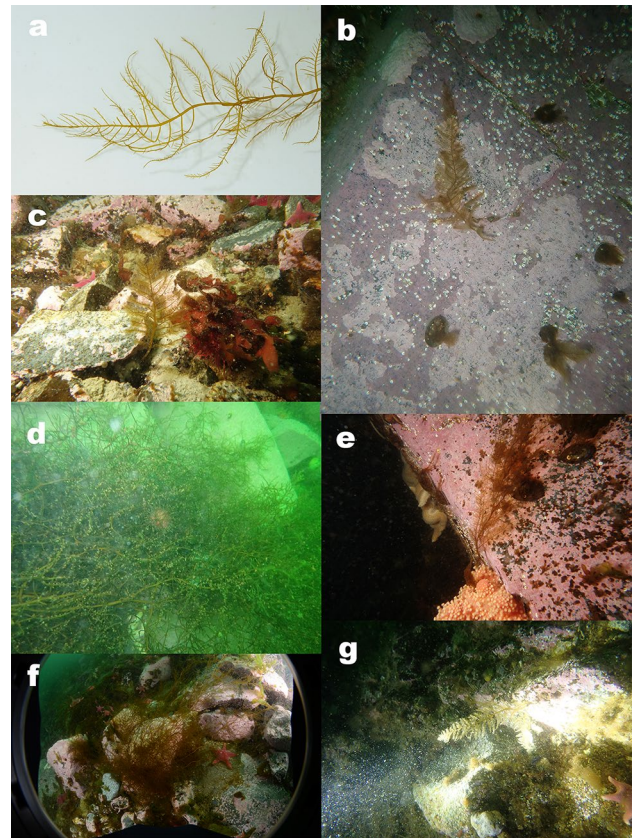
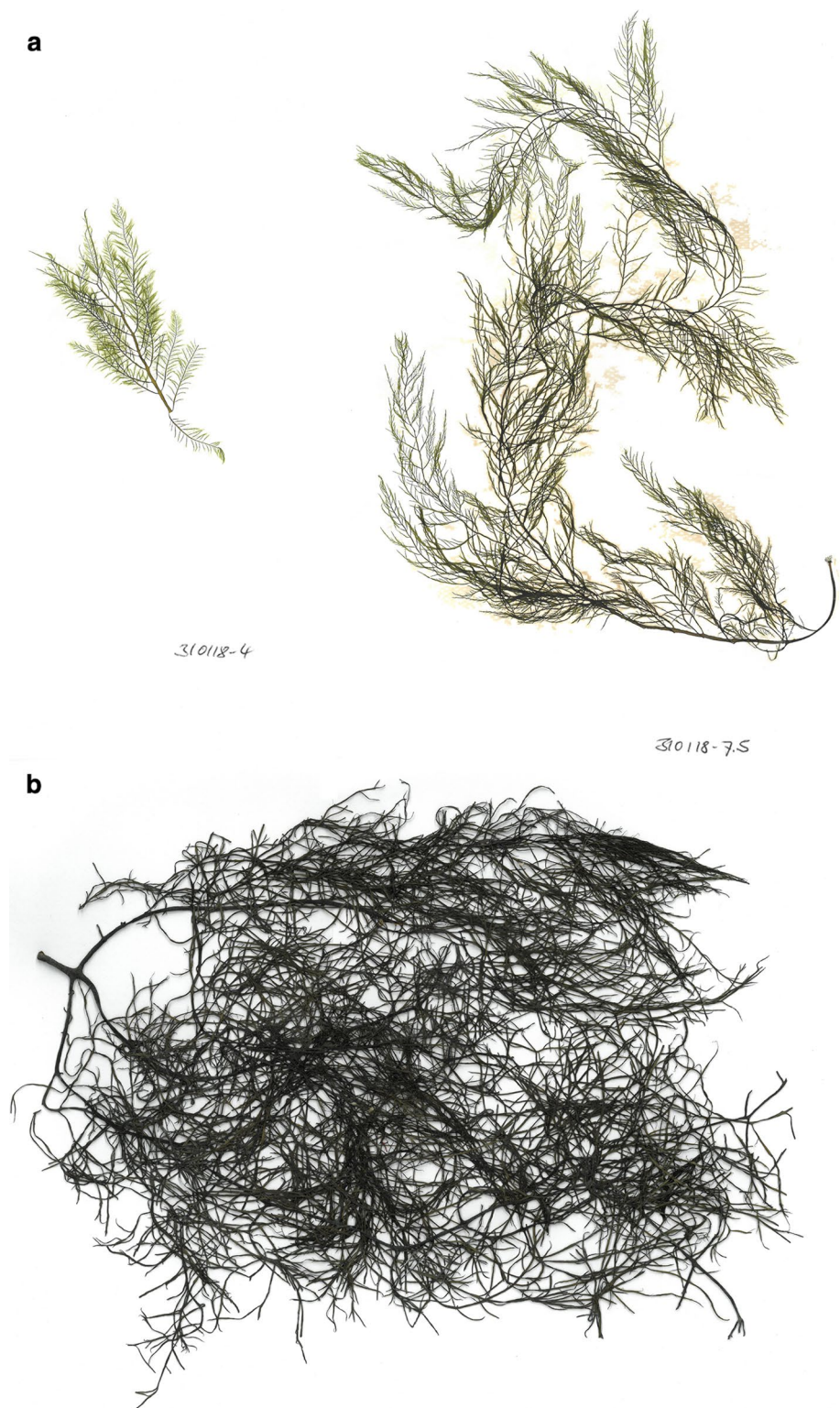


