



# Hydrological features above a Southern Ocean seamount inhibit larval dispersal and promote speciation: evidence from the bathyal mytilid *Dacrydium alleni* sp. nov. (Mytilidae: Bivalvia)

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## Abstract

The Maud Rise seamount (65°07.80'S 2°39.60'E), a distinct habitat in the Southern Ocean, was studied during the ANDEEP-SYSTCO expedition in 2007–2008 to describe its unique benthic assemblage, characterised by higher biomass and lower diversity than other SO locations. Epibenthic sledge deployments during the expedition revealed exceptionally high abundances of the small bivalve genus *Dacrydium* with a total of 516 specimens collected from this seamount, resembling up to 1860 bivalve individuals per 1000 m<sup>-2</sup>. The *Dacrydium* specimens were examined for taxonomic identification, population and reproductive biology. Shell and soft part morphology as well as life history characteristics were compared with all known congeners for which data are available. Hinge dentition, prodissoconch size and adult gill structure are notably different, supporting classification as a separate species, herein formally described as *Dacrydium alleni* sp. nov. *Dacrydium alleni* sp. nov. produces lecithotrophic larvae, capable of long-distance dispersal, yet is apparently restricted to the Maud Rise area, supporting the hypothesis that larval dispersal at isolated seamounts may be constrained by hydrographic rather than biological features. In addition to providing insight into the benthic assemblage at Maud Rise, this work also summarises the current taxonomic status of the genus *Dacrydium* in the Southern Ocean.

**Keywords** Antarctic · Deep sea · Bivalve · Maud Rise · Taylor column · Larval dispersal · Endemic species

## Introduction

The Maud Rise seamount rises over 3000 m from the sea floor in the Southern Ocean about 700 km north of the Antarctic continent, with its crest just under 1000 m depth (Brandt et al. 2011). Standing in the path of the Weddell Gyre, the Maud Rise influences the flow of circumpolar deep-water and warm deep-water currents, creating a halo of warm water up to 1 °C around a central Taylor column over

the mount (Holland 2001), representing the upper end of the thermal niche experienced by many Antarctic marine taxa (Windisch et al. 2011). Water above the mount is retained in a cold eddy. Although not isolated from surrounding water bodies, the transport of larvae with short pelagic stages may be inhibited, increasing the likelihood of some benthos being endemic to the seamount (Brandt et al. 2011). This is reflected in the overall composition of benthic species, which differs significantly from comparison sites in the surrounding Southern Ocean (Brandt et al. 2011; Brandt and Würzberg 2014). Surface productivity is high in summer as a result of intense phytoplankton blooms initiated by early melting sea ice, supporting a high biomass of zooplankton and predators. Mesoscale upwelling of nutrients around the mount and the retention of organic materials within the Taylor column causes phytoplankton blooms to persist into the autumn and winter, creating a fluctuating but continual delivery of organic matter to the benthos year round (Brandt et al. 2011). The presence of warm and cold areas of water and wide depth range around Maud Rise has been suggested to provide a unique system within Antarctica to observe

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climate-driven shifts in community structure (Brandt et al. 2011). Although there are fewer bivalve species recorded at Maud Rise than from the Scotia and Weddell seas, species richness per sampling event was comparable (8–14 species) and taxonomic composition at the family level also resembled comparative Southern Ocean deep sea sites sampled by epibenthic sledge (Linse 2004). However, abundance with up to 1860 bivalve ind 1000 m<sup>-2</sup> was 25 to 50 times higher at the seamount than other deep sea locations (Linse 2004; Brandt et al. 2011) and comparable to the high bivalve abundances reported from the Ross Sea continental shelf in 200–500 m (Schiaparelli et al. 2014). The bivalve community at Maud Rise was dominated by three species, *Vesicomya sirenkoi*, *Yoldiella* cf. *sabrina*, and the *Dacrydium* sp. 1, described herein (Brandt et al. 2011).

Species of mytilid bivalves of the genus *Dacrydium* are widespread throughout the world's oceans, from shallow to deep sea depth and from the Tropics to polar regions (Allen 1998). To date, 28 valid species are recognised on the World Register of Marine Species (Bouchet and Gofas, 2017). The bathymetric range of the genus is wide, with *Dacrydium hyalinum* recorded at < 30 m in the Mediterranean (Önen and Doğan 2007) and *Dacrydium hedleyi* recorded down to 5900 m depth in the Guyana Basin (Allen 1998). Some species also exhibit extreme eurybathy with depth ranges spanning more than 2000 m, including *Dacrydium ockelmanni* (100–3100 m), *Dacrydium sandersi* (587–3783 m) and *Dacrydium abyssorum* (1913–5280 m) (Allen 1998), enabling widespread colonisation of deep sea habitats (Table 1).

Species have been differentiated based on shell morphology, with details of the hinge teeth of primary importance for distinguishing between species (Salas and Gofas 1997; Allen 1998). Shells are usually colourless, translucent and smaller than 6 mm in length (Allen 1998). Valve shape has been suggested to be highly variable between conspecifics, leading to different morphs being incorrectly classified as separate species (Allen 1998; Lemaitre et al. 2009).

Unusually for mytilids, some species of *Dacrydium* brood their young inside the mantle cavity, releasing small numbers of crawling veliger larvae (Ockelmann 1983). Specimens of *Dacrydium hyalinum*, for example, have been recorded with broods of 5–10 larvae of differing stages of development (Ockelmann 1983; Salas and Gofas 1997). In total, Salas and Gofas (1997) reported three brooding species, plus an isolated seamount form of *D. hyalinum*, from the Atlantic deep sea.

