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THE DEEP-WATER SPECIES OF *DACRYDIUM* TORELL, 1859 (DACRYDIINAE: MYTILIDAE: BIVALVIA), OF THE ATLANTIC

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ABSTRACT

Species of the genus *Dacrydium* are ubiquitous, mostly at bathyal and abyssal depths within the world's oceans. Here, 11 species are described from the Atlantic at depths greater than 500 m, and of these six are described for the first time. In addition, a bibliography of the world's species described to date is appended. The Dacrydiinae are neotenous mytilids, many being associated with sponges to which they are byssally attached. Multiple fine byssal threads are produced, which may form a nest. The shells are small, rarely more than 4 mm total length, fragile, and transluscent, white or pale cream in colour. Ornamentation, when present, consists of fine concentric striae, sometimes with very fine radial lines and occasionally a scattering of tiny shell granules. The hinge is narrow, with fine, multiple, nepioconch teeth retained throughout life. The ligament is small, internal, and amphidetic. Ventral to the posterior hinge plate is a shell buttress parallel to the dorsal shell margin, which probably provides necessary strength to an extremely fragile shell at times subject to adduction. The viscera occupy the dorsal-most third of the mantle cavity, the organs within being arranged parallel to the dorsal shell margin. Sexes are separate. The palps and gills are reduced in size. The outer demibranch, if present, develops late in life at the time the gonads are begining to mature. At most, it occupies a third of the gill axis and acts as a repository for sperm or eggs when they are first released. At the same time, the fused inner folds of the posterior mantle edge, ventral to the point of the attachment of the gill axis, enlarge and form an aperture that is probably related to the release of sperm or eggs, or spat in the case of those species that brood.

Key words: *Dacrydium*, Mytilidae, Bivalvia, deep-sea, Atlantic.

INTRODUCTION

Of the mytilids present in the deep sea (>500 m), the vast majority belong to the genus *Dacrydium* Torell, 1859. The first species to be described was *Dacrydium vitreum* (Møller, 1842) from off West Greenland and which is now known to occur in relatively shallow water at shelf and upper slope depths in northern seas (Appendix 2). Although a shallow-water species, *D. hyalinum,* was described by Monterosato (1870, 1875, 1878) from the Recent of Sicily and another, *D. occidentale,* by Smith (1885) from the Caribbean, and six varieties of *D. vitreum* were recognized by Locard (1898), until 1959 all records from the North Atlantic were referred to *D. vitreum.* Then, Ockelmann (1959), recognizing differences in shell shape and shell characters in specimens from northern seas, tentatively identified three species that he referred to as species a, b, and c, one of which (b) he was later to describe as *D. viviparum* (Ockelmann, 1983). In the years between Ockelmann's two papers, others also recognized that species other than *D. vitreum* occurred in the North Atlantic (Soot-Ryen, 1966; Allen, 1979). One of these, *D. ockelmanni,* was described by Mattson & Warén (1977).

Elsewhere, species of *Dacrydium* had been described from Australasian waters (Hedley, 1904, 1906), from the Southern Ocean (Pelseneer, 1903; Theile, 1912), and the Pacific (Dall, 1916).

With the upsurge of deep-sea exploration in the last 25 years, a number of new species have been described from the world oceans (Okutani, 1975; Bernard, 1978; Knudsen, 1970; Poutiers, 1989; Okutani & Izumidate, 1992; Hayami & Kase, 1993; Salas & Gofas, 1997), bringing the total, prior to this paper, to 28 known species in the world oceans. This total includes five species that have not yet been given specific names and may yet prove to be synonymous with other species. A list of all the above species and a bibliography to

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them is given in Appendix 2. Unknown until shortly before publication, Salas & Gofas (1997) and the present author had been working simultaneously on Atlantic species of the genus. This paper takes account of their work.

Apart from *D. ockelmanni* (Mattson & Warén, 1977), *D. angulare* and, to a lesser degree *D. viviparum* (Ockelmann, 1983), and a note on their nephridia by Odhner (1912), the species of *Dacrydium* are known from their shell features alone. Here are added details of their internal morphology.

MATERIAL AND METHODS

The species described here were present in the deep-sea samples taken by the research vessels of the Natural Environment Research Council, U.K.; of the Woods Hole Oceanographic Institution, U.S.A.; and of the Centre National pour l'Exploration des Oceans, France. These ships and the names of the various expeditions are included in the list of material in Appendix 1. For the most part, the specimens were collected with a Sanders epibenthic sledge (ES) or some variant of it (Oban - OS; Wormley - WS), and a few were collected by other means, namely, Anchor Dredges (AD, DP), Beam Trawls (CP, CLG), Agassiz Trawl (CV), Reineck Box Corer (KR), large Boillet Trawls (GBO, GBS), small Boillet Trawl (PBS).

The samples were elutriated on board, using sieves (mesh 0.42 mm USA and UK; 0.25 mm and 0.50 mm France), fixed in 4% or 10% formal saline and then after 24 h, washed and transferred to 70% or 95% ethanol. Internal morphology was studied using whole mounts stained lightly in Ehrlich's haematoxylin and sections cut at 10 µm and stained with Meyer's haemotoxylin and eosin and with Azan.

DESCRIPTIONS

Family Mytilidae Rafinesque, 1815

Subfamily Dacrydiinae Ockelmann, 1983

Adult shell eqivalve, markedly inequilateral, small, rarely more than 4 mm total length, homologous to nepioconch of other mytilids; sculpture of fine concentric lines, marked in some species; fine radial lines present in some species; colour white or, occasionally, cream, frequently hyaline; umbo far anterior and somewhat dorsal to anterior limit of shell; highest part of shell varying in position from anterior to posterior to the mid-vertical axis; hinge may have derivatives of provincular teeth adjacent to primary ligament, a dorsal series of fine, transverse nepioconch teeth persist, the posterior series usually much more numerous than anterior; "subligamental ridge" (Ockelmann, 1983), or dorsal buttress shelf, ventral to and more or less parallel to posterior hinge plate; antero-ventral ridge, in-

Abbreviations Used in Figures

AA	anterior adductor
AF	axial muscle fibres
AL	ascending lamella
AN	anus
AP	anterior (upper) palp
AR	anterior pedal retractor
BC	basiphyllic gland cells
BG	byssal groove
CG	cerebral ganglion
DD	digestive duct
DG	digestive diverticula
DL	descending lamella
EC	eosinophyllic gland cells
FM	posterior fused inner mantle fold
FT	foot
HG	hindgut
GA	gill axis
GF	gill filament
GS	gastric shield
GV	ventral margin of inner demibranch
HB	hinge buttress
ID	inner demibranch
LI	ligament
LP	lip
MI	mantle isthmus
MT	mouth
OD	outer demibranch
OE	oesophagus
OR	rudiment of outer demibranch
OV	ovary
PA	posterior adductor muscle
PG	pedal ganglion
PM	longitudinal pallial muscle
PP	posterior (lower) palp
PR	posterior pedal retractor muscle
RA	reproductive aperture
SB	suprabranchial cavity
SP	sperm
ST	stomach
TE	testis
UC	umbonal cavity
VE	ventricle
VG	visceral ganglion

ternal to anterior hinge plate, variously developed; primary ligament small, internal and amphidetic; if present, secondary ligament very small, slender, opisthodetic. Viscera occupying dorsal third of shell space, digestive glands and gonads elongate, following line of dorsal margin; mantle margins simple, unfused, except where gill axis attaches to mantle margin; adductor muscles sometimes subequal in size, but usually heteromyarian, with the posterior muscle the larger; labial palps minute, few, if any, palp ridges; inner demibranch of gill extending length of mantle cavity, but with relatively few filibranch filaments; when present, outer demibranch developing late in life as a small posterior triangular flap; foot relatively small, with functional byssus, producing many fine threads.

Genus *Dacrydium* Torell, 1859

Type species by monotypy, *Modiola? vitrea* Møller, 1842:92.

Description as for subfamily. Occurs from shelf to abyssal depths, most species being found from mid-slope to lower slope depths.

The genus *Quendreda* was proposed by Iredale (1936:271) but without diagnosis. He designated *D. fabale* Hedley, 1904, as the type species, remarking that it "differs in shape, form and sculpture from the Spitzbergen shell, the type of Torell's genus." There is debate as to whether this distinction is justified (Soot-Ryen, 1955; Bernard, 1978; Ockelmann, 1983).

Abbreviations of Museums

AHF	Allan Hancock Foundation (see LACMNH)
AMS	Australian Museum, Sydney
BMNH	Natural History Museum, London
IRSNB	Institut Royal des Sciences Naturelles, Belgique
LACMNH	Los Angeles County Museum of Natural History
MNHNP	Muséum National d'Histoire Naturelle, Paris
NMNZ	National Museum of New Zealand
NSMT	National Science Museum, Tokyo
SBMNH	Santa Barbara Museum of Natural History
SMNH	Naturhistoriska Riksmuseet, Stockholm
TRFRL	Tokai Regional Fisheries Research Laboratory
UMUT	University Museum, University of Tokyo
USNM	United States National Museum
ZMHU	Zoologisches Museum Humbolt-Universitat, Berlin
ZMUB	Zoological Museum, University of Bergen
ZMUC	Zoological Museum, University of Copenhagen

Dacrydium sandersi, new species

Figs. 1–3

Type Locality: Atlantis II, Sta. 66, North America Basin, 38°46.7'N 70°08.8'W, 2802 m.

Type Material: Holotype, BMNH 1996136; paratypes, BMNH 1996137.

Material: North America Basin: Atlantis II, sta. 62, 69 spec.; sta. 64, 175 spec.; sta. 66, 12 spec.; sta. 72, 132 spec.; sta. 118, 5 spec;

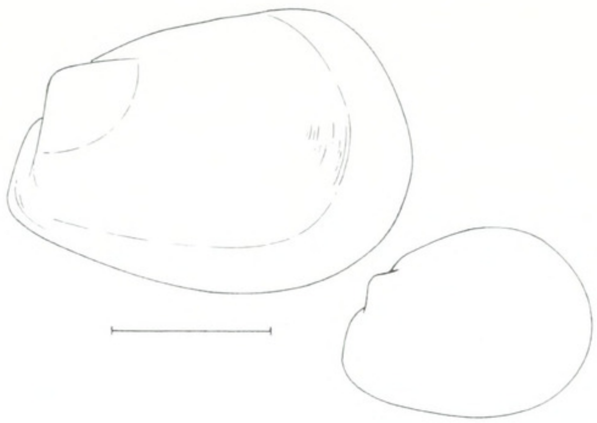

FIG. 1. *Dacrydium sandersi.* Lateral views from the left side of two specimens from Atlantis II sta. 72, North America Basin, 2864 m. Scale = 1 mm.

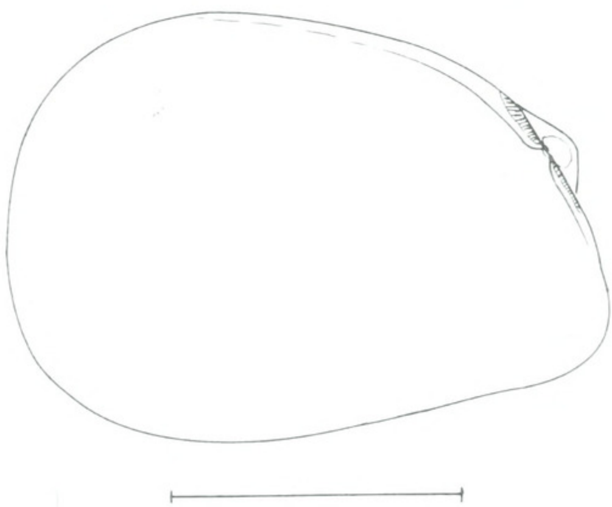

FIG. 2. *Dacrydium sandersi.* Lateral internal view of right valve from Biogas III sta. DS41, Bay of Biscay, 3548 m. Scale = 1 mm.

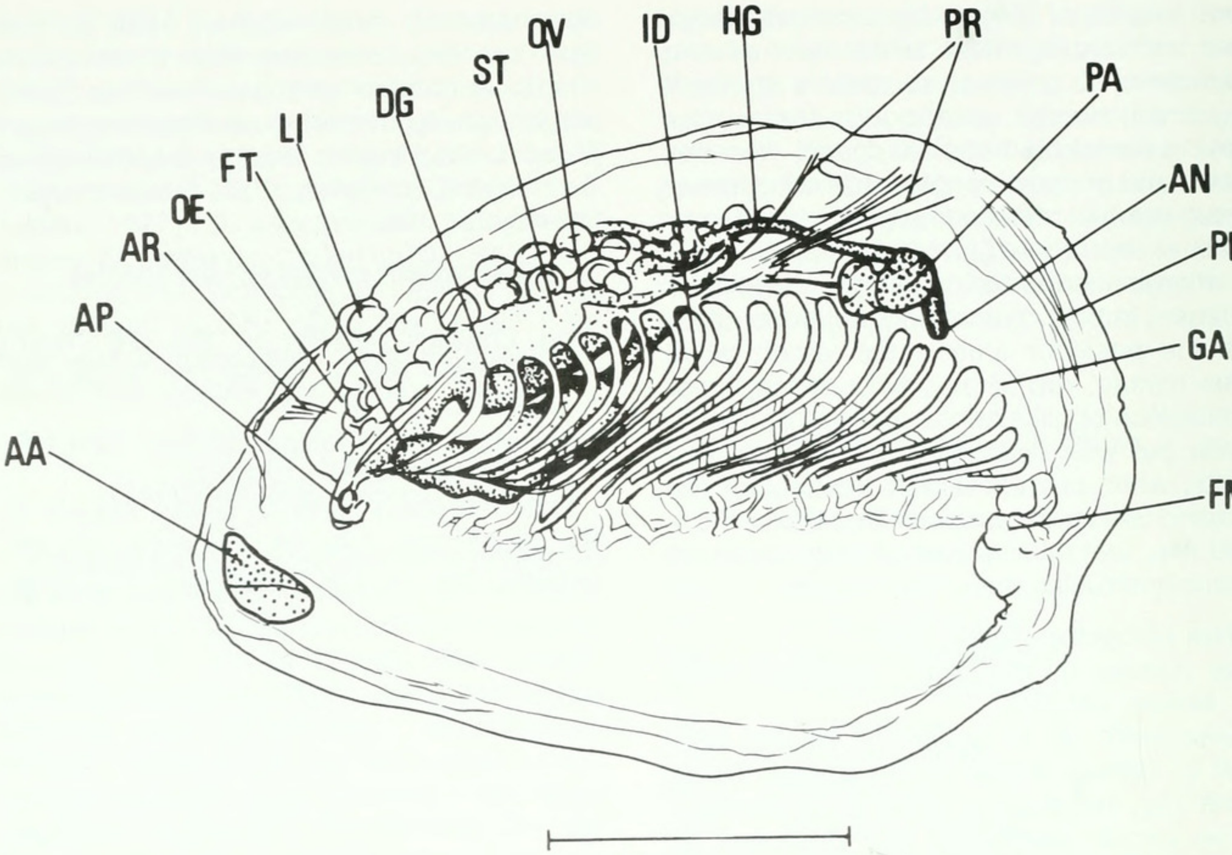

FIG. 3. *Dacrydium sandersi.* Semidiagrammatic view of the internal morphology of a specimen from the left side from Atlantis II sta. 72, North America Basin, 2864 m. Scale = 0.5 mm. Refer to Materials & Methods for list of abbreviations.

sta. 119, 32 spec.; Chain, sta. 76, 133 spec. Brazil Basin: Atlantis II, sta. 155, 90 spec.; sta. 156, 396 spec.; sta. 167, 39 spec.; sta. 169, 17 spec. West European Basin: Biogas II, sta. DS31, 10 spec.; Biogas III, sta. DS41, 61 spec.; Biogas IV, sta. DS58, 6 spec.; sta. DS59, 2 spec.; Biogas VI, sta. 74, 17 spec.; sta. CV38, 7 spec. Azores Mid Atlantic Ridge: Biacores, sta. 126, 19 spec.

Distribution: Occurs most commonly at lower slope depths (2500–3000 m), although the overall range is much wider (587–3783 m). It occurs across the Atlantic, predominantly at boreal latitudes in the North America and West European basins, although in the West Atlantic it has been taken from the northern part of the Brazil Basin.