Fig. 2 *Desmarestia menziesii* from the sublittoral in the vicinity of Rothera Point, Adelaide Island. The juvenile form described here **a** Macrophotograph in the laboratory; **b**, **c**, **e**, and **g** in situ in the sublittoral. For comparison, **d**, **f** the perennial form in situ with the morphology so far described in the literature

investigators by its regular pinnate (feathery) appearance with opposite laterals, which did not appear in accordance with the more irregular branching in adult *D. menziesii*. The morphology rather resembled juvenile *D. anceps* Montagne (Wiencke et al. 1996), which had not been reported from the Adelaide Island area.

Since it was impossible to identify it using keys based on morphology-based criteria (in particular, Wiencke and Clayton 2002), a molecular approach, relying on sequencing ITS1 (Internal Transcribed Spacer 1) was chosen. A partial sequence was obtained (MK506123) and aligned with ITS1 sequences of other *Desmarestia* species (Genbank accession number MK506123; Suppl. Fig. S1). It showed 100% identity with *D. menziesii* from King George Island, obtained from a male gametophyte isolated in 1986 (accessions Z84448 and HE866886) and a public sequence identified only to genus (accession MF419243), also from King George Island, and high similarity with adult *D. menziesii* collected at Candlemas Island in 1998 (AJ243781; two indels which could have been misreadings in manually sequenced AJ243781). Other *Desmarestia* species were

Fig. 3 Herbarium specimens of *Desmarestia menziesii* originating from this study deposited at PC. **a** Juvenile and **b** adult morphology



more different. The sequence of sub-Antarctic *D. chordalis* (HE866859) differed by two C-T substitutions, and the sequences of Antarctic *D. anceps* and *D. antarctica* were evidently more different (Supplementary Fig. S1).

Subsequently, a survey of 15 sites between Marguerite Bay and southern Anvers Island recorded the typical morphology of *D. menziesii* from the southernmost end of the survey (Terra Firma Islands) and two other sites in Marguerite Bay but did not observe the feathery form there. The

feathery form was observed at the South Saffery Islands (S 66° 05.4') and four other sites between there and southern Anvers Island (Fig. 1b; Table S1). At the South Saffery Is. site, the typical *D. menziesii* was observed at a depth ranging from 5 to 12 m depth range with the smaller feathery form seen only at a depth range from 15 to 30 m. However, at other sites, the feathery form and normal forms of *D. menziesii* and/or *D. anceps* were found throughout the 5–35-m depth range surveyed.