Currently, two species of *Dacrydium* are recognised from Antarctic waters, *Dacrydium albidum* Pelseneer, 1903 and *Dacrydium knudseni* Allen, 1998 (Allen 1998; Lemaitre et al. 2009). A third, *Dacrydium alleni* sp. nov., is described in this study. *Dacrydium* species are widespread in the Southern Ocean, and have been recorded from the continental shelves and slopes of the Ross, Bellingshausen,

Amundsen and Weddell seas (Engl 2012). The depth distribution of *D. albidum* ranges from 122 to 752 m in the Ross Sea to 1437 m north of Livingstone Island (following Allen 1998). *Dacrydium modioliforme* Thiele, 1912, recorded from depths of down to 4636 m (Lemaitre et al. 2009) was later reclassified as synonymous with *D. albidum* (Nicol, 1966, in Allen 1998). However, this was based on a type specimen of *D. modioliforme* collected at 385 m—well within the bathymetric range of *D. albidum*. Allen (1998) examined *Dacrydium* specimens sampled from 3697 m depth and concluded that a second species was indeed present, based on significant differences in hinge dentition, prodissoconch length and gill structure. Rather than resurrect the name *D. modioliforme*, Allen (1998) described *D. knudseni* distributed from the southern Weddell Sea to Burdwood Bank at abyssal depths ranging from 3111 to 4636 m. Previous cruise reports and publications have often reported *Dacrydium* specimens as *Dacrydium albidum*, *Dacrydium* cf. *albidum* or *Dacrydium* sp. without considering *D. knudseni*, thus artificially grouping at least two species records together under the *D. albidum* name. As several older records of *D. albidum* may refer to *D. knudseni*, we mapped the known distribution records for *Dacrydium* in the Southern Ocean and for nominal *D. albidum* outside the Southern Ocean separated by 1500 m depth (Fig. 1).

A deep-water *Dacrydium* sp. 1 was recorded from the bathyal top of the Maud Rise seamount (Brandt et al. 2011), and is herein described and referred to as *Dacrydium alleni* sp. nov.

## Methods

### Study sites and sample collection

During ANT-XXIV/2 in the Antarctic 2007/08 season, Maud Rise was studied with RV Polarstern (Bathmann 2010; Brandt et al. 2011). Macrobenthic samples from the top of the seamount were collected with an epibenthic sledge (Brenke 2005). On arrival on deck, samples were sieved through 500 µm and fixed in pre-cooled 96% ethanol and stored at – 20 °C for at least 48 h before sorting under a stereomicroscope. Samples were kept in 96% ethanol.

The epibenthic sledge was deployed at station 39–17 on 4 January 2008 in 2151 m depth at the location 64° 17'S and 002° 52'E.

### Shell morphology and morphometrics

Individual valves from specimens opened to examine internal contents were retained wherever possible and the viscera removed. High-resolution images of the valve outline, hinge teeth and prodissoconch were obtained using a JEOL

**Table 1** Comparison of morphological and geographic characteristics in *Dacrydium*. Sources: Knudsen, 1970; Hiyami & Kase, 1993; Salas & Gofas, 1997; Allen, 1998; Van der Linden & Moolenbeek, 2004; Huber, 2010

Species	Size (mm)	Ant.T	Post.T	PD I (µm)	Adult gill	Region	Recorded depth (m)
<i>D. abyssorum</i>	< 5	5–9	42	191–204	Simple	Atl	1913–5280
<i>D. albidum</i>	< 5	7–8	50–55	213	Simple	SO	122–1437
<i>D. alleni sp. nov.</i>	< 4.5 (4.09)	4–6	38–49	151–165	Complex	SO	2151
<i>D. angularae</i>	< 4	3–7	20–28	159–170	Simple	Atl	1849–3136
<i>D. balgimi</i>	< 1.5	15	15	315		Atl	2035
<i>D. dauvini</i>	< 1.5	11–13	13–15	170		IO	280–330
<i>D. elegantulum</i>	< 4.5					PO	45–200
<i>D. fabale</i>	2 mm					PO	180–200
<i>D. filiferum</i>	< 1.5	11–15	11–15	200		IO	330
<i>D. gloriosense</i>	2.7					IO	3700–3718
<i>D. hedleyi</i>	< 5	10–15	10–15	167	Simple	Atl	3859–5867
<i>D. hendersoni</i>	< 4	5–10	5–10 + 25–30	145		Atl	50–546
<i>D. hyalinum</i>	< 2.5	10–13	10–13 + 10–15	210–220		Atl, Med	23–521
<i>D. knudseni</i>	< 4	15–17	15–17	195	Simple	SO	3111–4636
<i>D. leucoguttatum</i>	< 3					Atl	25–2000
<i>D. nipponicum</i>	8.2					Jap	1000–1600
<i>D. occidentale</i>	< 4.5	8–9	8–9 + 40	170		Atl	364–846
<i>D. ockelmanni</i>	< 4.5	5–7	33–38	140–150	complex	Atl	100–3100
<i>D. pacificum</i>	< 4					PO	80–2562
<i>D. panamense</i>	< 5					PO	850–4096
<i>D. pelseneeri</i>	< 2.5					PO	200–310
<i>D. rostriferum</i>	6.8					PO	2532–2865
<i>D. sandersi</i>	< 4	13–15	10–12	123		Atl	587–3783
<i>D. speculum</i>	< 2	18–20	18–20	155		IO	3660–4580
<i>D. vitreum</i>	< 6	5–7	55–65	100–136		NA,NP	5–2200
<i>D. viviparum</i>	< 3			270–275	complex	Atl, Med	1070–1760
<i>D. wareni</i>	< 5	12–14	12–14 + 20–25	160–170	simple	Atl	700–1500
<i>D. zebra</i>	< 2.3	10	30	176–225		PO	12–40 m

Ant. T Anterior teeth, Post. T Posterior teeth, PD I Length of prodissoconch. Where two values are given for anterior dentition, the original description counts two adjacent but distinct groups of teeth. Regions: Atl. Atlantic, SO. Southern Ocean, PO. Pacific Ocean, NP. North Pacific, SP. South Pacific, Med. Mediterranean, IO. Indian Ocean, Jap. Sea of Japan

6060LV scanning electron microscope operating in secondary electron imaging mode at 15 kV acceleration voltage. ImageJ1.48 V image analysis software (Schindelin et al. 2015) was used to measure larval shell dimensions. Shell morphology and dentition were compared with the exhaustive catalogue of *Dacrydium* species descriptions compiled by Allen (1998) and the review of deep sea Atlantic species by Salas and Gofas (1997). Prodissoconch measurements were compared to the criteria for distinguishing different reproductive modes in bivalves in general (Jablonski and Lutz 1983) and in the genus *Dacrydium* (Salas and Gofas 1997).