Shell Description (Figs. 1, 2). Shell small (<4 mm), fragile, modioliform, greatest shell height posterior to mid-vertical axis, relatively wide, transluscent white, occasional growth lines and faint concentric striations, otherwise smooth; umbones large, distant from antero-ventral limit of shell margin; ventral margin convex in small specimens, with slight sinuosity anteriorly in larger specimens; posterior margin broadly curved; dorsal margin very slightly concave, slightly angled where posterior limit of hinge meets margin; anterior margin relatively long and straight, except close to umbo where it curves inwards; hinge plate interrupted by ligament pit; anterior hinge plate moderately elongate, with 13–15 nepioconch teeth; posterior hinge plate approximately the same length as anterior but broader, with 10–12 nepioconch teeth; narrow buttress shelf extending from anterior limit of posterior hinge plate along the dorsal margin to the highest point of the shell; a narrower buttress shelf extending from posterior limit of the anterior hinge plate along the anterior margin to a point where the margin starts to curve to the ventral margin; ligament small, internal, amphidetic, separating anterior and posterior hinge plates. Prodissoconch length: 123 μm.

Internal Morphology (Fig. 3). The mantle margin has outer, middle sensory and inner muscular folds. Posteriorly, there is fusion of the latter to form an extensive exhalent aperture. The area of fusion is relatively broad and is much more prominant in large than small specimens. The gill axes attach to the dorsal edge of the fused tissue. In large specimens, the area of fusion might be mistaken for an inturned and contracted inhalent siphon (Fig. 3), but in the present specimens neither whole mounts nor sections reveal a clear lumen from the exterior to the mantle cavity, although sections show that there is an inner cavity. It will be seen that in fully mature specimens of other species a lumen does connect the mantle cavity to the exterior, and it would appear that the aperture when formed is used for the discharge of eggs and sperm. Neither Mattson & Warén (1977) nor Ockelmann (1983) mention this, despite its presence in the species that they describe.

The adductor muscles are small and equal in size. The gills consist of only the inner demibranchs. No rudiment of an outer demibranch is present, even in specimens with maturing ova. The inner demibranchs comprise of a relatively broad descending lamella and an ascending lamella about half the length of the descending. The filaments are typically filibranch without interlamellar and interfilamentar junctions. The main axes are attached dorsally to the body wall and to the mantle posterior to the foot.

The palps are very small, slight enlargements to the lateral limits of the lips. The mouth opens to an oesophagus that has a lumen with six longitudinal grooves. The course of the oesophagus is straight, opening to the anterior part of the stomach. The latter is also elongate and tubular, lying along the antero-posterior axis. There is an extensive gastric shield that extends over much of the dorsal and left lateral walls of the stomach. The ciliation on the remaining wall appears to be relatively simple; however, there is a major typhlosole that extends the length of the combined style sac and mid gut. The hind gut turns immediately dorsal to the style sac, first taking an anterior course as far as the mid point of the stomach, and then turns sharply on itself and continues directly and mid-dorsally over the posterior adductor muscle to the anus. There is a very short digestive duct opening from what appears to be a simple caecum on the left side of the stomach. The duct connects with a digestive diverticulum that forms a longidinal tube on the left ventral side of the viscera. There is also a second duct opening anteriorly on the right side of the stomach. This branches, one branch connecting with a longitudinal diverticulum on the right side that parallels the one on the left, the other branch connecting with a smaller diverticulum ventral to the stomach. The right and left diverticula are finger-like and extend one each side of the oesophagus and terminate a short distance anterior to the mouth.

Dorsal to the paired diverticula are a pair of tubular gonads dorso-lateral to the digestive system. Sexes are separate; 30–35 ova (68 μm diameter) were present in a specimen 2 mm in length.

The kidneys are a pair of simple sacs posterior to the posterior adductor. The nervous system is of the typical bivalve design; however, all the ganglia are small in size.

Diagnosis: *D. sandersi* is characterized by the greatest shell height being posterior to the mid-vertical axis, the posterior hinge being short and of similar length to the anterior, the umbo being relatively distant from the antero-ventral point of the shell, and the adductor muscles being small and dimyarian.

Other species of similar shell shape are *D. rostriferum*. *D. occidentale* and *Dacrydium* sp. of Poitiers (1989), but these differ from the present species in that the posterior hinge is significantly longer than the anterior. The position of the umbo in *D. occidentale* and *Dacrydium* sp. is much closer to the antero-ventral limit of the shell (see Poitiers, 1989: fig. 3)

Dacrydium vitreum (Møller, 1842)
Figs. 4–7

Type Locality: West Greenland.

Type Material: originally ZMUC; appears to be lost (Warén, 1991).

Original description: Møller, 1842: 92 (for other references, see Appendix 2).

Cited specimen (figured in text): BMNH 1996144

Material: North America Basin: Atlantis, sta. D, 3 spec.; Chain, sta. 88, 34 spec.; sta. 105, 43 spec.; Knorr, sta. 346, 3 spec.

Also, specimens from off East Greenland identified and donated by Kurt Ockelmann to Howard Sanders of the Woods Hole Oceanographic Institution, have been examined.

Distribution: In the past, *D. vitreum* has been recorded widely from the North Atlantic south to the Azores and Florida (Ockelmann, 1959; Abbott, 1974), but it is now clear that southern specimens have been misidentified. It is a cold-water, panarctic species (Ockelmann, 1959; Mattson & Warén, 1977; Warén, 1991) and possibly circumglobal (Bernard, 1983; Salas & Gofas, 1997). Although the present specimens come from the shelf edge off Cape Cod at a boreal latitude, these relate to the southward extension of the Labrador Current,

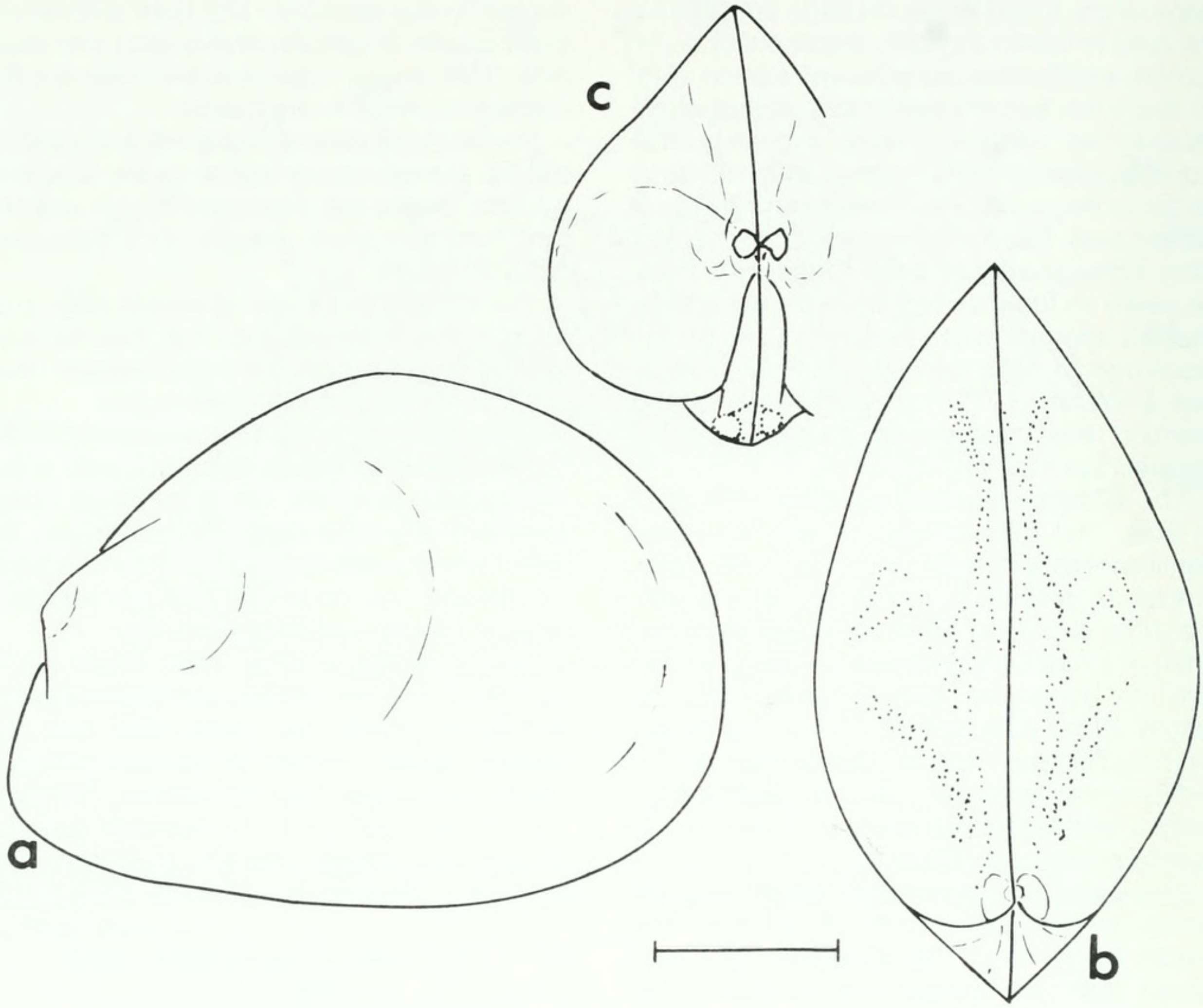

FIG. 4. *Dacrydium vitreum.* Three views of a shell from Knorr sta. 346, North America Basin. 475 m. (a) lateral from left side; (b) dorsal; (c) anterior. Scale = 1 mm.

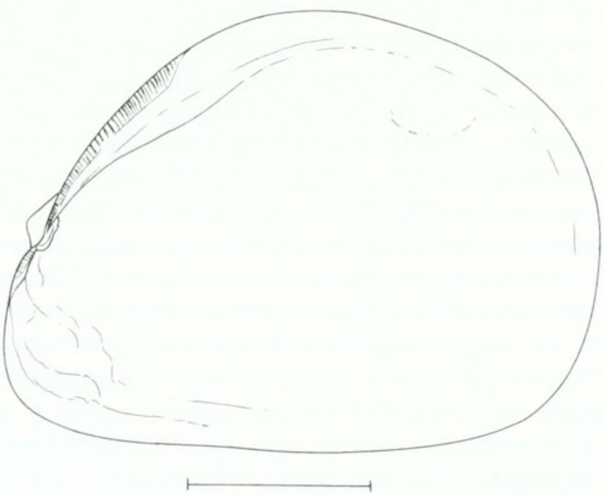

FIG. 5. *Dacrydium vitreum.* Lateral internal view of right valve from Atlantis 227 sta. D, 466–508 m. Scale = 1 mm.

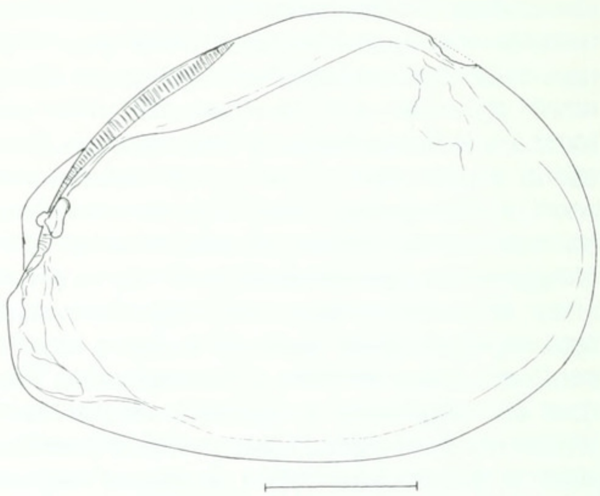

FIG. 6. *Dacrydium vitreum.* Lateral internal view of right valve of a specimen from off East Greenland (Ockelmann, 1953: 175). Scale = 1 mm.

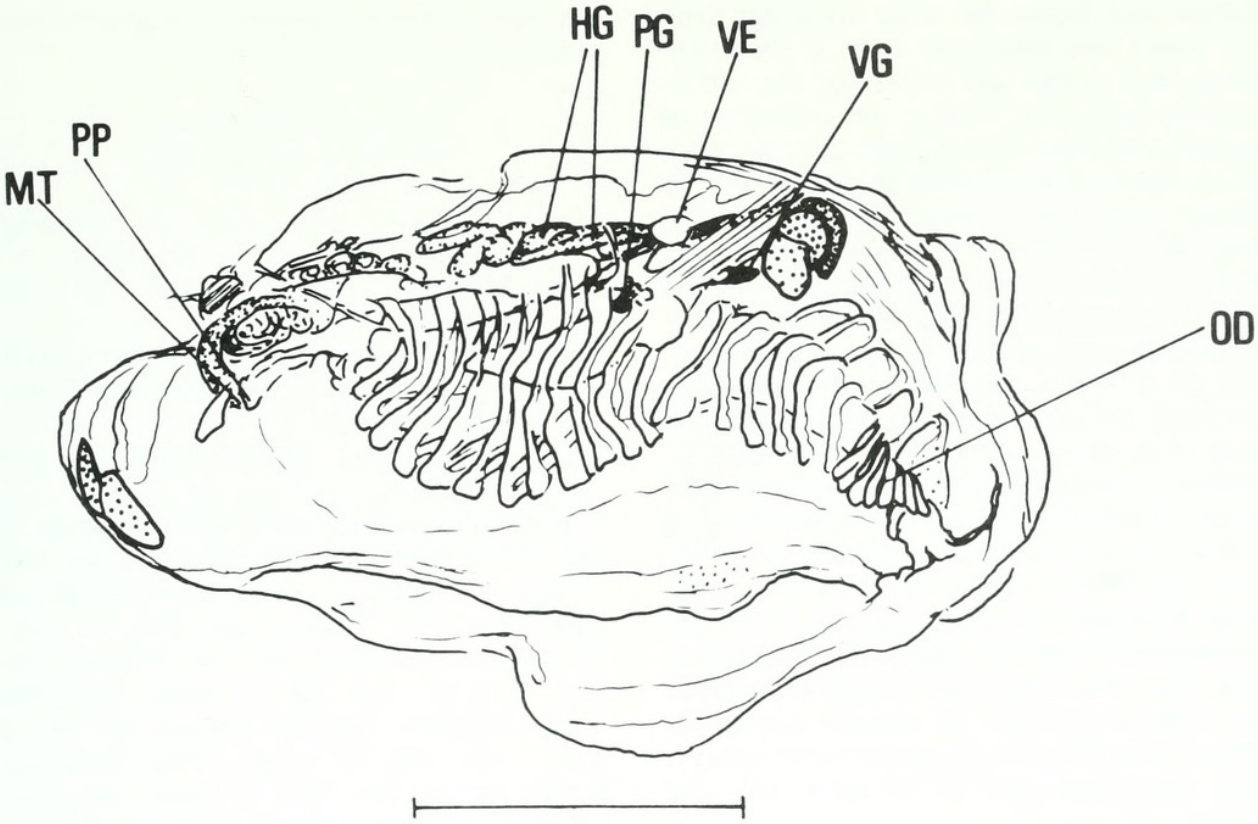

FIG. 7. *Dacrydium vitreum.* Semidiagrammatic view of the internal morphology of a specimen from the left side from Chain 58 sta. 105, North America Basin, 530 m. Scale = 1 mm. Refer to Materials & Methods for list of abbreviations and Fig. 3 for identification of other parts.

other species of Arctic bivalves are found at the same stations (Allen et al., 1995). Depth range: 5–698 m, deeper records down to 2258 m need to be confirmed (Ockelmann, 1959).

Shell Description (Figs. 4–6). Sars (1878) gave good descriptions and figures of the shell (Mattson & Warén, 1977), and since then other good figures and photographs have been provided by Ockelmann (1959, 1983), Mattson & Warén (1977), Warén (1991), and Salas & Gofas (1997). For completeness and for comparative purposes, shells from the North America Basin and from East Greenland are figured and described and, for the first time, the internal anatomy is described.