A search of BM and PC did not uncover any specimens corresponding to the morphology of the *Desmarestia* found at Rothera. However, a search of the UC Herbarium revealed five specimens that correspond to the juvenile morphology (UC 1,571,530, 1,571,531, 1,571,533 and 1,571,534 from Arthur Harbor, Anvers Island; 1,571,532 from Lavebrua Island, Deception Island). Interestingly, they are labelled “*D. menziesii*”, but this morphology has not been described anywhere (R.L. Moe, personal communication). A subsequent search of voucher material in the personal herbarium of C.D. Amsler from a March–April 1989 survey at several sites off Anvers Island (Amsler et al. 1995) revealed multiple individuals with the juvenile morphology. These were collected throughout the 2–20-m depth range surveyed in the study along with the typical morphological forms of both *D. menziesii* and *D. anceps*.

Discussion

The juvenile form of *D. menziesii* described in this paper was identified using a partial ITS1 sequence (MK506123) aligned with published sequences. For this marker, numerous sequences from other *Desmarestiales*, including all other *Desmarestia* species known from Antarctica, had previously been obtained (van Oppen et al. 1993; Peters et al. 1997; Yang et al. 2014). The sequence of a highly variable part of the barcode marker ITS1 obtained from the unknown entity collected during the diving surveys around Rothera corresponds unambiguously to that of *D. menziesii* from King George Island. Beyond any doubt, this supports the conclusion that the previously unknown entity described here, which we collected at Rothera, is not a new species or a new record of another known *Desmarestia* species occurring elsewhere in the Antarctic, but a hitherto-unknown life form of a very common Southern Ocean seaweed. Indeed *D. menziesii* is of one of the major canopy-forming seaweeds in Antarctic waters. The small size of our specimens and clear early-stage colonization in the majority of cases makes it reasonable to conclude that the morphology of this entity is a juvenile form of *D. menziesii* (Fig. 3a for herbarium specimens), and that the established wiry morphology of *D. menziesii* as it is described in the literature corresponds to the adult/perennial form. This latter adult wiry morphology

occurs widely in the *D. menziesii* canopy around Rothera (Fig. 2 in situ; Fig. 3b for a herbarium specimen).

In culture, juvenile *D. menziesii* sporophytes with opposite and alternate laterals have been observed (Wiencke et al. 1995). However, one-level intercalary meristems have never been seen in both opposite laterals (Wiencke, personal communication). An intercalary meristem developed in one of the opposite laterals only, not in both. The other opposite lateral degenerated and later vanished (Wiencke, personal communication).

A search of BM and PC did not uncover any specimens corresponding to the morphology described here for our field samples, yet a search in UC uncovered five specimens of this morphology. All specimens held in BM and PC and labelled “*D. menziesii*” have the known, wiry morphology, likely belonging to the perennial adult form (Fig. 3b), suggesting that previous investigations have missed the juvenile form, and live cultures do not seem to have been raised to this size yet.

In this context, it has to be mentioned that there seems to be some uncertainty attached to the application of the name *D. menziesii*. When providing the initial description, J. Agardh (Agardh 1848) stated that it was based on specimens collected by Menzies in the South Shetland Islands and by Bory in Concepción, Chile. But Menzies had retired from the Navy long before the South Shetland Islands were discovered, and it is unlikely that the same species of *Desmarestia* occurs in temperate Chile and the high Antarctic (R. L. Moe, pers. comm.). The species collected by Bory at Concepción is *D. confervoides*.

The reasons for the strong dimorphism within *D. menziesii* and other Antarctic *Desmarestia* species remain unknown at present, but a plausible hypothesis is that the samples with a seemingly novel morphology is the juvenile form, appearing briefly before spending winter under sea ice, while the entity with the well-documented morphology in the literature (Wiencke and Clayton 2002) is the long-lived, perennial form. This is consistent with the specimens collected in 1989 and 2019, all of which were from late in the growing season (March to May) when young plants might be expected to become apparent. This is also a time when relatively few scientists make diving collections along the WAP, which may explain why the morphology has been rarely seen and never before documented in the literature. Indeed, survival during prolonged periods under sea ice, possibly in combination with ice abrasion and at least potential intense herbivory, may be a strong factor resulting in a more sturdy morphology in certain polar seaweeds. A few analogous cases are known. The first is that of *Desmarestia chordalis* J.D.Hooker & Harvey, where juvenile individuals were described under the name *D. rossii* J.D.Hooker & Harvey (Reviere unpublished observations in Kerguelen Islands, 1977; Fischer et al. 1987; Ricker 1987).