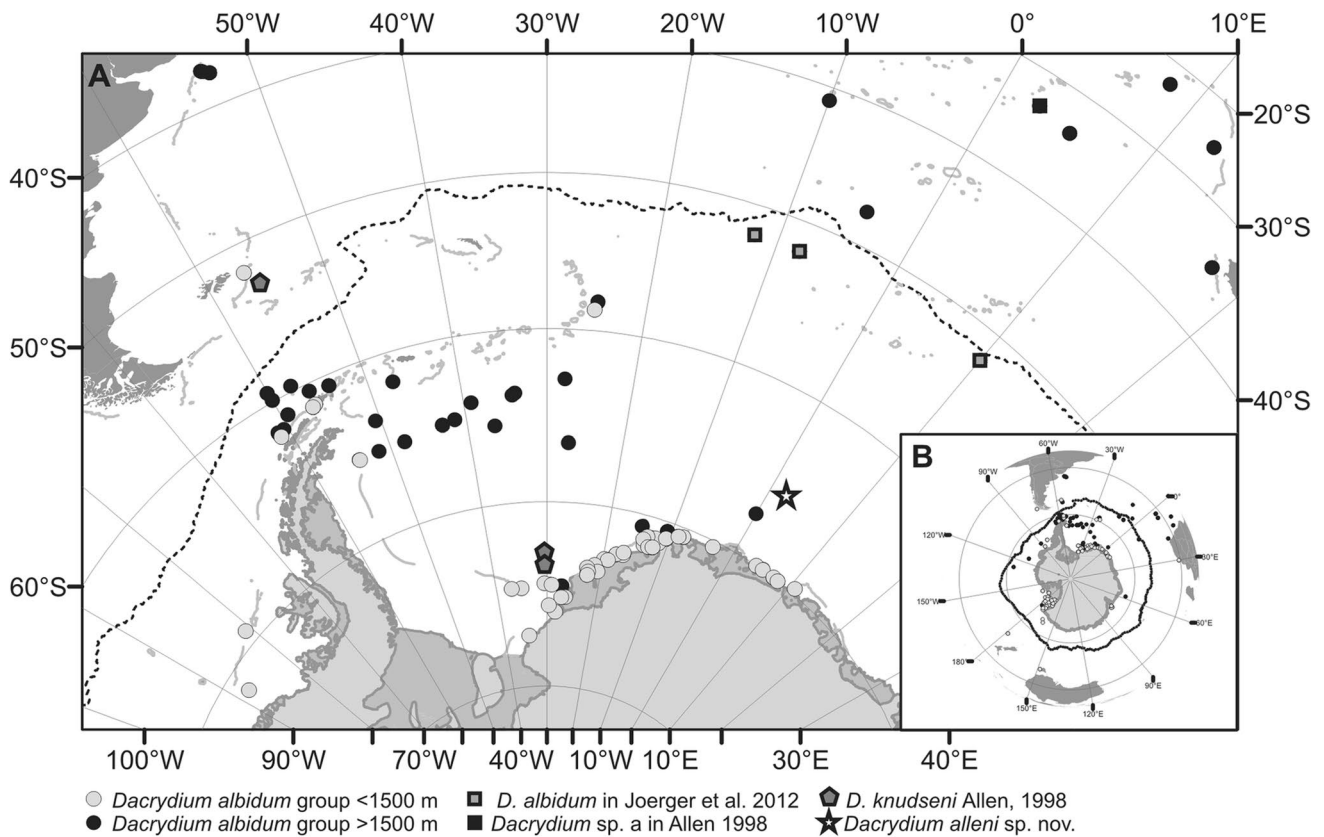
Individual size was measured using the dimensions employed by Salas and Gofas (1997) which are similar to those used by Ockelmann (1983) and are illustrated in Fig. 2. Length is defined as the maximum distance across the shell on a line parallel to the horizontal midline. Shell height was

measured as the maximum distance across the shell from ventral to dorsal margins, parallel to the vertical midline.

Multiple images were recorded for each specimen and ImageJ was used to generate measurements of shell length and height accurate to 0.001 mm. A subsample was also measured using digital callipers accurate to 0.01 mm to validate the results generated by image analysis. IBM SPSS Statistics 22 was used to produce histograms of size frequency and these results were further investigated with R version 3.4.3 (R Core Team 2017) using the package MixDist (Macdonald and Du 2012).

### Soft part morphology

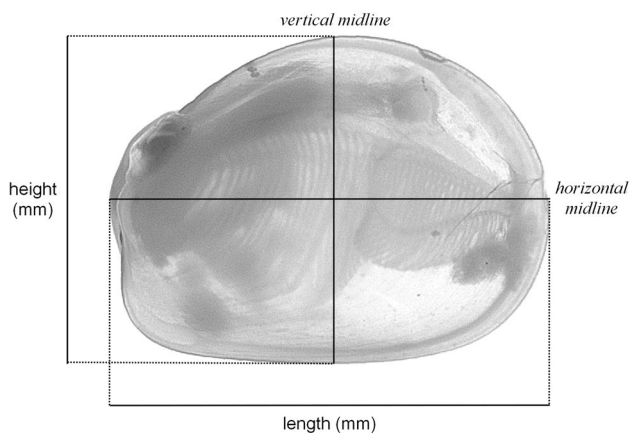
A total of 296 specimens were analysed under a stereomicroscope equipped with a Leica MC120HD digital camera. A combination of delicate, translucent shells and



**Fig. 1** Locations of records for *Dacrydium* in the Southern Ocean. **a** Records of *Dacrydium* species in study area, **b** Records of *Dacrydium albidum* group in the Southern Ocean and Neighbouring areas. The dotted/solid line represents the polar front

careful positioning of backlighting enabled observation of ontogeny of gill structure and internal organs including opaque paired gonads between the dorsoanterior shell buttress and viscera. All individuals were inspected for evidence of brooding. Females containing objects inside

the mantle cavity were opened and the objects examined to confirm the presence or absence of brooded larvae. Female gonads and unidentifiable objects removed from female shells were examined further using the combination of a compound microscope with MC120HD digital camera and SEM imaging. Valves imaged under SEM were transferred from 96% ethanol to acetone, cleaned and subsequently evaporation dried using hexamethyldisilazane as a low surface tension transition liquid. Specimens were mounted pairwise on stubs and sputter coated with gold.



**Fig. 2** *Dacrydium* shell shape and dimensions used for measurements

### Type repositories

The holotype specimen is deposited in the mollusc collection at the Zoological Museum, Hamburg in the Centre of Natural Sciences CeNaK, paratypes as well as the specimens used in the morphometric analysis are deposited in the Zoological Museum, Hamburg, the Natural History Museum, London, UK (NHMUK), the Cambridge Zoology Museum, Cambridge, UK (CAMZM), and the Muséum national d'Histoire naturelle (MNHN), Paris, France.