Shell small (<6 mm total length), semi-transparent or opaque, white, periostracum cream in larger specimens, semi-ovate, equivalve; shell relatively high, maximum height measurement immediately posterior to mid-vertical axis; umbo prominant, dorsal, slightly posterior to the anterior limit of the shell; ventral margin a shallow convex curve; posterior margin smoothly rounded; postero-dorsal margin broadly convex; antero-dorsal margin a shallow convex curve indented at juxtaposition of umbo and internal ligament; posterior hinge plate elongate, occupying 1/3 posterior dorsal margin, present specimens with 55–65 nepioconch teeth (number increasing with size); posterior hinge plate strengthened by broad buttress shelf thickened along ventral edge ("subligamental ridge" of Ockelmann, 1983); shelf extending just posterior to summit of dorsal shell margin, thereafter merging with pallial line of shell; anterior hinge plate short, with 5–8 nepioconch teeth; antero-ventral corner of shell somewhat thickened where anterior adductor muscle inserts; insertion of posterior adductor close to postero-dorsal pallial line posterior to buttress shelf; ligament internal, amphidetic, with very short fine external extensions not usually visible unless shell is dissolved. Prodissoconch length: 120–136 µm (Ockelmann, 1983; Salas & Gofas, 1997).

Internal Morphology (Fig. 7). The morphology is similar to that described for *D. sandersi.* The mantle margins are relatively unmodified, with three simple folds that are unfused, except posteriorly where the gill axes meet the margin and where the inner muscular folds are fused and thickened over a short distance. No papillae are present on the middle sensory lobe, and there is no extension of sensory and inner folds to form siphons. Very fine scattered radial pallial muscle fibres are present as a band internal to the inner muscular fold. The adductor muscles are relatively well developed, the anterior being of a similar size to the posterior, except that it is crescent-shaped in cross section as opposed to oval. The gill axes are attached latero-ventrally to the body and to the mantle posterior to the body. The inner demibranch, with approximately 25 filaments in a specimen 3 mm total length, is well developed, with the descending and ascending lamellae of similar size. The outer demibranch is restricted to a small, posterior, triangular structure close to where the axis meets the mantle margin, and it has up to nine short filaments. The anterior filament of the inner demibranch is situated somewhat distant from the minute palps, there being a long distal oral groove between gill and mouth.

The viscera are confined to a narrow band in the dorsal third of the shell cavity. This restriction is reminiscent of the condition in the deep-sea limopsids, in which the viscera occupy less than a third of the available mantle space (Oliver & Allen, 1980). Thus, in *D. vitreum,* the oesophagus, stomach, style sac and intestine are arranged in a longitudinal fashion within the body. The oesophagus is relatively elongate, joining the stomach anteriorly, the midgut is combined with the style sac; the hind gut is first reflected anteriorly, along the dorsal 2/3rds of the length of the stomach, and then posteriorly, passing through the heart and dorsal to the posterior adductor, to the anus. The major portion of the digestive diverticula comprise a pair of parallel tubules, one each side of the stomach and oesophagus. In addition, there are a few short tubules ventral to the stomach. The gonads are paired elongate tubes lying dorsal to the oesophagus and stomach. The sexes are separate. The kidney lies ventral to the hindgut, anterior to the posterior adductor. The foot joins the viscera posterior to the style sac. In preserved specimens, it is small and cylindrical enclosed by the gill lamellae. There is a functional byssus gland at the postero-ventral limit of the foot, and clearly in life the latter must be capable of considerable extension. Two paired posterior pedal retractor muscles insert immediately anterior to the posterior adductor, and a pair of fine anterior pedal retractors attach to the shell immediately dorsal to the umbones.

Dacrydium ockelmanni
Mattson & Warén, 1977
Figs. 8–15

Type Locality: Korsfjorden, W. Norway, 60°08.58′N 05°00.67′W, 260–290 m.

Type Material: Holotype ZMUB 58 633; paratypes ZMUB 58 634.

Original Description: Mattsen & Warén, 1977: 2, figs. 4–6, 10–13 (for other references, see Appendix 2).

Cited Specimens: BMNH 1996138 and 1996139.

Material: North America Basin: Atlantis II, sta. 73, 90 spec.; sta. 115, 50 spec.; sta. 119, 24 spec.; sta. 128, 37 spec.; Chain, sta. 87, 16 spec.; sta. 103, 1 spec.; sta. 210, 77 spec. Brazil Basin: Atlantis II, sta. 142, 89 spec.; sta. 144, 2 spec.; sta. 147, 9 spec. Argentine Basin: Atlantis II, sta. 239, 9 spec.; sta. 240, 2 spec.; sta. 245, 21 spec. West European Basin: Sarsia, sta. S33/2, 1 spec.; sta. S44, 19 spec.; sta. S50, 52 spec.; sta. S66; 1 spec.; Discovery, sta. 7601, 1 spec.; Challenger, sta. E80-73, 24 spec.; Biogas I, sta. DS11, 1 spec.; Polygas, sta. DS15, 9 spec.; sta. DS17, 2 spec.; DS18, 5 spec.; sta. DS25, 1 spec.; sta. DS31, 4 spec.; Biogas II, sta. DS32, 3 spec.; Biogas III, sta. DS36, 1 spec.; sta. DS37, 3 spec.; sta. DS38, 1 spec.; sta. DS50, 7 spec.; Thalassa, sta. Z397, 5 spec.; sta. Z400, 13 spec.; sta. Z413, 2 spec.; sta. Z417, 4 spec.; sta. Z427, 1 spec.; sta. Z447, 1 spec.; Biogas IV, sta. DS52, 13 spec.; sta. DS61, 4 spec.; sta CP01, 2 spec.; sta. DS62, 8 spec.; sta. DS63, 6 spec.; sta. DS64, 14 spec.; Biogas VI, sta. CP08, 3 spec.; sta. CP09, 7 spec.; sta. DS71, 3 spec.; sta. DS86, 36 spec.; sta. CP23, 1 spec.; sta. DS87, 30 spec.; Incal, sta. DS01, 12 spec.; sta. CP01, 41 spec.; sta. DS02, 31 spec.; sta. CP08, 1 spec.; Chain, sta. 313, 7 spec.; sta. 318, 1 spec.; sta. 321, 24 spec. Canary Basin: Discovery, sta. 6701, 13 spec.; sta. 6704, 5 spec. Azores Mid Atlantic Ridge: Biacores, sta. 105, 2 spec.; sta. 120, 1 spec.

Distribution: Ockelmann (1958), Mattson & Warén (1977) and Warén (1991) reported *D. ockelmanni* as occurring WSW and SE of Iceland, SW of the Faroes, NW of Ireland and probably Bay of Biscay. The species is confirmed as common in the Bay of Biscay and, further, as being present throughout most of the Atlantic, with the possible exception of the Angola and Cape basins. It is also reported as

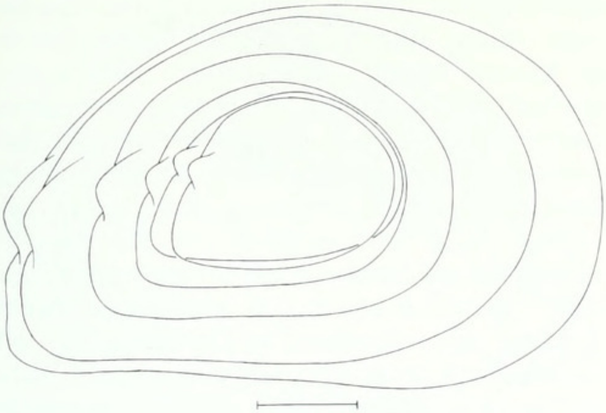

FIG. 8. *Dacrydium ockelmanni*. Lateral views of six shells from the left side to show variation in shell outline with increasing size. Specimens taken from Atlantis II sta. 73, North America Basin, 1330–1470 m. Scale = 0.5 mm.

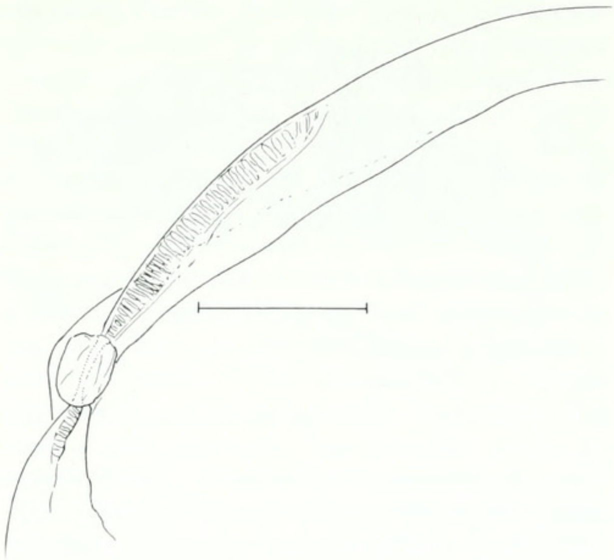

FIG. 10. *Dacrydium ockelmanni*. Detail of the hinge of a right valve from Atlantis II sta. 240, Argentine Basin, 2195–2323 m. Scale = 0.5 mm.

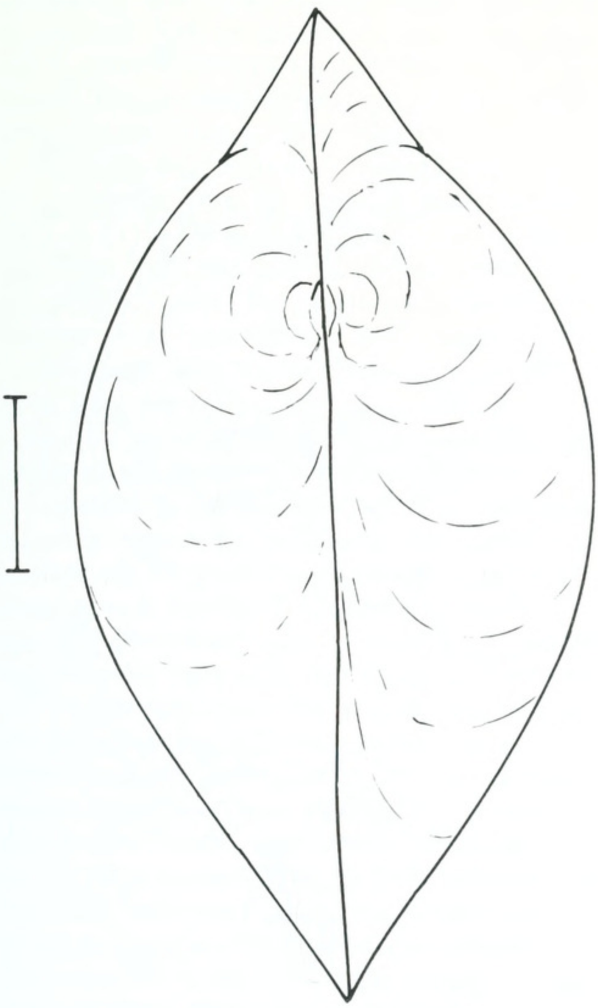

FIG. 9. *Dacrydium ockelmanni*. Dorsal view of shell from Atlantis II sta. 73, North America Basin, 1330–1470 m. Scale = 0.5 mm.

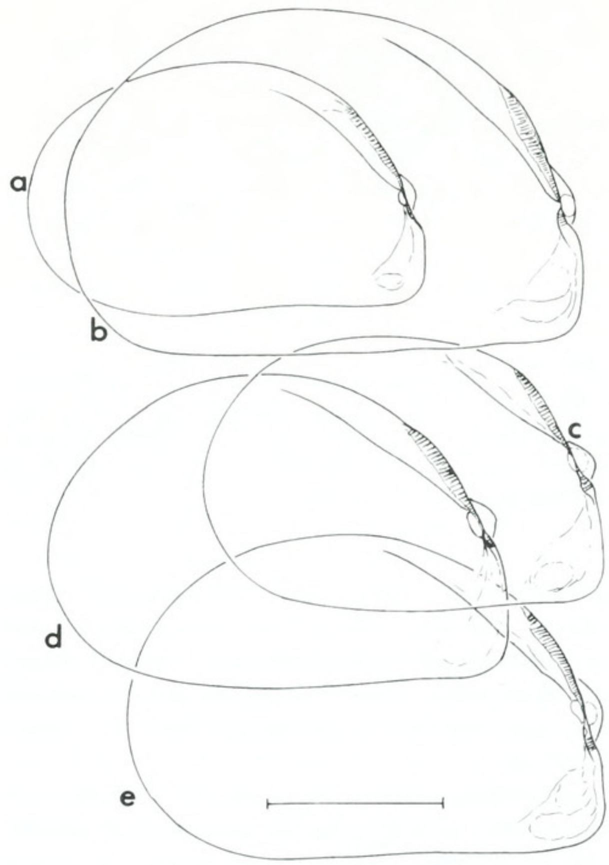

FIG. 11. *Dacrydium ockelmanni*. Lateral internal views of five right valves to show variation in form. (a) Discovery sta. 6704, Canary Basin, 2129 m; (b) Sarsia sta. S44, Bay of Biscay, 1739 m; (c) Atlantis II sta. 142, Brazil Basin, 1624–1796 m; (d) Atlantis II sta. 239, Argentine Basin, 1661–1669 m; (e) Atlantis II sta. 73, North America Basin, 1330–1470 m. Scale = 1 mm.

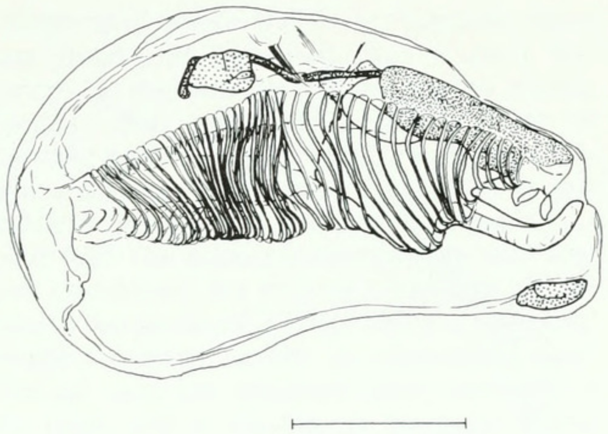

FIG. 12. *Dacrydium ockelmanni.* Semidiagrammatic view of the internal morphology of a male specimen from Atlantis II sta. 73, North America Basin, 1330–1470 m. Scale = 1 mm. See Fig. 3 for identification of the parts.

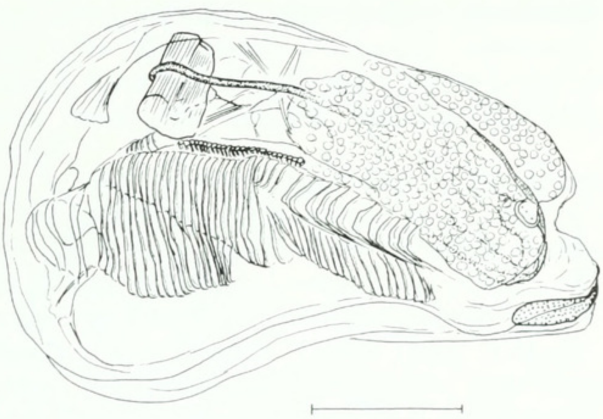

FIG. 13. *Dacrydium ockelmanni.* Semidiagrammatic view of the internal morphology of a female specimen from Atlantis II sta. 73, North America Basin, 1330–1470 m. Scale = 1 mm. See Fig. 3 for identification of the parts.

a Pleistocene fossil from the Mediterranean (Salas & Gofas, 1997). It occurs at lower shelf to lower slope depths with an extreme range of 100–3100 m, but most of the above records are from mid to lower slope depths (1000–2500 m).

Shell Description (Figs. 8–11). The shell is described and figured by Mattson & Warén (1977), Warén (1991), and Salas & Gofas (1997). Here further detail is added.