The juvenile sporophytes of *D. menziesii* resemble juvenile sporophytes of *D. anceps*, which may be a typical feature of field material (Wiencke et al. 1996). Another one is that of the Arctic *Platysiphon glacialis* (Kawai et al. 2015), replacing two previously separately described entities: *Platysiphon verticillatus* R.T. Wilce and *Platyarticus glacialis* (Rosenvinge) R.T. Wilce & P.M. Pedersen.

The description here of a newly reported juvenile morphology of *D. menziesii* has wider implications for understanding the recruitment of canopy-forming seaweed communities in Antarctica, and we can only conjecture as to how many more examples there may be of undescribed juvenile forms of Antarctic macroalgae. Given the extreme variations in open water and ice scour from year to year and from place to place and given the difficulty of longitudinal observation in the Antarctic, environmental sequencing might reveal cryptic diversity in the form of endophytic or endozoic stages. Further, significant questions in this context are whether the gametophytes have special requirements, and whether they are long lived and were present even where no sporophytes are found.

Acknowledgements We are grateful to the UK Natural Environment Research Council for funding to FCK (grants NE/D521522/1 and NE/J023094/1), in particular through the Collaborative Antarctic Science Scheme (Grant CASS-134, 2017) to FCK and LSP. Funding for cruise-based observations in 2019 was from US National Science Foundation award OPP-1744550 to CDA. We thank Kate Stanton, Teresa Murphy and Ben Robinson (British Antarctic Survey) for support with diving operations around Rothera in January–February 2018, and also Richard L. Moe (UC Berkeley) for locating specimens corresponding to the morphology described here in the UC collection. Special thanks are due to Charlie Bibby (Financial Times) for taking professional photographs of the unknown *Desmarestia* sp. in the aquarium of the Bonner Lab at Rothera (Fig. 2a). We would also like to thank Richard L. Moe (UC Berkeley) and Christian Wiencke (AWI Bremerhaven) for their very helpful reviews of this paper. Also, the MASTS pooling initiative (Marine Alliance for Science and Technology for Scotland, funded by the Scottish Funding Council and contributing institutions; grant reference HR09011) is gratefully acknowledged for supporting FCK. This research contributes to the SCAR Ant-ERA research programme.

Compliance with ethical standards

Conflict of interest There are no conflicts of interest to disclose.