## Results

### Taxonomic results

#### Order MYTILIDA Férussac, 1822

#### Superfamily MYTILOIDEA Rafinesque, 1815

#### Family MYTILIDAE Rafinesque, 1815

#### Genus *DACRYDIUM* Torell, 1859

#### *Dacrydium alleni* sp. nov.

#### ZooBank registration: urn:

*Dacrydium* sp. 1 – Brandt et al. 2011: 1969, 1971 Table 7, 1974.

**Type material:** Holotype [CeNak Museum number to be added after acceptance of manuscript ZMHK-xxxxx1,] mature male, 3.97 mm in length 2.96 mm in height.

Paratypes [CeNak Museum numbers to be added after acceptance of manuscript ZMHK-xxxxx2-ZMHK-xxxxx7] numbered by increasing size – 6 specimens of ontogenetic changes in valve shape shown in Fig. 3.

Paratypes [CeNak Museum numbers to be added after acceptance of manuscript ZMHK-xxxxx8-ZMHK-xxxxxY] – 14 specimens on SEM stubs.

Paratype series each containing 20 specimens including juveniles, females and males across the size range are [CeNak Museum numbers to be added after acceptance of manuscript ZMHK-xxxxxY + 1-ZMHK-xxxxxY + 19], [NHMUK Museum numbers to be added after acceptance of manuscript NHMUK2017.xxXY-NHMUK-2017.xxXY + 19], [CAMZM Museum numbers to be added after acceptance of manuscript CAMZN 2017.x.x-19] and [MNHN Museum numbers to be added after

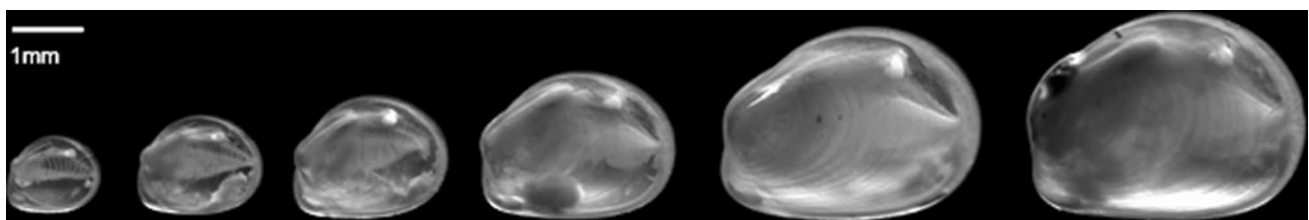
acceptance of manuscript MNHM IM-xxxx-xxxxx – MNHN IM-xxxx-xxxxx + 19].

**Type locality:** Maud Rise Seamount, Eastern Lazarev Sea north of the Antarctic Continent, 64°17'S and 002°52'E, depth 2151 m, sampled 4 January 2008, station 39–17 during RV Polarstern ANT-XXIV/2. Sediment soft: 60–80% foraminiferous ooze with sub-fractions of diatomic and radiolarian detritus.

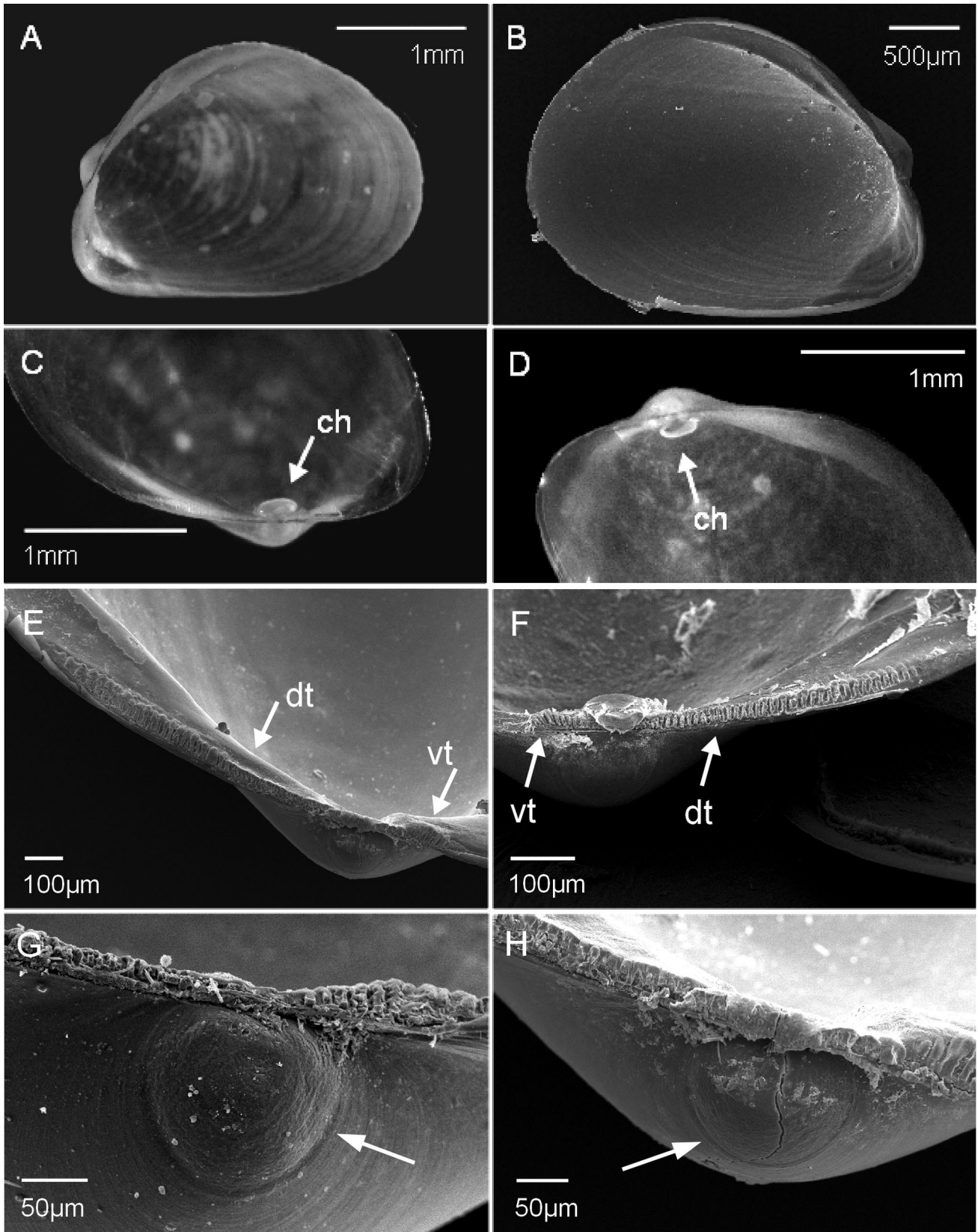
**Additional material:** 295 specimens have been measured next to the type material for the morphometric study and are deposited at the NHM, London. Further 230 specimens and shells from the type locality are held at British Antarctic Survey, Cambridge.