Shell small (<6.0 mm), semi-transparent, white or tinged with yellow/green, semi-ovate, greatest height coincident with mid-vertical axis or, in largest specimens, posterior to it; umbo moderate in size; ventral shell margin slightly concave in smallest specimens, as length increases ventral margin first becomes

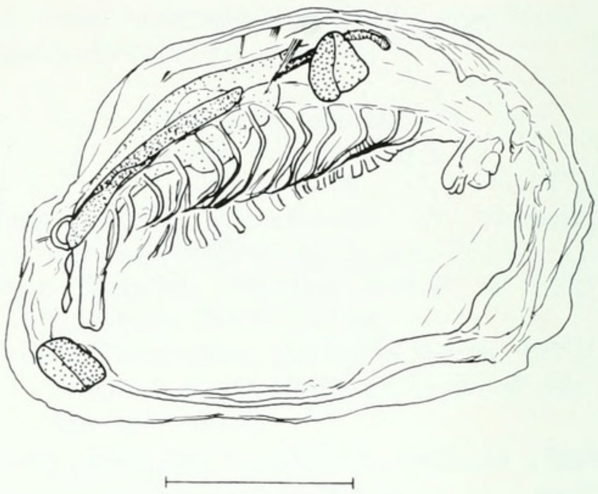

FIG. 14. *Dacrydium ockelmanni.* Semidiagrammatic view of the internal morphology of an immature specimen from Atlantis II sta. 142, Brazil Basin, 1624–1796 m. Scale = 0.5 mm. See Fig. 3 for the identification of the parts.

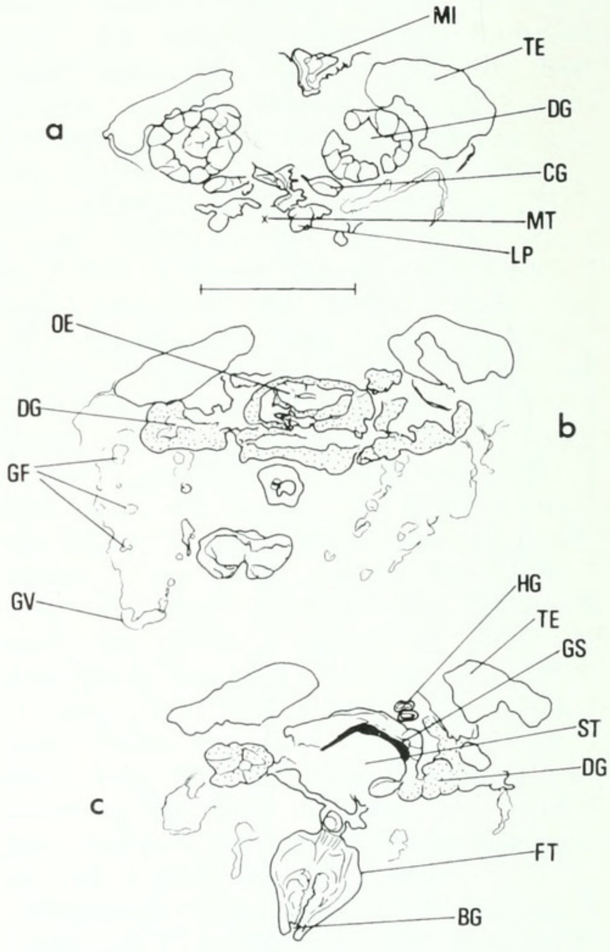

FIG. 15. *Dacrydium ockelmanni.* Transverse vertical 10 μm sections through a specimen from Atlantis II sta. 73, North America Basin, 1330–1470 m. (a) through region of mouth; (b) through oesophagus; (c) through stomach and gastric shield. Scale = 0.5 mm. Refer to Materials & Methods for list of abbreviations.

straight and then slightly convex; posterior and dorsal margins forming smooth, broad, convex curve; antero-dorsal margin dorsal to umbo almost straight, ventral to umbo slightly sinuate, then straight for short distance before curving sharply to meet ventral margin; posterior hinge plate occupying <1/4 dorsal shell margin, with 33–38 nepioconch teeth in present specimens (larger numbers are present in larger specimens, e.g. Salas & Gofas, 1997: fig. 8), supported by relatively wide buttress shelf that extends beyond hinge for a similar distance but short of the highest point of the shell; in intact specimens, ventral edge of buttress usually visible through shell; posterior limit of hinge plate frequently marked by slight angulation of shell margin; anterior hinge plate short with 5–7 nepioconch teeth, very small provincular tooth at proximal limit of anterior hinge plate; antero-ventral part of shell slightly thickened, with inner ventral ridge originating at anterior limit of anterior hinge plate; ligament internal, amphidetic, seated in pit between hinge plates. Prodissoconch length: 141–150 μm (Ockelmann, 1983).

Dacrydium ockelmanni (height/length 0.72–0.77) differs from *D. vitreum* (height/length 0.63–0.71) in being slightly more elongate and less high, with the ventral margin concave in larger specimens. The posterior hinge plate is shorter in *D. ockelmanni* with fewer nepioconch teeth, and the buttress shelf is somewhat less wide. The antero-dorsal margin is straighter and the umbo smaller and less distant from the antero-ventral limit of shell.

Ockelmann (1959) reported on a number of possible species, including one later described as *D. ockelmanni,* within a relatively small area of the North Atlantic off Iceland. The species described here, including *D. ockelmanni,* have fairly wide distributions. Because it is known that shell shape and internal morphology changes with increasing size, internal shell characters from specimens from different basins have been figured (Fig. 11), as well as differences in shell outline with increasing size from a large sample (Fig. 8). This confirms the variation, with that seen in a single sample being as great as the interbasinal differences. The variation is not consistant enough to warrent naming subspecies or varieties.

Internal Morphology (Figs. 12–15). Although their figures are diagrammatic, the morphology of *D. ockelmanni* is well described by Mattson & Warén (1977). Immature and mature whole mounts are illustrated here, and additional information given. Thus, the anterior adductor muscle is more round in cross-section and smaller than the posterior adductor. The gill filaments on the inner demibranch are more widely spaced compared with those of the outer demibranch, and specimens 1.6 mm in length have only a rudiment of the outer demibranch (Fig. 14). Ventral to the attachment of the gill axis with the mantle margin, the inner muscular mantle fold is fused and thickened over some distance and extended inwards to form an internal "collar." This structure is much more developed in larger specimens, particularly so in specimens that have mature gonads. The posterior pedal retractor muscles are not particularly well developed. The presence of a longitudinal pallial muscle is confirmed, and is perhaps better developed than the diagrammatic drawing of Mattson & Warén (1977) might indicate. Sexes are separate, and large female specimens from Station 73 were mature, with approximately 400 eggs (75 μm diameter) in specimens >4 mm total length (Figs. 13, 14).

Dacrydium abyssorum, new species
Figs. 16–19

Type Locality: Knorr 25, Station 287, Guyana Basin, 13°16.0′N 54°52.2′W 13°15.8′N 54°53.1′W, 4980–4934 m.

Type Material: Holotype BMNH 1996140; paratype BMNH 1996141.

Material: Newfoundland Basin: Chain, sta. 331, 2 spec.; North America Basin: Atlantis II, sta. 70, 3 spec.; sta. 93, 1 spec.; Chain, sta. 80, 1 spec.; sta. 83, 2 spec.; sta. 84, 5 spec.; sta. 84, 8 spec. Guyana Basin: Knorr, sta. 287, 27 spec.; sta. 288, 14 spec.; sta. 306, 2 spec.; Vema, sta. CP02, 2 spec.; sta. DS05, 2 spec. West European Basin: Biacores, sta. 245, 11 spec.; Polygas, sta. DS20, 89 spec.; sta. DS21, 26 spec.; sta. CV13, 17 spec.; sta. DS22, 59 spec.; sta. DS23, 21 spec.; sta. DS26, 9 spec.; Biogas II, sta. DS30, 12 spec.; Biogas III, sta. DS42, 1 spec.; sta. DS44, 4 spec.; sta. DS45, 8 spec.; sta. DS46, 3 spec.; sta. DS48, 2 spec.; Biogas IV, sta. 54, 4 spec.; sta. DS55, 264 spec.; sta. KR31, 1 spec.; sta. DS56, 15 spec.; sta. KR35, 2 spec.; Biogas V, sta. DS67, 23 spec.; sta. DS68, 10 spec.; sta. DS69, 4 spec.; sta. CP07, 1 spec.; Biogas VI, sta. DS75, 1 spec.; sta. DS76, 579 spec.; sta. CP13, 32 spec.; sta. CP14, 53 spec.; sta. KR60, 5 spec.; sta. KR64, 2 spec.; sta. DS77. 148 spec.; sta. DS78, 21 spec.; sta. CP16, 13 spec.; sta. DS79, 9 spec.; sta. CP17, 17 spec.; sta. CP18, 1 spec.; sta. DS80, 2 spec.; sta. DS81, 1 spec.; sta. CP21, 2 spec.; sta. DS87,

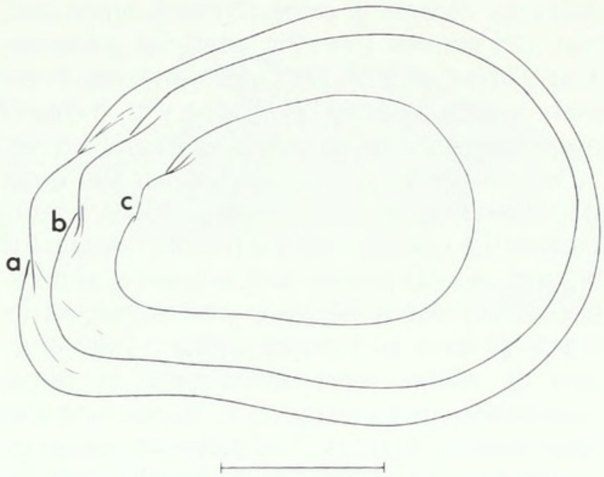

FIG. 16. *Dacrydium abyssorum.* Lateral views of three shells from the right side. (a & c) Chain 50 sta. 85, North America Basin, 3834 m; (b) Knorr sta. 287, Guyana Basin, 4980–4934 m. Scale = 0.5 mm.

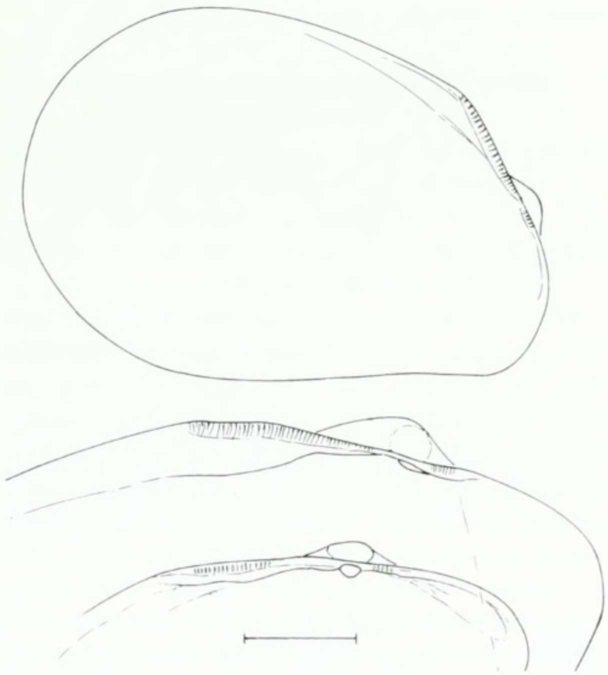

FIG. 17. *Dacrydium abyssorum.* Lateral internal view of right valve of a specimen from Knorr sta. 288, Guyana Basin, 4417–4429 m, and the detail of the hinge of two right valves from Chain 50 sta. 85, North America Basin, 3834 m. Scale = 0.5 mm.

13 spec.; Incal, sta. CP10, 6 spec.; sta. DS11, 5 spec.; sta. CP11, 30 spec.; sta. WS02, 64 spec.; sta. OS03, 19 spec.; sta. OS05, 26 spec.; sta. KR14, 3 spec.; sta. WS07, 388 spec.; sta. DS14, 73 spec.; sta. DS15, 42 spec.; sta. DS16, 123 spec.; sta. WS08,

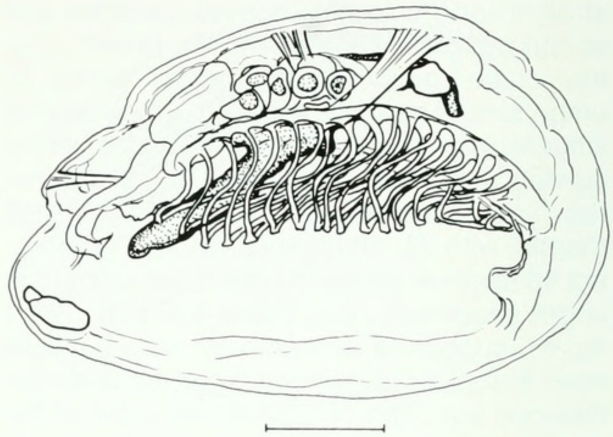

FIG. 18. *Dacrydium abyssorum.* Semidiagrammatic view from the left side of the internal morphology of a mature female from Knorr sta. 287, Guyana Basin, 4980–4934 m. Scale = 0.5 mm. See Fig. 3 for the identification of the parts.

274 spec.; sta. OS06, 63 spec.; sta. OS07, 515 spec.; sta. WS09, 111 spec.; sta. WS10, 280 spec.; sta. OS08, 145 spec. Sierra Leone Basin: Atlantis II, sta. 148, 1 spec.; sta. 149, 13 spec. Cape Basin: Walvis, sta. DS02, 2 spec.; sta. KG14, 1 spec.; sta. DS05, 39 spec.; sta. DS06, 43 spec.; sta. DS07, 2 spec.

Distribution: *Dacrydium abyssorum* is widespread at abyssal depths throughout the Atlantic. It occurs at depths from 1913–5280 m, but predominantly at depths >4000 m.

Shell Description (Figs. 16, 17). Shell small, modioliform, fragile, transluscent, white, greatest height posterior to mid-vertical transverse axis; umbo relatively large, distant from the antero-ventral limit of shell; antero-ventral margin broadly rounded; ventral margin sinuous; posterior margin a smooth, broad curve; postero-dorsal margin a smooth convex curve; antero-dorsal margin much less convex, angulate at posterior limit of hinge plate; antero-dorsal margin almost straight; anterior margin dipping slightly where umbo meets margin; anterior and posterior hinge plates continuous, although edentulous section below umbo narrow; anterior hinge-plate short, but relatively broad, with 5–9 nepioconch teeth; posterior hinge-plate elongate, broadening distally, with approximately 42 nepioconch teeth in specimen 4.5 mm total length; buttress shelf broad, except ventral to the anterior half of the posterior hinge plate, where it narrows, usually making a sinuous curve with the broader posterior part; internal ridge from anterior limit of hinge plate curving postero-ventrally, forming margin of antero-

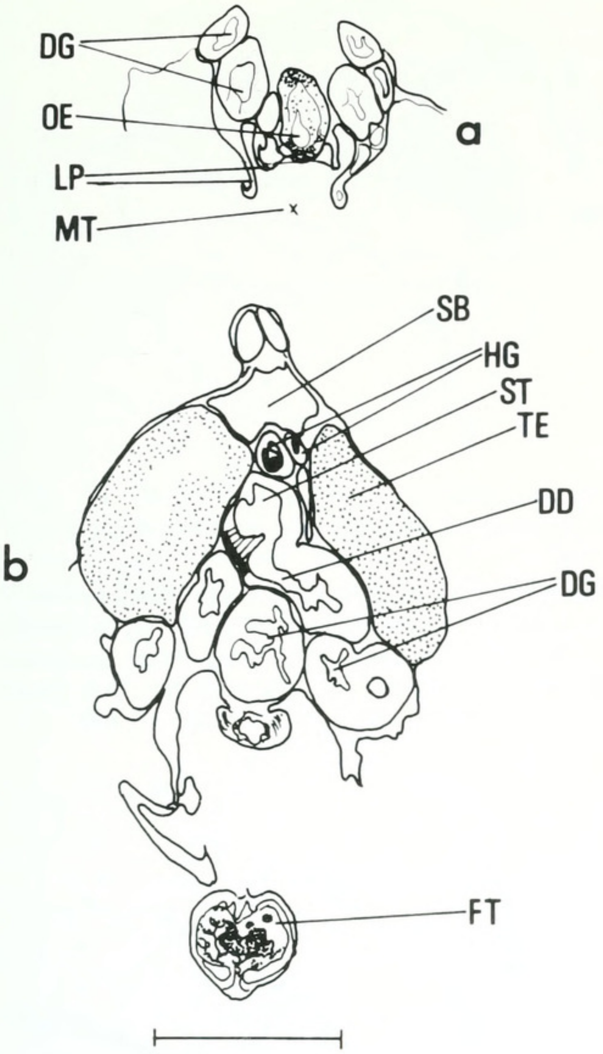

FIG. 19. *Dacrydium abyssorum.* Transverse vertical 10 µm sections through a mature male specimen from Knorr sta. 287, Guyana Basin, 4980–4934 m, (a) through the mouth; (b) through the stomach. Scale = 0.5 mm. Refer to Materials & Methods for list of abbreviations.

ventral triangular area to which anterior adductor muscle attaches; ligament small, internal, amphidetic. Prodissoconch length: 191–204 µm.