Open Access This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

References

- Agardh J (1848) Species genera et ordines algarum, seu descriptiones succinctae specierum, generum et ordinum, quibus algarum regnum constituitur. Volumen Primum. Algae fucoideas complectens. C.W.K. Gleerup, Lundae
- AlgaeBase. World-wide electronic publication. <https://www.algaebase.org> (2018) National University of Ireland, Galway. <https://www.algaebase.org>. Accessed 11/08/2018
- Amsler CD, Rowley RJ, Laur DR, Quetin LB, Ross RM (1995) Vertical distribution of Antarctic Peninsular macroalgae-cover, biomass and species composition. *Phycologia* 34:424–430. <https://doi.org/10.2216/i0031-8884-34-5-424.1>
- Barnes DKA, Souster T (2011) Reduced survival of Antarctic benthos linked to climate-induced iceberg scouring. *Nat Clim Chang* 1:365–368. <https://doi.org/10.1038/nclimate1232>
- Barnes DKA, Fenton M, Cordingley A (2014) Climate-linked iceberg activity massively reduces spatial competition in Antarctic shallow waters. *Curr Biol* 24:R553–R554. <https://doi.org/10.1016/j.cub.2014.04.040>
- Barnes DKA, Fuentes V, Clarke A, Schloss IR, Wallace MI (2006) Spatial and temporal variation in shallow seawater temperatures around Antarctica Deep-Sea Research Part II. *Top Stud Oceanogr* 53:853–865. <https://doi.org/10.1016/j.dsr2.2006.03.008>
- Fischer W, Hureau J-C, eds (1987) Fiches FAO d'identification des espèces pour les besoins de la pêche. Océan Austral (Zones de pêche 48, 58 et 88) (Zone de la Convention CCAMLR). Publication préparée et publiée avec l'aide de la Commission pour la conservation de la faune et de la flore marines de l'Antarctique. vol 1. FAO, Rome
- Gachon CMM, Strittmatter M, Müller DG, Kleinteich J, Küpper FC (2009) Differential host susceptibility to the marine oomycete pathogen *Eurychasma dicksonii* detected by real time PCR: not all algae are equal. *Appl Environ Microbiol* 75:322–328
- Kawai H et al (2015) Reproductive morphology and DNA sequences of the brown alga *Platysiphon verticillatus* support the new combination *P. glacialis*. *J Phycol* 51:910–917. <https://doi.org/10.1111/jpy.12331>
- Lane CE, Mayes C, Druehl LD, Saunders GW (2006) A multi-gene molecular investigation of the kelp (Laminariales, Phaeophyceae) supports substantial taxonomic re-organization (Vol 42, pg 493). *J Phycol* 42:962–962. <https://doi.org/10.1111/j.1529-8817.2006.00253.x>
- Moe RL, Silva PC (1977) Antarctic marine flora: uniquely devoid of kelp. *Science* 196:1206–1208. <https://doi.org/10.1126/science.196.4295.1206>
- Mystikou A et al (2014) Seaweed biodiversity in the south-western Antarctic Peninsula: surveying macroalgal community composition in the Adelaide Island/Marguerite Bay region over a 35-year time span. *Polar Biol* 37:1607–1619. <https://doi.org/10.1007/s00300-014-1547-1>
- Peck LS (2018) Antarctic marine biodiversity: adaptations, environments and responses to change. *Oceanogr Mar Biol Annu Rev* 56:105–236
- Peck LS, Convey P, Barnes DKA (2006) Environmental constraints on life histories in Antarctic ecosystems: tempos, timings and predictability. *Biol Rev* 81:75–109. <https://doi.org/10.1017/s1464793105006871>
- Peters AF, van Oppen MJH, Wiencke C, Stam WT, Olsen JL (1997) Phylogeny and historical ecology of the Desmarestiaceae (Phaeophyceae) support a southern hemisphere origin. *J Phycol* 33:294–309
- Ricker RW (1987) Taxonomy and biogeography of Macquarie Island seaweeds. British Museum Natural History, London

- Skottsberg C (1907) Zur Kenntnis der subantarktischen und antarktischen Meeresalgen. I. Phaeophyceen. Kungl. Boktryckeriet. P.A. Norstedt & Söner, Stockholm
- van Oppen MJH, Olsen JL, Stam WT, Wiencke C (1993) Arctic-Antarctic disjunctions in the benthic seaweeds *Acrosiphonia arcta* (Chlorophyta) and *Desmarestia viridiswillii* (Phaeophyta) are of recent origin. *Mar Biol* 115:381–386
- Waller CL, Barnes DKA, Convey P (2006) Ecological contrasts across an Antarctic land-sea interface. *Austral Ecol* 31:656–666. <https://doi.org/10.1111/j.1442-9993.2006.01618.x>
- White TJ, Bruns T, Lee S, Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols: a guide to methods and applications. Academic Press Inc., New York, pp 315–322
- Wiencke C, Clayton MN (2002) Antarctic seaweeds. A.R.G Gantner, Liechtenstein
- Wiencke C, Clayton MN, Langreder C (1996) Life history and seasonal morphogenesis of the endemic Antarctic brown alga *Desmarestia anceps* Montagne. *Bot Mar* 39:435–444. <https://doi.org/10.1515/botm.1996.39.1-6.435>
- Wiencke C, Clayton MN, Schulz D (1995) Life history, reproductive morphology and development of the Antarctic brown alga *Desmarestia menziesii*. *J Agardh Bot Acta* 108:201–208
- Wiencke C, Gomez I, Dunton K (2009) Phenology and seasonal physiological performance of polar seaweeds. *Bot Mar* 52:585–592
- Yang EC et al (2014) Ligulate *Desmarestia* (Desmarestiales, Phaeophyceae) revisited: *D. japonica* sp. nov. and *D. dudresnayi* differ from *D. ligulata*. *J Phycol* 50:149–166. <https://doi.org/10.1111/jpy.12148>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.