**Etymology:** The new species is named after John A Allen in recognition of his contributions to Malacology in general and in particular for his work on *Dacrydium*.

**General shell description:** Paratype specimens ranged from 1.36 to 3.97 mm length and were rather stout. Very small individuals had a broadly subovate shell which assumed a more modioliform shape with age (Fig. 3), the roughly semi-circular posterior margin expanding away from the umbo and the ventral margin becoming almost straight. The dorsal buttress is wide and extends almost to the vertical midline in small- to medium-sized individuals (Fig. 3). In larger specimens, the dorsal buttress falls short of the vertical midline as the shell becomes more elongated. The antero-ventral region is short and rounded. Umbo is moderately large, and prodissoconch appeared denser and more opaque than the surrounding dissoconch shell. Only the prodissoconch I is present, with a length of 151–165 µm. Average prodissoconch I size is 156 µm with a standard deviation of 4.8 µm ( $n = 14$ ). The prodissoconch II is absent. The chondrophore is spoon shaped and not overly large (Fig. 4c, d). There is a cluster of 4–6 narrow teeth anterior to the primary ligament on the short anterior hinge plate, plus 3–4 underdeveloped and rather indistinct adjoining teeth evident under scanning electron microscopy only. An extensive ridge of 38 to 49 posterior teeth on the elongated posterior hinge plate extends up to half the length of the dorsal buttress, with



**Fig. 3** Ontogenetic changes in valve shape of *Dacrydium alleni* sp. nov. (CeNak numbers of paratypes ZMHK-xxxxx2-ZMHK-xxxxx7)



**Fig. 4** Shell characteristics in *Dacrydium alleni* sp. nov. **a** Adult, left valve Paratype ZMHK-xxxxx8, **b** Adult, right valve ZMHK-xxxxx9. **c, d** Detail of the chondrophore (ch) **c** Paratype ZMHK-xxxxx, **d** Paratype ZMHK-xxxxx8. **e, f** Hinge dentition visible using SEM imagery. Six anterior teeth (at) are visible anterior hinge plate of the primary ligament and 38 to 49 (pt) on the elongated posterior hinge plate **e** Paratype ZMHK-xxxxx, **f** Paratype ZMHK-xxxxx. **g, h** Prodissoconch I (indicated by arrow) clearly visible on two different specimens **g** Paratype ZMHK-xxxxx, **h** Paratype ZMHK-xxxxx

crenulations becoming indistinct in proximity to primary dentition (Fig. 4e, f). Co-marginal lines were evident under magnification on all but the smallest individuals. At time of collection, the soft parts of these specimens seen through the translucent shells were green in colour, possibly as a result of recent phytoplankton consumption.

**General soft part description:** Shells are translucent and, when backlit under magnification, internal organs were visible (Fig. 5).

The foot is tongue-shaped with a central ventral groove and was often visible curving around the gills. Gills structure varied with size, increasing from initially 6 + filaments on the inner demibranch in juveniles to 22 or more in large adults. Juvenile *D. alleni* sp. nov. exhibited a very simple gill structure with initially only six descending lamellae on the inner demibranch. The outer demibranch was entirely absent in small individuals. Sub-adults gradually develop both ascending and descending lamellae on the filaments of the inner demibranch, and fully developed adults had both inner and outer demibranch filaments with ascending and descending lamellae.

Large paired gonads were also visible in adults, dorsal to the viscera.

### Differential diagnosis

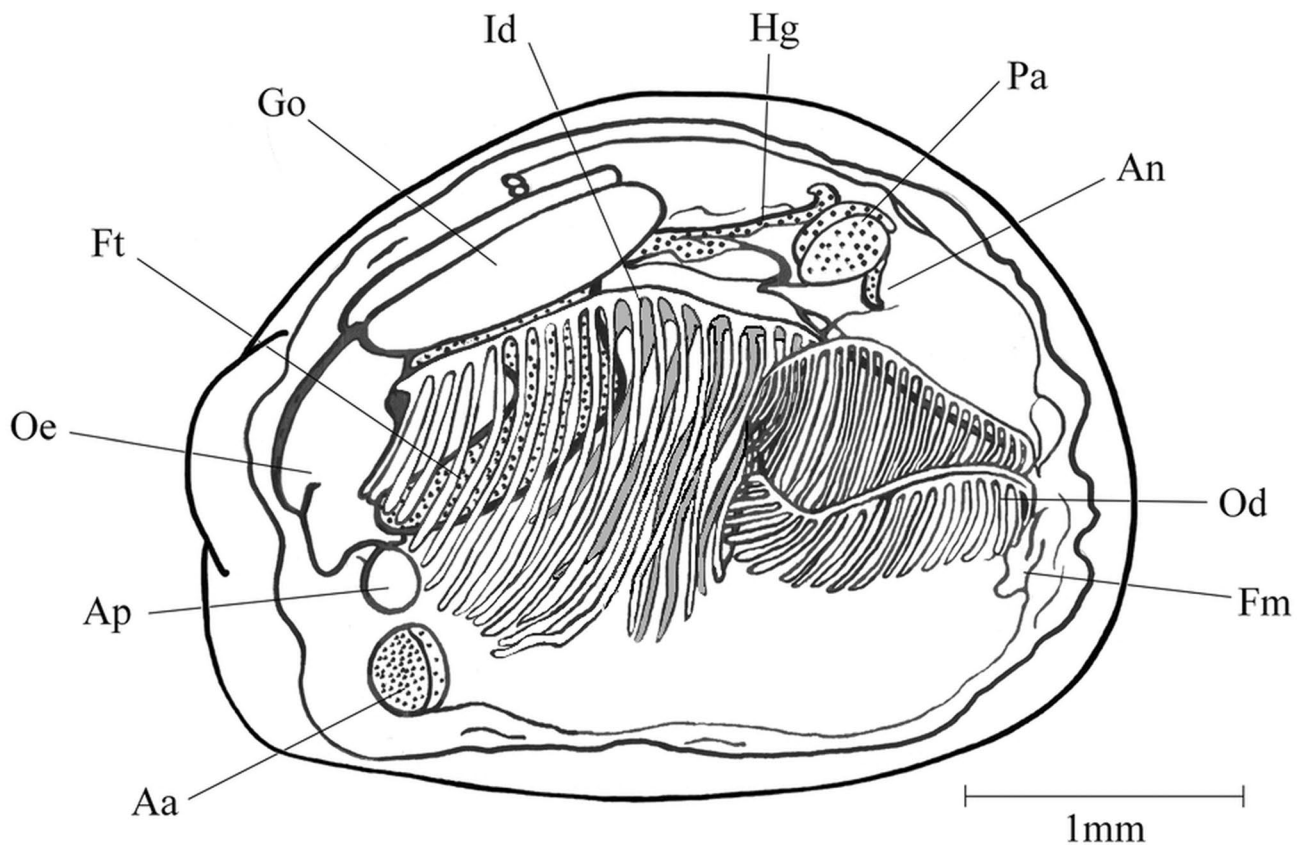
As noted by Dell (1990, in Allen 1998), valve shape alone is not a reliable taxonomic feature. The outlines of *D. alleni* sp. nov. and *D. albidum* shells resemble each other closely, whilst the few differently shaped individuals in this sample resembled *D. knudseni*. There are also similarities to *Dacrydium angulare* (Ockelmann 1983) described from the west coast of South Africa. However, the finer details of shell morphology differ considerably between species. Allen (1998) studied deep-water specimens of the invalid species *Dacrydium modioliforme* Thiele 1912, previously revised by Nicol (1966) as synonymous with *D. albidum*, and described *D. knudseni* based on significant dissimilarities in the arrangement of primary and secondary dentition, prodissoconch length and gill structure. This is in agreement with Salas and Gofas (1997), who asserted that species of Atlantic *Dacrydium* could be effectively differentiated by the quantity and distribution