Internal Morphology (Figs. 18, 19). The internal morphology is similar to that of *D. sandersi.* The adductor muscles are small, the anterior slightly larger in size. The gill is without an outer demibranch, and the inner demibranch comprises both ascending and descending lamellae. There are relatively few filaments, 17 and 27 in the demibranchs of specimens 1.8 mm and 3.0 mm total length, respectively. There are no interfilamentar connectives and no interlamellar connectives. The posterior mantle margin is thickened at the point where the gill axes attach to it and also ventral and dorsal to the point of attachment. Fusion of the inner mantle folds occurs at the point where the gill axes meet the mantle margin and ventral to this. In mature specimens, through this is a channel from mantle cavity to the exterior, homologous to an inhalent aperture, which is probably used for the passage of sexual products. Inhalent repiratory and feeding currents pass through the extensive pedal gape. Internally, the margin of this reproductive aperture is characteristically curved, forming a funnel. Anteriorly, the lips and mouth also form a wide buccal funnel; this is directed postero-ventrally and so placed to receive material traveling the length of the gill margin. The palps are reduced to slight thickenings at the extremities of the lips, and it would appear that little or no sorting of incoming material can occur. The oesophagus is wide and the stomach relatively voluminous. The digestive diverticula are more branched than in *D. sandersi,* but similar in their distribution. The pedal musculature is relatively stout compared with that of *D. sandersi.* Mature specimens were present in the samples, 10 and 24 large eggs (115 µm max. dimension) were present in specimens 1.8 mm and 3.0 mm total length, respectively.

Diagnosis: *Dacrydium abyssorum* is a species in which the maximum shell height is posterior to the vertical mid-line and thus is similar to *D. sandersi.* It differs from the latter in the more pronounced angulation of the shell margin opposite the posterior limit of the hinge, the more sinusoidally curved ventral margin of the shell, and in the difference in length of the hinge plates and the numbers of nepioconch teeth.

Dacrydium wareni Salas & Gofas, 1997
Figs. 20–25

Type Locality: Off northwestern Morocco, 35°31′N 07°42′W, 1510 m.

Type Material: Holotype and paratypes MNHNP; paratypes SMNH.

Description: Salas & Gofas 1997: 271, figs. 94–96, 97–99 (for other references, see Appendix 2). Cited specimen: BMNH 1996146.

Material: North America Basin: Atlantis II, sta. 73, 2 spec.; sta. 118, 1 spec. West European Basin: Sarsia, sta. S61, 1 spec.; sta. S63, 4 spec.; Thalassa, sta. Z400, 1 spec.; sta. 435, 2 spec.; Biogas IV, sta. DS51, 1 spec. Canary Basin: Discovery, sta. 6696, 1 spec.

Distribution: This species occurs at mid-

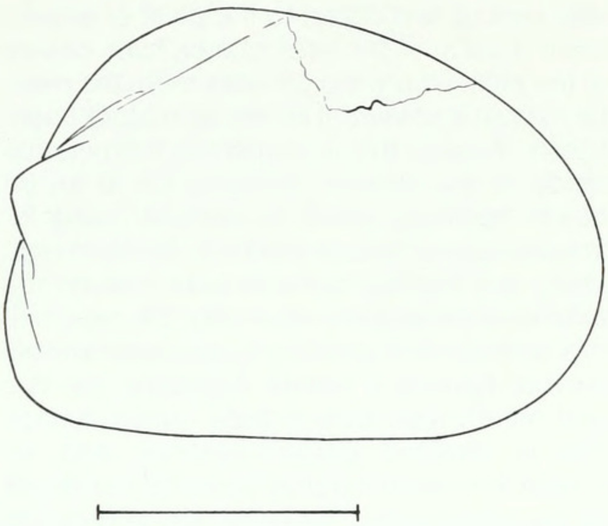

FIG. 20. *Dacrydium viviparum.* Lateral view from the left side of the shell of the paratype BMNH 1983035. Scale = 1 mm.

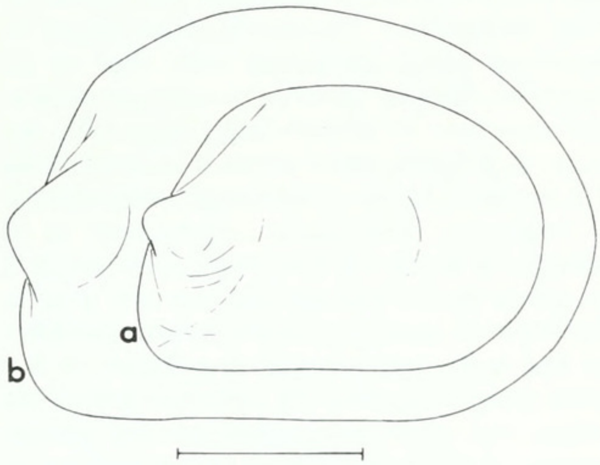

FIG. 21. *Dacrydium wareni.* Lateral view from the left side of two shells from (a) Sarsia sta. S63, Bay of Biscay, 1336 m and (b) from Atlantis II sta. 73, North America Basin, 1330–1470 m. Scale = 1.0 mm.

slope depths in the temperate North Atlantic and western Mediterranean (depth range: 952–2340 m). Maximum length of present specimens, 4.4 mm.

Shell Description (Figs. 20–23). Salas & Gofas (1997) give a description *D. wareni,* which is extended here. The present specimens were recognized as belonging to a new species before the description by the latter authors was published. The present specimens correspond in every respect with their excellent description. Salas & Gofas (1997) do not describe the internal morphology.

Shell small, transluscent white, semi-ovate,

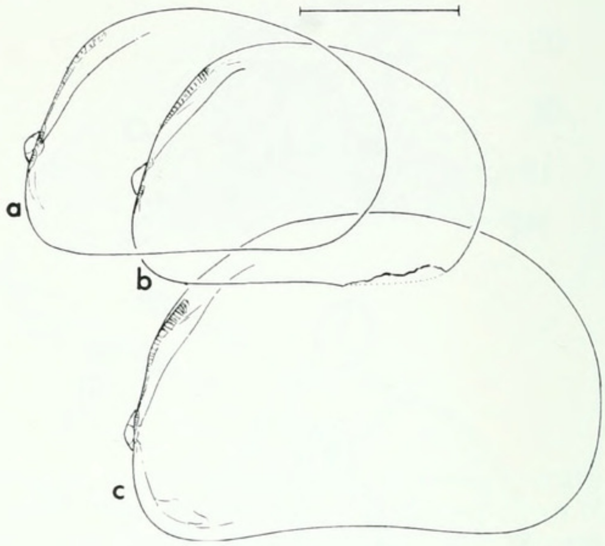

FIG. 22. *Dacrydium wareni.* Lateral internal views of right valves from (a) Sarsia sta. S63, Bay of Biscay, 1336 m; (b) Thalassa sta. Z400, West European Basin, 1175 m and (c) Atlantis II sta. 118, North America Basin, 1135–1153 m. Scale = 1 mm.

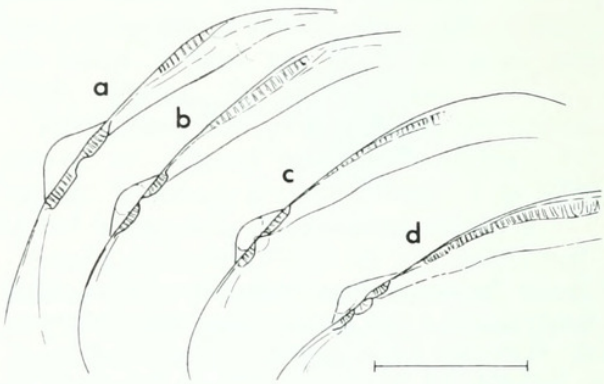

FIG. 23. *Dacrydium.* Comparative detail of the hinges of four left valves. (a) *Dacrydium viviparum.* Paratype, BMNH 1983035, Ingolf sta. 78, Reykjanes Ridge, 1505 m; (b) *Dacrydium wareni.* Thalassa sta. Z400, West European Basin, 1175 m, (c) Sarsia sta. S63, Bay of Biscay, 1336 m and (d) Atlantis II sta. 118, North America Basin, 1135–1153 m. Scale = 0.5 mm.

greatest height dimension usually anterior to mid vertical axis, but may be coincident or slightly posterior to axis in larger specimens; umbo small, distant from the antero-ventral limit of shell; maybe one or two faint radial lines from umbo to mid-dorsal and postero-dorsal margin respectively, faint incremental lines present; anterior shell margin ventral to umbo a shallow, convex curve dorsal to umbo almost straight, steeply inclined, meeting broadly convex dorsal margin in slight break

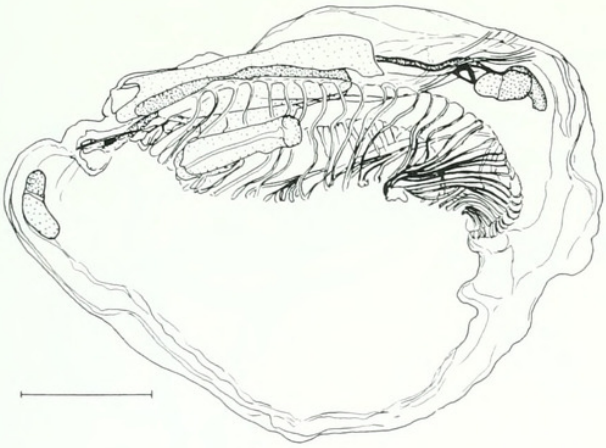

FIG. 24. *Dacrydium wareni.* Semidiagrammatic view from the left side of the internal morphology of a male specimen from Atlantis II sta. 73, North America Basin, 1330–1470 m. Scale = 0.5 mm. See Fig. 3 for the identification of parts.

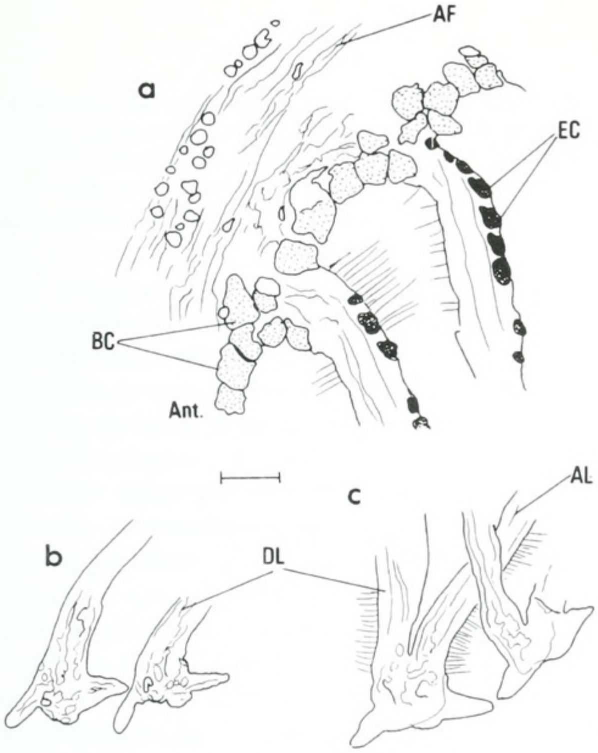

FIG. 25. *Dacrydium wareni.* Detail of (a) the distribution of gland cells at junction of the filaments of the inner demibranch with the gill axis; (b) ventral margin of two filaments of the outer demibranch and (c) of the inner demibranch. Scale = 50 μm. Refer to Materials & Methods for list of abbreviations.

opposite dorsal limit of hinge plate; dorsal and posterior margins forming a smooth curve; ventral margin almost straight or very slightly concave; hinge with short anterior plate with up to 8 teeth; posterior plate in two parts, that close to umbo is of similar length to anterior plate and with up to 8 teeth, narrow, edentulous posterior to this section, followed by elongate section with 16–34 nepioconch teeth (dependent on specimen size) similar to the posterior hinge plates of other species; relatively broad buttress extending from umbo to a point opposite highest point of shell; small ridge extending for short distance ventral to anterior hinge plate; internal ligament amphidetic, ventral to umbo; secondary external ligament, opisthodetic, slender, consisting of fused periostracum. Prodissoconch length: 121–130 μm.

Internal Morphology (Figs. 24, 25). The internal morphology is similar to that of *D. ockelmanni.* The adductor muscles are relatively small and similar in size. The anterior muscle is crescent-shaped in cross section, and the posterior adductor is oval. The gills have an inner demibranch comprising of descending and ascending lamellae and a short posterior outer demibranch comprising of a descending lamella. The size of the latter varies according to the length of the animal. In a specimen 2.4 mm total length, there are 16 closely arrayed filaments forming the outer demibranch. In the same specimen, there are 25 filaments in the inner demibranch, but these are much more widely separated than those of the outer demibranch. The latter occupies less than a fifth of the total gill area. The reflected ascending filament of the inner demibranch is approximately half the length of the descending. As in other species, at the tips of the filaments of the outer demibranch and at the point of reflection (ventral edge) of the inner demibranch, there are a pair of horn-like processes oriented along the horizontal axis and which bridge the interfilamentar gap. In addition, dorsally the gills are well supplied with gland cells (Fig. 25). These comprise 8–10 small eosinophilic cells on the outer posterior face of the filament close to where it joins the axis, and numerous large squamous basiphyllic cells lining the arch of axial tissue joining the filaments ventral to the axial muscle. The mouth is a particularly broad, shallow cone without palps on the lower lip and tiny palp rudiments on the upper lips, with traces of two or possibly three ridges. The viscera are similar to those of the previous species.

No mature specimens or specimens brooding eggs were present in the available samples.