of marginal teeth, form of the hinge and diameter of the early larval shell. *D. albidum* possesses 7–8 anterior teeth and a further 50–55 posterior teeth extending along the dorsal buttress (Allen 1998). In contrast, *D. knudseni* is characterised by an approximately equal amount of 15–17 teeth on both dorsal and ventral hinge plates (Allen 1998). *Dacrydium alleni* sp. nov. exhibited 4–6 teeth anterior to the primary ligament and 38–49 posterior teeth on the dorsal buttress. Prodissoconch length in the holotypes described by Allen was 213  $\mu\text{m}$  in *D. albidum* and 195  $\mu\text{m}$  in *D. knudseni*. SEM images of *D. alleni* sp. nov. showed a prodissoconch length of 151–165  $\mu\text{m}$  (156  $\mu\text{m}$  average, SD 4.83  $\mu\text{m}$ ,  $n = 14$ ), notably smaller despite the similar adult size.

### Taxonomic remarks

The description of *Dacrydium alleni* sp. nov. from the Maud Rise has extended the number of currently described species of *Dacrydium* in the Southern Ocean to three. Given the limited distinguishing characteristics known for this small-sized genus, and following Nicol (1966) synonymising *D. modioliforme* with *D. albidum*, finds of *Dacrydium* in the Southern Ocean were often assigned to the latter species (e.g. Hain and Arnaud 1992; Troncoso and Aldea 2008; Schiaparelli et al. 2014). Jörger et al. (2014) reported *D. albidum* in samples from the 2012 SYSTCO II expedition with RV Polarstern collected at depths from 2736–3994 m depth in the vicinity of the Antarctic Polar Front—the boundary between the South Atlantic and the Southern Ocean. These records may extend the known bathymetric range for *D. albidum*, or may indicate a further undescribed deep sea species within the *Dacrydium albidum* grouping. Hain and Arnaud (1992) reported a single female *D. albidum* containing brooded young in specimens collected in the Weddell Sea in 257–500 m depth. However, at 258  $\mu\text{m}$ , the prodissoconch length of this specimen was notably larger than that recorded by Allen (1998) for both *D. albidum* and *D. knudseni*. Additionally, as no other previously examined samples of *D. albidum* showed evidence of brooded offspring, this record may represent a separate undescribed brooding *Dacrydium* species (Hain and Arnaud, 1992). More recent finds of *Dacrydium* specimens in bathyal and abyssal depth of the Southern Ocean in the Atlantic sector were reported as *Dacrydium* sp. (Linse 2004; Brandt et al. 2011).

Bivalve collections held at the British Antarctic Survey include 43 lots with 1086 specimens assigned to the *Dacrydium albidum* group and collected from 365–5191 m depth across the Amundsen, Weddell and Scotia seas (Linse pers com).



**Fig. 5** Schematic anatomy of *Dacrydium alleni* sp. nov. holotype [CeNak Museum number ZMHK-xxxxx1,] mature male, 3.97 mm in length 2.96 mm in. Aa Anterior adductor, Ap Anterior palp, Oe

Oesophagus, Ft Foot, Go Gonad, Hg Hindgut, Pa Posterior adductor, An Anus, Id Inner demibranch, Od Outer demibranch, Fm Posterior fused inner mantle fold

### Ontogenetic and reproductive remarks

The gonadal tract could be seen in various stages of development from mid-sized juveniles upwards (Fig. 6). The minimum length at which oogenesis was observed was 2.25 mm shell length and specimens larger than this size were classed as reproductively mature. Half of the individuals at this size or above-contained variable numbers of clearly visible oocytes, the other half possessed a full-looking, opaque gonadal tract but no oocytes, indicating *Dacrydium alleni* sp. nov. is dioecious. Specimens displaying full gonads without eggs were classed as mature males and specimens with developing oocytes evident classed as mature females. No evidence of hermaphroditism was observed and there were no empty gonads in individuals of adult size. In juveniles, the gonadal tract, when present, was of varying size and definition, was translucent rather than opaque and did not appear full. Of the 296 specimens examined, 51% were classified as adult, based on size and fullness of the gonads and/or presence of oocytes as described, and males and females were equally represented in the adult population. 75 reproductively active female *Dacrydium alleni* sp. nov. were

examined and no brooded larvae were found. SEM images of female gonad sections confirmed the presence of reasonably uniform flask-shaped developing oocytes of approximately 100–110  $\mu\text{m}$  length with a diameter around 65–75  $\mu\text{m}$ . Oocytes were arranged in three or four overlapping rows around a central stem of gonadal tissue (Fig. 5e, f). Comparison of dissected and in situ gonads visible through the shell suggested mature females contain upwards of 60 oocytes.

The early ontogenetic shell was clearly discernible on SEM images of adult valves. Prodissoconch length, defined as the diameter of the prodissoconch I when measured parallel to the hinge line, varied between 151 and 165  $\mu\text{m}$  with a mean of 156  $\mu\text{m}$  ( $n = 14$ ). This is comparable to those described for lecithotrophic bivalves in Hain and Arnaud (1992) and Salas and Gofas (1997) and smaller than the prodissoconch I of brooding species. Prodissoconch II was absent on all individuals examined, indicating that no feeding occurs during the planktonic stage.



## Ecological remarks

Of 516 *Dacrydium alleni* sp. nov. specimens collected at a single station at Maud Rise, 296 were measured and examined for morphometric analysis and assessment of reproductive stage.

Size-frequency histograms for *Dacrydium alleni* sp. nov. indicated a non-normal distribution with two visible data modes (Fig. 7). Modality was tested using R package MixDist, which identified two modes of data at means of 1.04 mm shell length (Standard deviation 0.22 mm) and 2.07 mm shell length (Standard deviation 0.36 mm). To clarify this result, we split our data into cohorts of immature individuals (smaller than 2.25 mm length) and reproductively mature adults (larger than 2.25 mm length) and applied both Kolmogorov–Smirnov and Shapiro–Wilks tests to each group. We additionally split the adult cohort into male and female and tested size-frequency distribution for each. Results showed both juvenile and adult cohorts and also mature male and mature female groups were normally distributed. This distribution is suggestive of a synchronously reproducing population with slightly overlapping cohorts of mature specimens and new recruits. However, the periodicity of spawning events and the age of individuals cannot be determined from our specimens.

## Discussion

In January, when Brandt et al. (2011) investigated Maud Rise, fresh organic phytodetritus was recorded at around 2,000 m depth and carbon flux was shown to increase through February with a peak in March. It is notable that the specimens examined in this study, collected from 2151 m depth, were tinted green at the time of collection, presumably due to the recent ingestion of phytodetritus, and all sexually mature individuals studied appeared to be approaching a state of reproductive readiness, indicated by the observed uniformly developing oocytes in 100% of mature females and the apparently ripe gonads of mature males. The high numbers in the 1.4 mm valve length size class of the size-frequency histogram signal a peak in recruitment which we interpret as indicative of simultaneous spawning, perhaps triggered by the seasonal increase in carbon flux. Biological responses such as synchronised vitellogenesis, mediated by seasonal phytodetritus input, have been previously reported in deep sea invertebrates (Gooday 2002) and represent rare evidence of benthopelagic coupling from the surface to the deep sea floor.

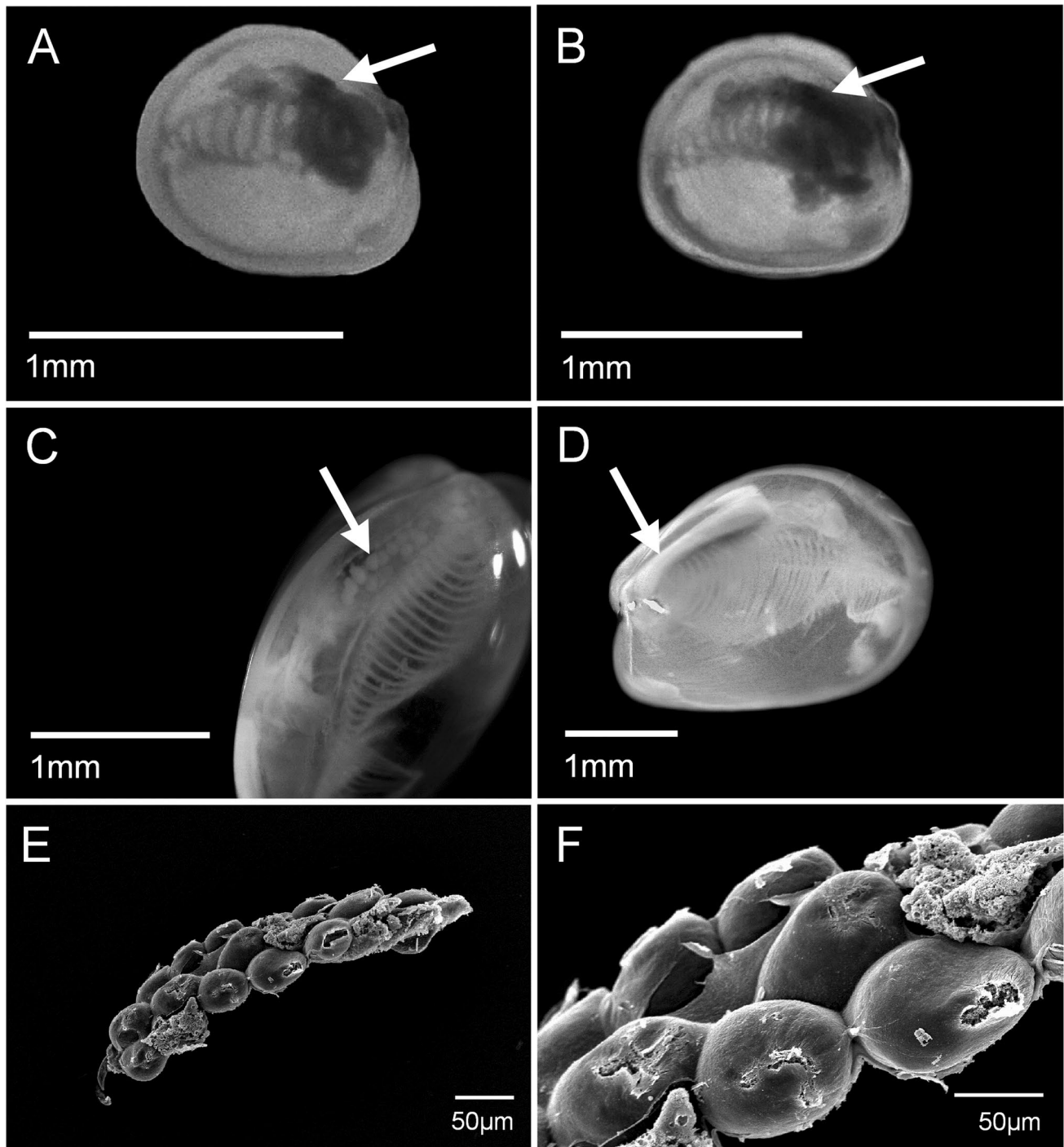
The size of adult *Dacrydium alleni* sp. nov., the length of prodissoconch I and the lack of brooded larvae indicate development via a lecithotrophic planktonic stage. This is the most common method of reproduction in Antarctic