Not mentioned by Salas & Gofas (1997) is the similarity in shell and hinge form to *D. vi-*

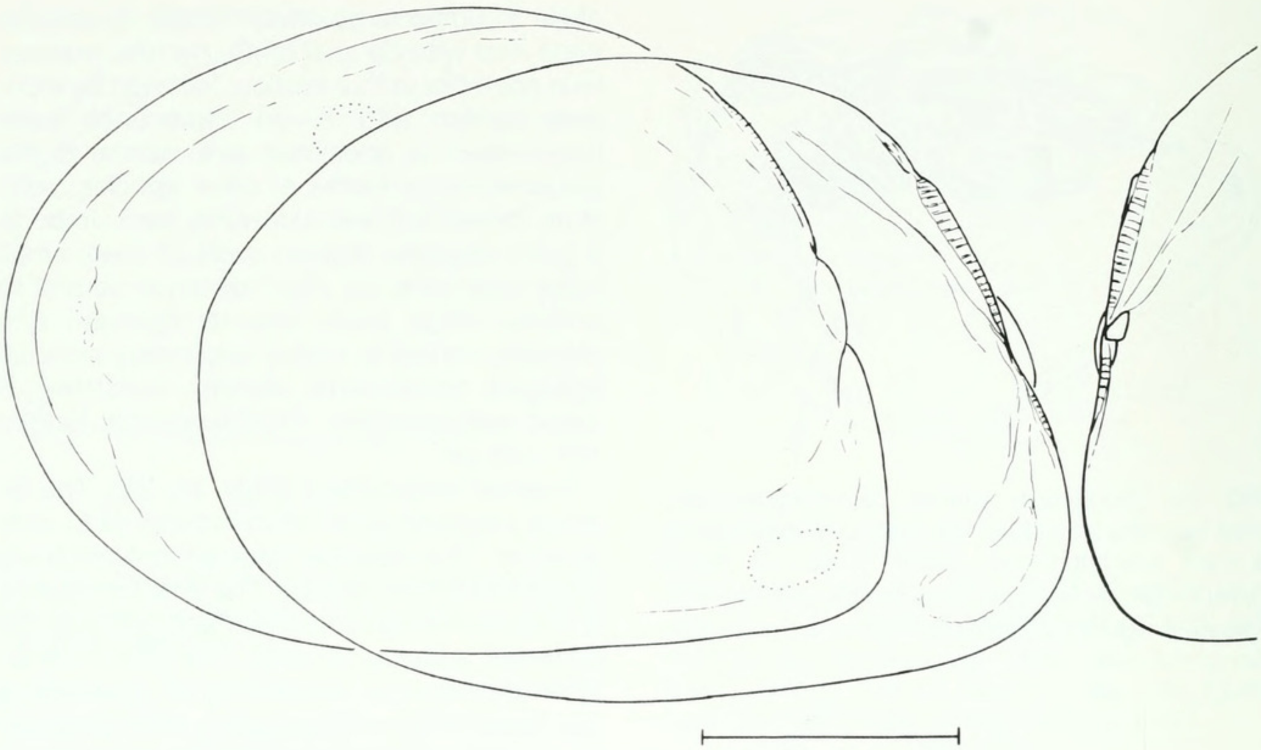

FIG. 26. *Dacrydium angulare.* Lateral view of a shell from the right side, an internal view of a left valve and detail of the hinge of a right valve from Atlantis II sta. 202, Angola Basin, 1427–1643 m. Scale = 0.5 mm.

viparum (Ockelmann, 1983) (Figs. 20–23). This might be within the range of variation to be expected within a species of *Dacrydium,* but, because of the great difference in size of the prodissoconch of specimens of *D. viviparum* described by Ockelmann (1983) (252–292 μm) and the lack of evidence of viviparity in the present specimens, the case for synonymy is doubtful. The Ockelmann material was taken from latitude 60°N–64N°, in comparison with 32°N–48°N for the present specimens, and it seems unlikely that there could be so much variation in egg size and development between northern and southern populations. Nevertheless, the prodissoconch length of *D. wareni* reported by Sales & Gofas (1997) is larger (approx. 170 μm) than that of the present specimens. This is the only difference in our respective descriptions.

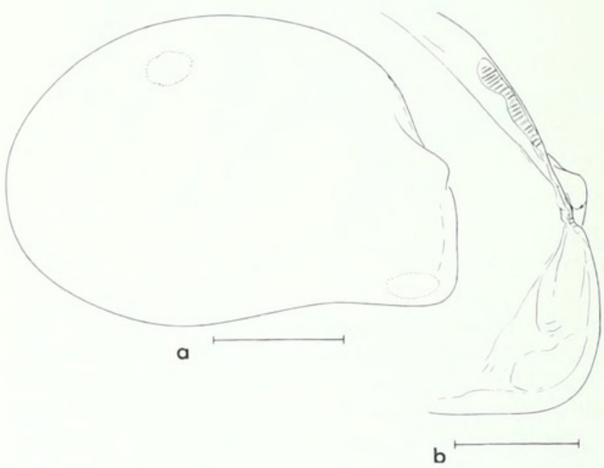

FIG. 27. *Dacrydium angulare.* Lateral view of shell from the right side and detail of the hinge of a left valve from J. Charcot Walda sta. DS13, Angola Basin, 3985 m. Scale a = 1 mm; scale b = 0.5 mm.

Dacrydium angulare Ockelmann, 1983
Figs. 26–28

Type Locality: Vema Sta. 54, Cape Basin, 34°35′S 17°31′E, 1849 m.

Type Material: Holotype and paratypes ZMUC; paratypes USNM 822398.

Original Description: Ockelmann 1983: 114, figs. 46–48, 51 (for other references, see Appendix 2).

Cited specimen: BMNH 1996147.

Material: Angola Basin: Walda, sta. DS13, 10 spec.; Atlantis II, sta. 202, 7 spec.

Distribution: This species occurs at lower slope to abyssal depths in the Cape Verde, Angola and Cape basins. Depth range 1427–3985 m.

Shell Description (Figs. 26, 27). Shell small (<4.0 mm), fragile, semi-transluscent, moderately elongate, greatest height coinciding with

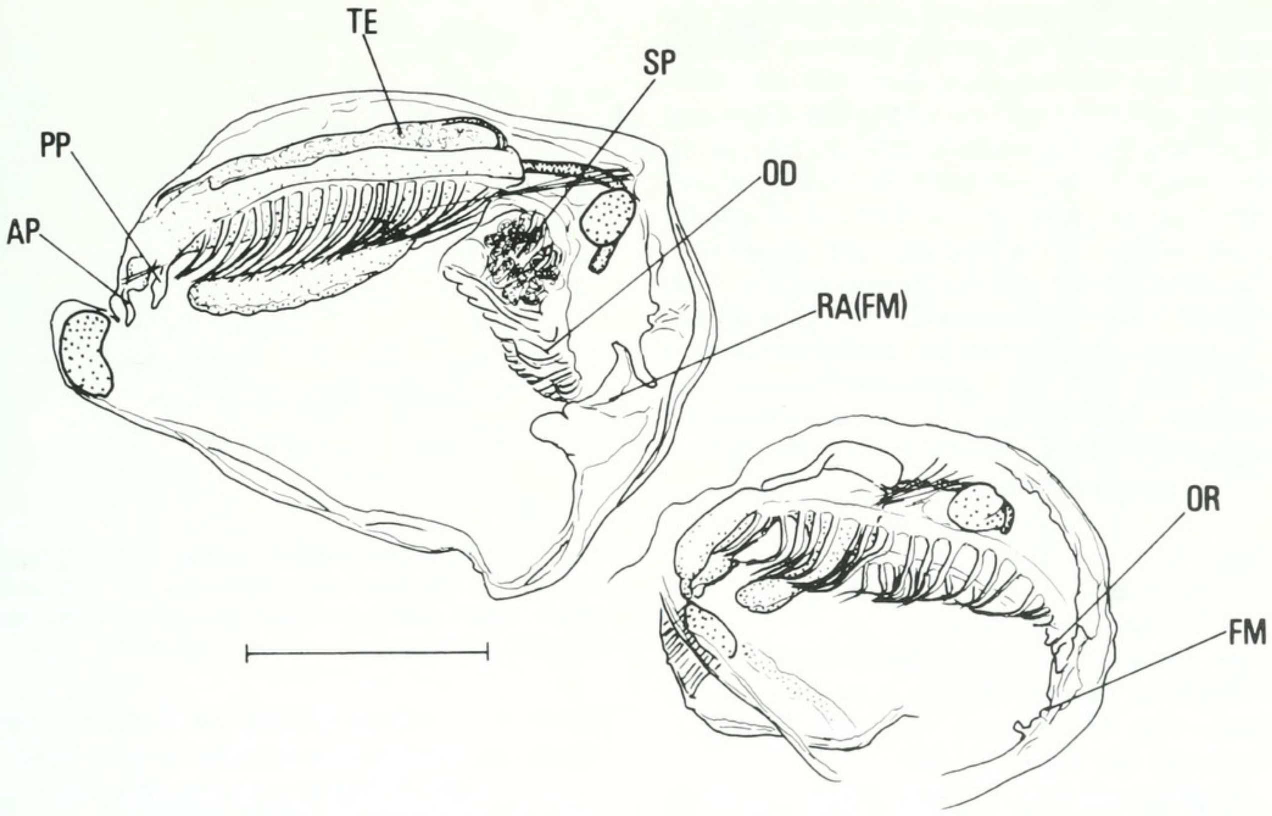

FIG. 28. *Dacrydium angulare*. Semidiagrammatic views from the left side of the internal morphology of a mature male and an immature specimen from J. Charcot Walda sta. DS13, Angola Basin. Scale = 1 mm. Refer to Materials & Methods for list of abbreviations and to Fig. 3 for identification of other parts.

the mid-vertical axis, extremely fine close concentric sculpture with faint growth lines; umbo moderately small, some distance from the antero-ventral limit of shell; ventral margin slightly sinuous in large specimens, otherwise broadly convex, joining posterior margin in smooth, deep curve; dorsal margin broadly convex, somewhat angulate at limit of posterior hinge plate; antero-dorsal margin slightly convex, high-angled in relation to ventral margin; anterior margin indented ventral to umbo particularly in large specimens, then slightly convex dorsal to antero-ventral margin; anterior hinge plate, narrow, short, with 3–7 indistinct nepioconch teeth, narrow edentulous subumbonal section joining relatively short posterior hinge plate, 20–28 nepiconch teeth; posterior buttress relatively broad, extending beyond dorsal limit of hinge plate to a point approximately twice the length of the posterior hinge plate; antero-ventral ridge short, extending to posterior limit of anterior adductor scar, less sharply deliniated than posterior buttress; ligament small, internal, amphidetic. Prodissoconch length: 159–165 μm (Ockelmann, 1983), 165–170 μm (Salas & Gofas, 1997), present specimens 170 μm.

The present specimens differ slightly from the excellent description given by Ockelmann (1983). The sinuous ventral shell margin of larger specimens is somewhat more pronounced than those described by Ockelmann (1983), but similar to those of Salas & Gofas (1997). The present specimens also have a more marked indentation ventral to the umbo and have a less extended anterior hinge plate with fewer teeth (see Ockelmann 1983: fig. 47). Such slight variation can be expected in specimens of differing size and from different basins.

Internal Morphology (Fig. 28). The internal morphology was described in detail by Ockelmann (1983), but, except for the oral field, not figured. Minor additions are given here. The adductor muscles are moderate and equal in size. Both inner and outer demibranchs are present in the largest specimens, and the filaments are relatively short. The first rudiments of the outer demibranch appear in specimens of approximately 2.0 mm length. The palps, although minute, are larger than other species examined. Ockelmann (1983) notes that "posterior fusion of the inner mantle folds large and muscular" and that "gills attach slightly below its upper border." He then further notes that the "inner mantle lobes surrounding the inhalent and pedal opening" are well developed. He clearly believes that the pedal and and inhalent openings are combined, although he has noted the thickened muscular development ventral to the gill attachment. It has been possible, in the present samples, to demonstrate that the posterior inner mantle fold enlarges as the outer demibranch develops and the gonads mature. One mature male was found with sperm packed in the space enclosed by the outer demibranch (Fig. 28), and this specimen showed the greatest development of the posterior inner mantle fold and a channel to the exterior.

Dacrydium hedleyi, new species
Figs. 29–31

Type Locality: Knorr Cruise 25 sta. 287, 13°16.0′N 54°52.2′W–13°16.8′N 54° 53.1′W, 4980–4934 m.

Type Material: Holotype BMNH 1996143.

Material: Guyana Basin: Knorr, sta. 287, 2 spec.; sta. 288, 9 spec.; sta. 291, 23 spec.; Biovema, sta. DS11, 2 spec.

Distribution: This species appears to be restricted to abyssal depths in the Guyana Basin. Depth range: 3859–5867 m.

Shell description (Figs. 29, 30). Shell small, fragile, modioloid, transluscent when fresh, turning opaque white on death or preservation, growth lines faint, without other ornamentation, greatest height anterior to mid-vertical axis; umbo relatively large, distant from the antero-ventral shell margin; ventral margin concave in smallest specimens, with slight antero-ventral sinuosity in larger specimens, joining posterior and postero-dorsal margins in a broad curve; postero-dorsal margin slightly angulate at posterior limit of hinge plate; anterior margin almost straight, angled to meet ventral margin in acute curve; antero-ventral margin less acute in larger specimens; hinge plates extremely narrow, barely wider than shell thickness; both anterior and posterior plates with 10–15 extremely fine nepioconch teeth; posterior and anterior buttresses faint, barely extending beyond the limits of the hinge plate; ligament small, internal, amphidetic, more or less globular, supported by two very small nymphs ventral to umbo. Prodissoconch length: 167 μm.

Internal Morphology (Fig. 31). The internal morphology differs little from any of the described species above. The adductor muscles are relatively small. The posterior inner mantle folds are fused in the manner described above. The gills comprise the descending lamella of the inner demibranchs. These comprise 12–13 widely spaced gill filaments, the distal half of which are typically angled anteriorly. No outer demibranchs were developed in any of the specimens in the collection.

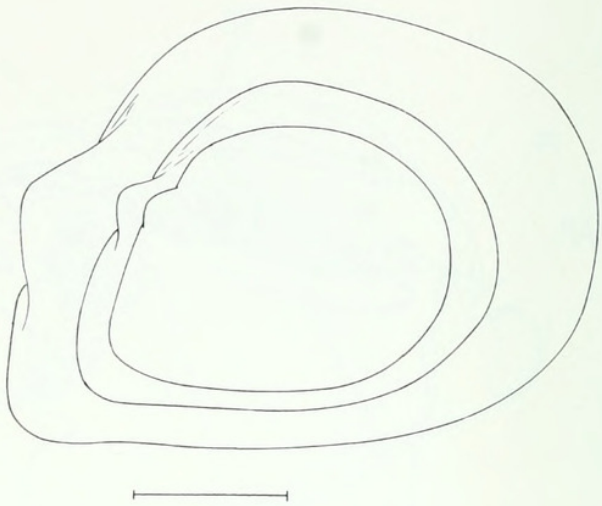

FIG. 29. *Dacrydium hedleyi.* Lateral views of three shells from left side from Knorr sta. 291, Guyana Basin, 3859–3868 m to show changes in shell outline with increasing size. Scale = 0.5 mm.

It is likely that the specimens are all juveniles. No maturing sperm or ova were seen.

The species is named after Dr. Charles Hedley who described Australiasian species of *Dacrydium.*

Diagnosis: This species is characterized by the slender hinge plates and that the greatest height measurement is anterior to the mid vertical shell axis. In shape, *D. hedleyi* resembles that of *D. nipponicum* (Okutani, 1975), but the ventral margin is less concave. The latter species also has stouter hinge plates and shell buttresses, and the adductor scars are much larger.

Dacrydium albidum Pelseneer, 1903
Figs. 32–34

Type Locality: S. Y. Belgica, Sta. 1046, 71°18′S 88°02′W, 400 m.

Type Material: IRSNB.

Cited Specimen: BMNH 1996145.

Material: Weddell Sea: IWSOE, sta. 001, 12 spec.; sta. 002, 3 spec.; sta. 004, 1 spec.; sta. 005, 1 spec.; sta. 007, 3 spec.; sta. 008, 2 spec.; sta. 010, 2 spec.

Distribution:Circum-Antarctic, occurring at outer shelf to mid-slope depths in the Ross, Davis and Weddall seas and off the South Shetland Islands (depth range: 122–1437 m).

Shell Description (Figs. 32, 33). The original description (Pelseneer 1903), although short, is accurate. The description was later extended by Nicol (1966).