bivalves (Brandt et al. 2011) and typical of the genus (Salas and Gofas 1997). Long-range transport of lecithotrophic larvae has been previously documented in the Antarctic, enabled in part by the decreased metabolic demands in cold Antarctic waters (Roterman et al. 2016). Although dispersal via currents of *D. alleni* sp. nov. lecithotrophic larvae does seem possible, the species has not previously been recorded from the neighbouring Lazarev and Weddell seas. As suggested by Brandt et al. (2011), local hydrological features, notably the retention of water in a Taylor column around Maud Rise, apparently limit the dispersal potential of non-swimming invertebrates and concentrate individuals in the area surrounding the seamount, promoting the development of an unusually abundant but less diverse community. This theory has been previously tested by Mullineaux and Mills (1997), who postulated that larval retention was a feature peculiar to geographically isolated seamounts only. However, although this effect may be driving high endemism due to local retention at Maud Rise, it should be noted that it would be unreasonable to expect 100% of larvae to be trapped and it is anticipated that future surveys may recover occasional singletons or ephemeral populations.

Given the importance and potential fragility of Antarctic marine ecosystems, it is imperative to establish robust ecological and taxonomic baselines against which to measure the impacts of our changing climate (Ingels et al. 2012; Brandt et al. 2014). Shelled, non-swimming molluscs are of primary importance in the modelling of biogeographical patterns as, in addition to not travelling large distances, they also leave long-term evidence of their presence in the form of shells (Schiaparelli et al. 2014). Bivalvia are considered a model taxon for exploring geographic trends in diversity (Linse et al. 2006; Jörger et al. 2014), therefore there is an increasing need to accurately quantify species richness, distribution and reproductive strategies in order to understand potential community and ecosystem level responses to environmental change (Linse et al. 2006; Ingels et al. 2012). Given the apparently extremely cosmopolitan and eurybathic distribution, differing reproductive strategies and variable shell morphology of Antarctic *Dacrydium*, plus evidence of historic mis-identification, we consider it likely there are further undescribed species and a requirement for a taxonomic investigation of the *Dacrydium albidum* group.

## Conclusion

Comparisons of *Dacrydium alleni* sp. nov. with related Antarctic and abyssal Atlantic *Dacrydium* species described by Allen (1998) and Salas and Gofas (1997) support the classification of *Dacrydium alleni* sp. nov. as a distinct species. Population structure in this sample is indicative of synchronous reproduction, further evidenced by the apparently

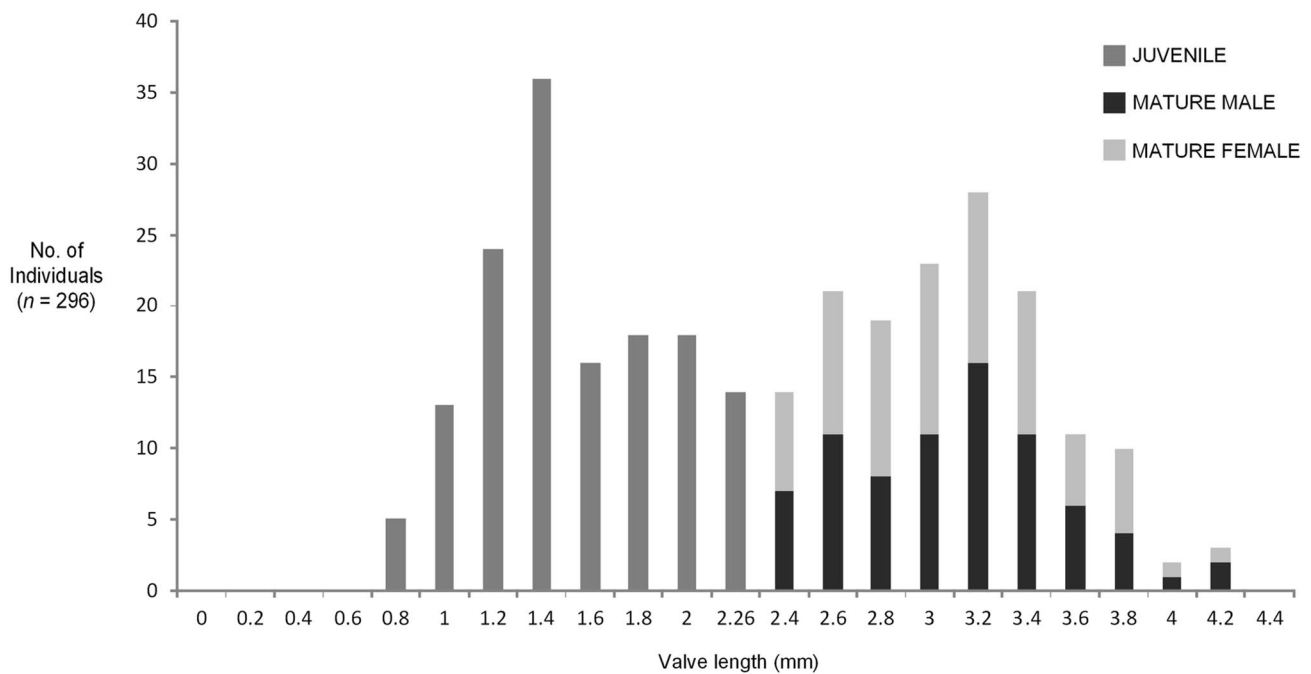


**Fig. 6** Reproductive development in *Dacrydium alleni* sp. nov. **a** Juvenile specimen with no visible gonad development Paratype ZMHK-xxxxx. **b** Early development of gonad structure at the anterodorsal margin of an immature specimen Paratype ZMHK-xxxxx. **c**

Mature female with visible oocytes Paratype ZMHK-xxxxx. **d** Mature female. Full, opaque gonads are evident Paratype ZMHK-xxxxx. **e, f** detail of oocytes. Note also the increased complexity of the gill from juveniles (**a, b**) to adults (**c, d**)

similar developmental stages of oocytes across a selection of individuals. Lifespan is unknown as, in common with other deep sea dacrydiines (Salas and Gofas 1997), growth marks in the dissoconch are inconsistent and largely absent.

Prodissoconch features such as D shape, large prodissoconch I and lack of prodissoconch II growth are consistent with species that produce lecithotrophic larvae.



**Fig. 7** Size-frequency histogram of *Dacrydium alleni* sp. nov

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### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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