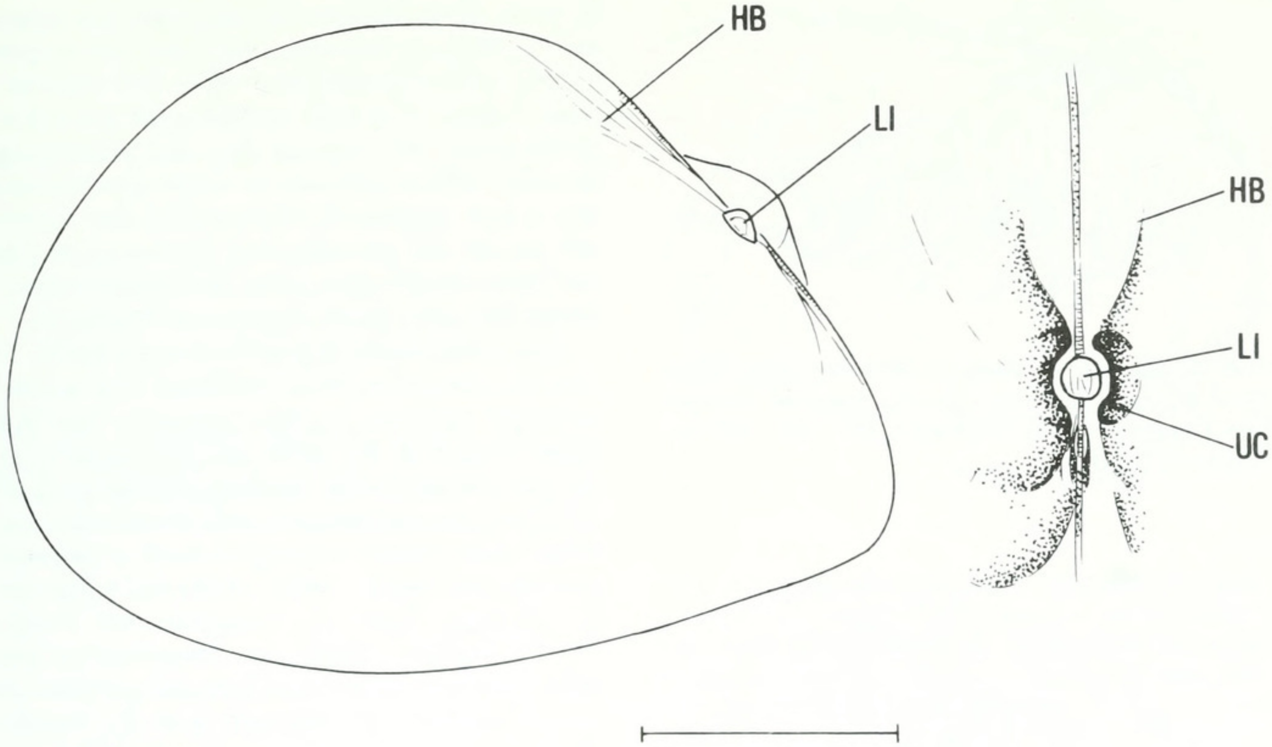

FIG. 30. *Dacrydium hedleyi.* Internal view of a left valve and internal view of an intact hinge and ligament of specimens from Knorr sta. 291, Guyana Basin, 3859–3868 m. Scale = 0.5 mm. Refer to Materials & Methods for list of abbreviations.

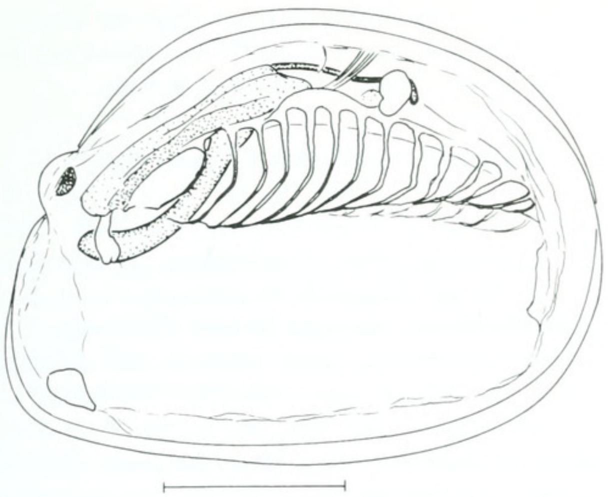

FIG. 31. *Dacrydium hedleyi.* Semidiagrammatic view of the internal morphology as seen through the transparent shell of a specimen from Knorr sta. 291, Guyana Basin, 3859–3868 m. Scale = 0.5 mm. See Fig. 3 for identification of parts.

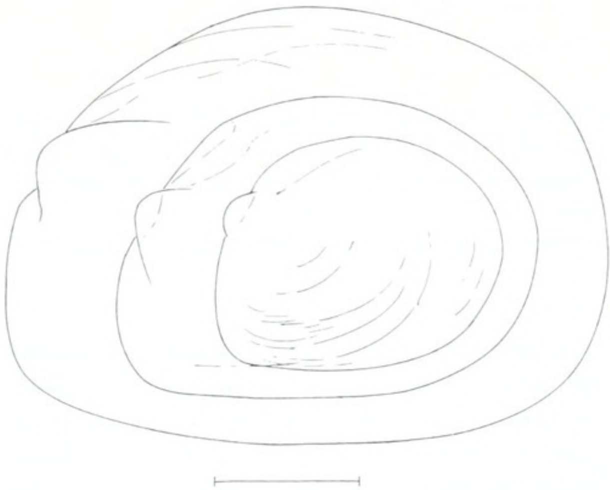

FIG. 32. *Dacrydium albidum.* Lateral views of three shells from the International Weddell Sea Oceanographic Expedition sta. 002, 412 m, to show differences in outline with increasing growth. Scale = 0.5 mm.

Shell small (<5 mm), fragile, greatest height varies from slightly anterior to mid-vertical axis to slightly posterior, opaque white or hyaline, with faint growth lines, periostracum very pale brown; umbo moderately large, relatively distant from antero-ventral limit of shell; ventral margin almost straight, in large specimens sometimes very slightly sinuous; posterior margin broadly rounded, joining postero-dorsal margin in a smooth curve; anterior margin ventral to umbo relatively elongate, convex, slightly incurved at umbo; antero-ventral margin smoothly rounded; anterior hinge plate short, slightly expanded internally, with 7–8

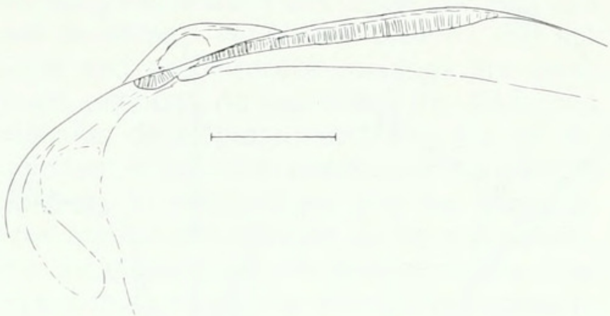

FIG. 33. *Dacrydium albidum.* Detail of hinge of right valve of a specimen from the International Weddell Sea Oceanographic Expedition sta. 001, 728 m. Scale = 0.5 mm.

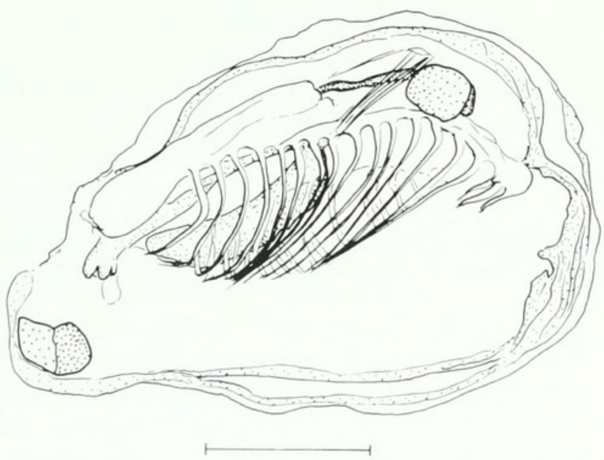

FIG. 34. *Dacrydium albidum.* Semidiagrammatic view from the left side of the internal morphology of a specimen from the International Weddell Sea Oceanographic Expedition sta. 004, 793 m. Scale = 0.5 mm. See Fig. 3 for identification of the parts.

nepioconch teeth; short edentulous section dorsal to ligament connecting with long posterior plate, terminating just short of the highest point of shell, with 50–55 nepioconch teeth; broad posterior buttress extending from ligament and slightly angled to hinge plate, terminating opposite highest point of shell; short, curved antero-ventral buttress terminating dorsal to anterior adductor muscle; ligament internal, ventral to umbo, amphidetic, elongate-oval. Prodissoconch length: 213 µm.

Nicol (1966) orientated the shell such that his dorsal margin equates with the anterior margin as described here and by others. He also overlooked the anterior nepioconch teeth.

Internal Morphology (Fig. 34). The internal morphology differs little from those described above. The adductor muscles are larger than in most other species. In addition, the outer palps, although still much reduced, are larger than in other species and have two well-defined ridges. The gills comprise of the inner demibranch, with descending and ascending lamellae and a rudiment of outer demibranch with a few unreflected filaments at the posterior end of the gill axis. In a specimen of 2.5 mm total length, the outer demibranch comprises two very short unreflected filaments.

Dell (1990) figure a specimen from the R. V. Eltanin collections from the Ross Sea which, although identical in other respects, has the highest point of the shell slightly posterior to the mid-vertical axis, and he refered to shell variation, though without definition, when he stated that "valves varying to such a degree" that he, like Nicol (1966), could not separate *D. albidum* from *D. modioliforme* Theile (1912). Poitiers (1989) also remarked on the confusion and refers to a bathyal complex of forms involving *D. albidum* and *D. modioliforme.*

The original description of *D. modioliforme* (Theile, 1912) does differ little from the description of *D. albidum,* and the type specimen came from a depth (385 m) within the range of the latter species. Specimens identified as *D. modioliforme* from abyssal depths (e.g., Theile & Jaeckel, 1931) do differ from *D. albidum* (Knudsen, 1970) (see below).

Dacrydium knudseni, new species

Figs. 35–37

Type Locality: International Weddell Sea Oceanographic Expedition sta. 023, 72°47.6′S 30°29.7′W, 3697 m.

Type Material: Holotype BMNH 1996142.

Material:Weddell Sea: IWSOE, sta. 022, 3 spec.; sta. 023, 6 spec.; sta. 027, 10 spec.

Distribution: This species is distributed at abyssal depths in the Weddell Sea. Depth range: 3111–4636 m.

Shell Description (Figs. 35, 36). Shell small, fragile, relatively short, maximum height more or less coincident with mid-vertical axis, opaque white, with fine concentric growth lines; umbo moderately large, distant from antero-ventral limit of shell; ventral margin a shallow convex curve in small specimens, straight and sometimes faintly concave in larger specimens; postero-ventral and posterior margins forming a smooth, broad curve; postero-dorsal margin slightly flattened in most specimens; anterior margin slightly indented ventral to umbo, forming a relatively long convex curve, making a characteristic

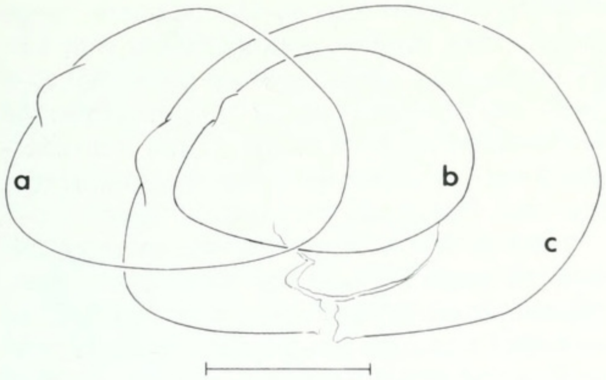

FIG. 35. *Dacrydium knudseni*. Lateral views of three shells from the International Weddell Sea Oceanographic Expedition sta. (a) 022, 3111 m; (b & c) 023, 3697 m, to show variation in outline. Scale = 1 mm.

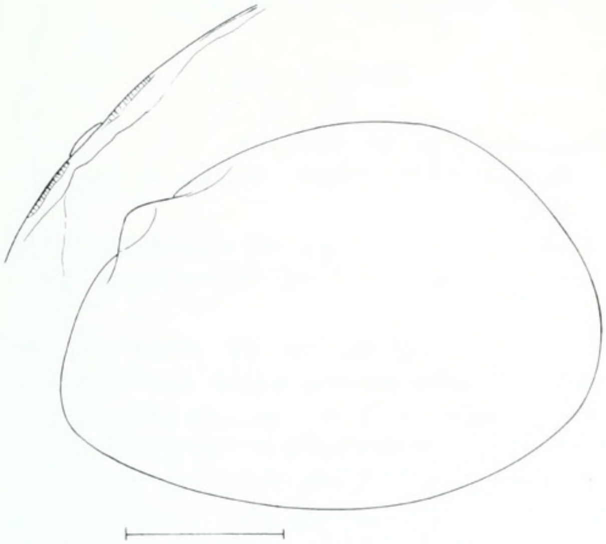

FIG. 36. *Dacrydium knudseni*. Lateral view of a shell from the left side and detail of the hinge of a right valve. Specimens taken by the International Weddell Sea Oceanographic Expedition sta. 023, 3697 m. Scale = 0.5 mm.

acutely rounded antero-ventral shell margin; anterior and posterior hinge plates narrow, each with 15–17 nepioconch teeth, moderately long, narrow edentulous section ventral to umbo joining the toothed parts; posterior hinge plate short; posterior buttress moderately narrow, extending from anterior limit of posterior hinge plate to a short distance posterior to the posterior plate buttress, continuing ventral to umbo and accommodating the resilifer; ligament ventral to umbo, amphidetic, oval. Prodissoconch length: 195 μm.

Internal morphology (Fig. 37). The internal morphology is similar to that of *D. albidum*. Differences include smaller adductor muscles, gills that comprise only the descending

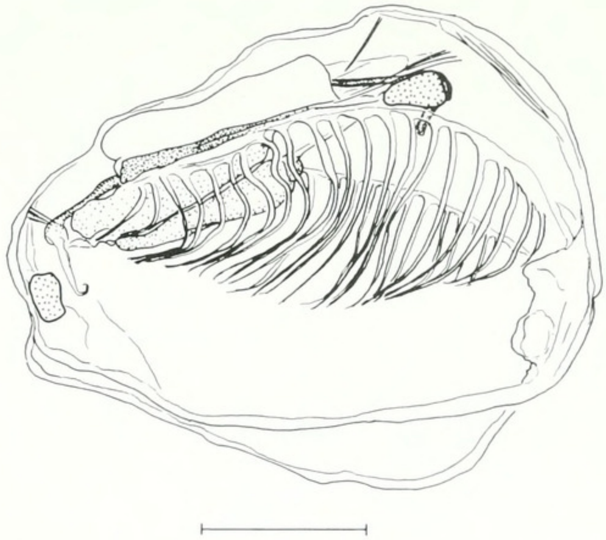

FIG. 37. *Dacrydium knudseni*. Semidiagrammatic view of the internal morphology of a specimen from the International Weddell Sea Oceanographic Expedition sta. 027, 4575 m. Scale = 0.5 mm. See Fig. 3 for the identification of parts.

lamellae of the inner demibranchs and no outer demibranchs. The dorsal lip is characteristically elongate and with a minute palp rudiment.

Dacrydium knudseni is named after Dr. Jørgen Knudsen, distinguished deep-sea malacologist who first recognized that there was a clear difference between the deep-water Antarctic specimen collected by the R. V. Valdivia and the more shallow water species *D. albidum*.

Diagnosis: *Dacrydium knudseni* is characterized by an acutely angled antero-ventral shell margin and approximately equal numbers of nepioconch teeth on the anterior and posterior hinge plates. It most closely resembles *D. panamensis* Knudsen, 1970, the latter differing in having a more foreshortened antero-ventral shell margin, a shorter anterior hinge plate with fewer teeth, a shorter edentulous section, and a more extensive inner buttress.

Dacrydium sp. a

Figs. 38, 39

Specimen: MNHNP

Material: Cape Basin: Walvis, sta. DS05, 2 spec.

Distribution: These are juveniles of an abyssal species that has only been recorded from one locality at abyssal depth (4560 m) immediately south of the south west extremity of the Walvis Ridge.

Shell Description (Figs. 38, 39). Shell tiny,

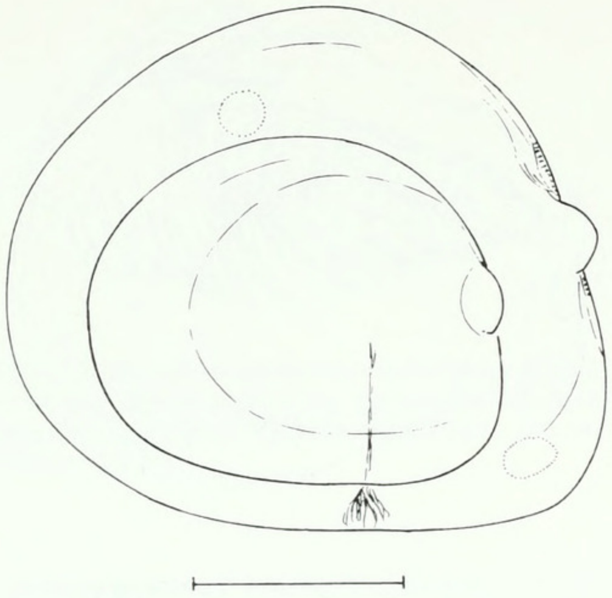

FIG. 38. *Dacrydium* sp. a. Lateral views of two shells from the left side from J. Charcot Walvis Expedition sta. DS05, Cape Basin, 4560 m. Scale = 0.5 mm.

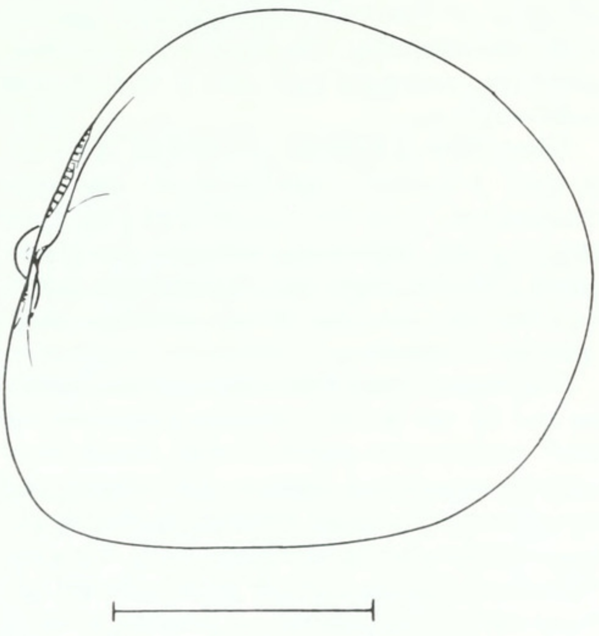

FIG. 39. *Dacrydium* sp. a. Internal view of a right valve from J. Charcot Walvis Expedition sta. DS05, Cape Basin, 4560 m. Scale = 0.5 mm.

broadly ovate, semitranslucent, with a few faint growth lines; greatest shell height very slightly anterior to the mid-vertical axis, only slightly longer than high; umbo moderately large, prominent, distant from the antero-ventral margin; ventral margin almost straight, at most slightly convex; posterior and dorsal margins broadly rounded; anterior margin in hinge region almost straight, antero-ventrally meeting ventral margin in a broad curve; hinge plates short, narrow; posterior plate with 12–14 nepioconch teeth; anterior plate with 2–4 teeth; plates reinforced by narrow buttresses that parallel the shell margin rather than deviating from it; ligament internal, amphidetic, rounded. Prodissoconch length 185 μm.

Internal Morphology. The internal morphology, as seen through the transparent shell, appears to be similar to that of *D. hedleyi*. The adductor muscles are moderately large, and only the inner demibranch is present. The foot is particularly slender and secretes a byssus composed of many extremely fine strands.

Although the shell shape with its great height is so distinctive, because only two tiny, fragile, juvenile specimens (1 mm and 1.5 mm total length) were taken, it was decided not to name a new species at this stage.

Dacrydium sp. b
Fig. 40

Specimen: BMNH 1996148.

Material: Brazil Basin: Atlantis II, sta. 167, 20 spec.

Distribution: This species was taken at one mid-slope station in the Brazil Basin, 943–1007 m.

Shell Description (Fig. 40). Shell, tiny, extremely fragile, broadly ovate, with very fine, close, concentric lines, opaque white, greatest height coincident with or slightly anterior to mid-vertical axis; umbo relatively large, distant from antero-ventral shell margin; ventral shell margin straight or slightly convex; posterior margin broad, rounded, joining dorsal margin in a smooth curve; antero-dorsal margin angulate at limit of posterior hinge plate; anterior margin straight, almost vertical to rounded antero-ventral margin; ventral margin varies from slightly convex in smallest specimens, through straight, to slightly concave in largest specimens; hinge plates relatively short, narrow; posterior plate with 15–16 nepioconch teeth; anterior plate slightly shorter with 9–10 teeth; posterior shell buttress, narrow, not extending far beyond limit of hinge faint anterior buttress extending short distance towards anterior adductor; ligament internal, amphidetic, relatively large, globular. Prodissoconch length: 122–129 μm.

Internal Morphology (Fig. 40). The internal morphology is similar to that of the preceeding species. The adductor muscles are small and round, the anterior somewhat smaller than the posterior. Mantle fusion is similar to that in other species but little thickened, suggesting

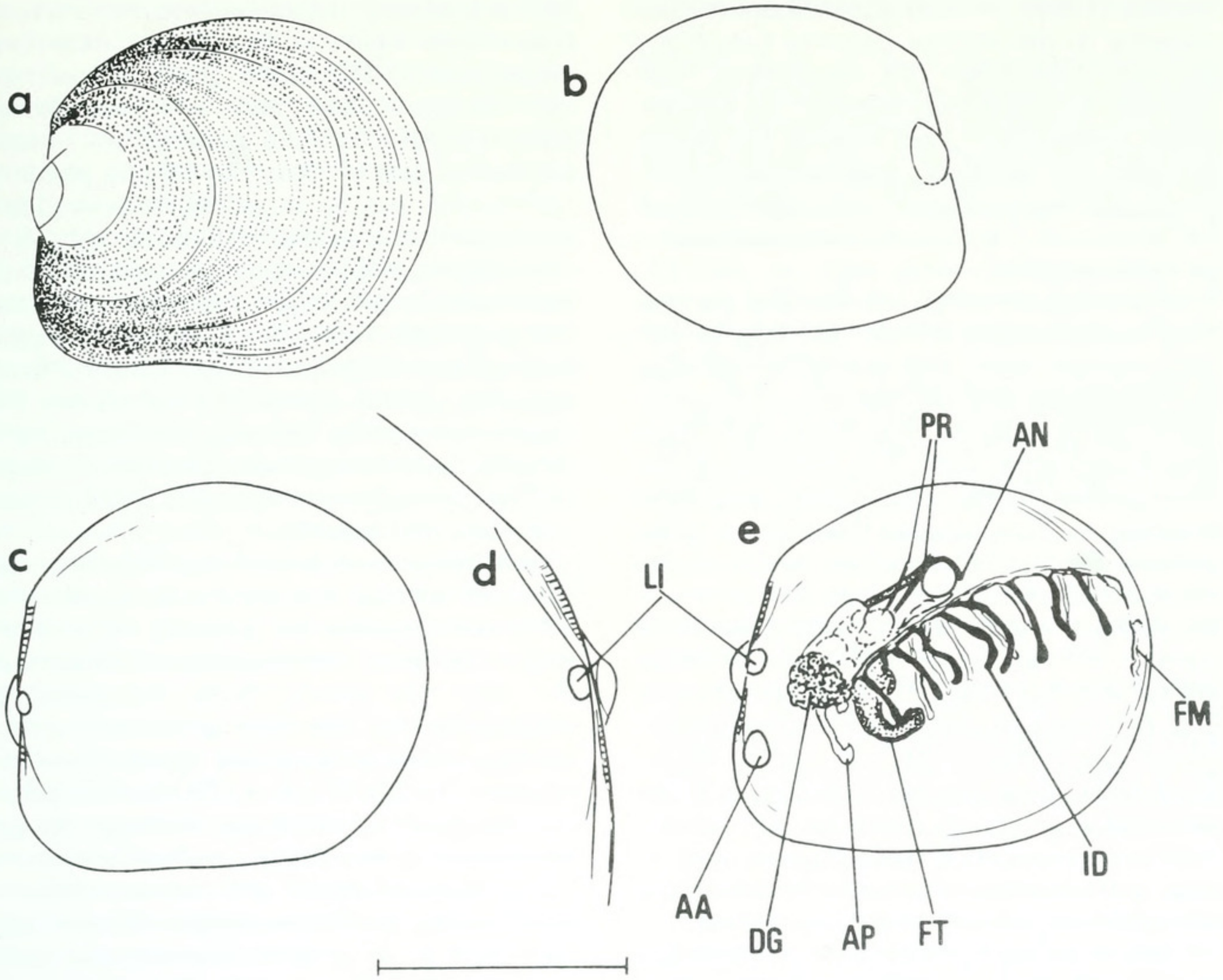

FIG. 40. *Dacrydium* sp. b. Lateral view of (a) shell from the right side; (b) outline of shell from left side; (c) internal view of right valve; (d) detail of hinge of left valve; (e) semidiagrammatic view of the internal morphology as seen through a transparent shell from the left side. Specimens from Atlantis II sta. 167, Brazil Basin, 943–1007 m. Scale = 1 mm a, b, c and e; = 0.5 mm d. Refer to Materials & Methods for list of abbreviations.

that these are juvenile specimens. There is no outer demibranch, and the inner demibranchs consists of 10–12 unreflected descending filaments in a specimen of 1.7 mm total length. Unlike other species, in which the foot extends anteriorly within the canopy of the gill filaments, here the foot is recurved so that the tip is facing posteriorly, but this is is likely to be an artifact of preservation. The palps are small, distal enlargements of the lips, the upper of which are extended. The course of the gut is similar to that of other species, but the digestive diverticula comprise of a pair of sacs lateral to the stomach. In this, they resemble the post-larval gut of other bivalves.

The internal features all suggest that these specimens are the juveniles of a larger species rather than neotenous adults of a miniature species. In addition, the shell shape is reminiscent of the nepioconch stage in mytilid development. It is for these reasons, and the fact that the shells of all but two or three of the specimens have disintegrated, that this species is not named, even though it has characters unlike those any other described species.

DISCUSSION

The species of the genus *Dacrydium* are present throughout the world's oceans and, for the most part, in deep waters (>500 m). They are anchored by a fine tuft of byssus threads and may form nesting congregations incorporating fine sediment, without the shell fragments and sediment particles that form the nests of *Lima hians,* as described by

Gilmour (1967). In many cases, there is clear evidence in the form of attached tissue and spicules that they are associated with sponges. It is not known whether this is a universal association. Other mytilids are known to occur with sponges, tunicates and, even, skulls of whales, although not necessarily all the species of a genus are associated with a particular phylum.

All species are small (<6 mm and the majority approximately 3 mm) and fragile, with unpigmented shells that are either transluscent or opaque and with little or no ornamentation. Some species may have faint radial and/or concentric lines. The species can be distinguished by the shell outline and hinge morphology. This includes the position of the greatest height of the shell in relation to the mid-vertical axis of the shell, the extent of the anterior and posterior hinge plates, the number of nepioconch teeth on the hinge plates, and the degree of development of a shell buttress associated with the hinge plate. Ockelmann (1983) points out that the dacrydines have shells that are homologous to the nepioconch stage of other mytilids, sometimes with provincular teeth present, and always with a series of anterior and posterior teeth homologous with nepioconch teeth.

There is a degree of variation in the shape of the shell outline and hinge features in all species, and this has been noted by other authors (e.g., Nicol, 1966; Poitiers, 1989). This involves variation irrespective and respective of size. The curvature of the ventral margin changes with growth, becoming straighter or more concave or more sinuous. In addition, the position of maximum shell height tends to shift posteriorly with growth.

The internal morphology displays a number of features characteristic of the genus. While the adductor muscles vary in size and, as in the case of other mytilids, the anterior may be smaller than the posterior, the latter is always relatively well-developed. The posterior adductor muscle is not excessively enlarged. There must be a balance between the size and strength of the muscle and the strength of such a thin, fragile, shell. It is clear that the buttresses play a part in the balance of adductor forces and shell strength. The mantle margins are specialized in only one respect, namely the development of an aperture coincident with gonad maturity. It is homologous with the inhalent aperture of other lamellibranchs. It would appear that it develops as a channel for the release of sexual products and is probably not concerned with the inhalent flow, which is through the extensive pedal gape. The "inhalent" aperture is formed from the inner mantle folds, which are developed inwards. There no development of tentacles or papillae from the middle sensory mantle fold, and the structure has never been seen extended beyond the shell margins. It is more developed in the larger specimens of each species and only in specimens with maturing gonads has a lumen to the exterior been clearly identified. Prior to discharge, the eggs and sperm appear to be shed into the space enclosed by the outer demibranchs of species that develop them. Like the aperture, the full development of the outer demibranchs coincides with maturity.

The gills are unusual. In the juveniles, and in some species the mature adult, only the inner demibranchs are present. Species in which the outer demibranchs are absent in the adult are among those that occur at abyssal depths. The inner demibranchs consist of a relatively few widely spaced filaments (approx. 10–20). There are no interlamellar or interfilamentar connectives. Although the gill filaments in a few of the smallest specimens hang vertically within the mantle cavity, in most others the filaments are characteristically bent in an anterior direction at a point half way along their length. The outer demibranchs develop from gill rudiments at the posterior limit of the axes. The outer demibranchs at maximum extend anteriorly to about a third of the axial length. Their filaments are more closely set together and are not bent forward. It is hypothesized that the aperture and, when present, the outer demibranch combine to form a reproductive mechanism that canalizes the movement of eggs and sperm to ensure successful fertilization and the release of eggs or larvae. Sexes are separate. Although Ockelmann (1983) and Salas & Gofas (1997) showed that in *D. viviparum, D. hyalinum* and *D. balgimi* the eggs are incubated in the suprabranchial chamber, none of the species described here had embryos developing within the mantle cavity. Egg and prodissoconch size varies considerably among species, but it appears in general that those of abyssal and high latitude species are significantly larger than those of bathyal or shelf species in lower latitudes.

Other features characteristic of the genus include the dorsal position of the viscera. The oesophagus, stomach and combined style sac, and midgut are elongate and lie parallel to the antero-posterior axis close to the shell buttress. Similarly, the foot is elongate and tubular and in the contracted state also lies parallel with this axis within the space enclosed by the inner demibranchs. The shell buttress provides the attachment surface for the pedal retractors.

Another unusual feature involves the palps and lips. The palps are extremely small, with no more than the rudiments of two small ridges being present. However, the upper lips tend to be elongate and attached vertically to the mantle such that they form a collecting area immediately ventral to the mouth, at the point where food particles from the filaments accumulate. The ventral margin of the filaments of the inner demibranch, which is construed as the main food collector, are laterally extended so that the lateral cilia interlock with those of the adjacent filaments. It is likely that there is little sorting of food particles on gills and palps.

The combination of these features gives a unique functional design, which fully supports Ockelmann (1983) in his decision to erect a new subfamily. Ockelmann (1983) argues that the dacrydines are probably derived from the crenellines rather than the modiolines as suggested by Soot-Ryen (1969), and the present study supports this view.

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APPENDIX 1.
Stations from which material was collected

Cruise	Station	Depth (m)	Latitude	Longitude	Date	Gear
			NEWFOUNDLAND BASIN			
Chain 106	331	4793	41°13.0′N	41°36.7′W	29.8.72	ES
			NORTH AMERICA BASIN			
Atlantis 277	D	466–508	39°54.5′N	70°35.0′W	23.5.62	AD
Atlantis II 12	62	2496	39°26.0′N	70°33.0′W	21.8.64	ES
	64	2886	38°46.0′N	70°06.0′W	21.8.64	ES
	66	2802	38°46.7′N	70°08.8′W	21.8.64	ES
	70	4680	36°23.0′N	67°58.0′W	23.8.64	ES
	72	2864	38°16.0′N	71°14.0′W	24.8.64	ES
	73	1330–1470	39°46.5′N	70°43.3′W	25.8.64	ES
Atlantis II 17	93	4926–5007	34°39.0′N	66°26.0′W	14.12.65	ES
Chain 50	76	2862	39°38.3′N	67°57.8′W	29.6.65	ES
	80	4970	34°49.8′N	66°34.0′W	2.7.65	ES
	83	5000	34°46.5′N	66°30.0′W	3.7.65	ES
	84	4749	36°24.4′N	67°56.0′W	4.7.65	ES
	85	3834	37°59.2′N	69°26.2′W	5.7.65	ES
Chain 50	87	110	39°48.7′N	70°40.8′W	6.7.65	ES
	88	478	39°54.1′N	70°37.0′W	6.7.65	ES
Chain 58	103	2022	39°43.6′N	70°37.4′W	4.5.66	ES
	105	530	39°56.6′N	71°03.6′W	5.5.66	ES
Atlantis II 24	115	2030–2050	39°39.2′N	70°24.5′W	18.8.66	ES
	118	1135–1153	32°19.4′N	64°34.9′W	18.8.66	ES
	119	2095–2223	34°15.8′N 32°16.1′N	64°31.6′W- 64°32.6′W	19.8.66	ES
Atlantis II 30	128	1254	39°46.5′N	70°45.2′W	16.12.66	ES
Chain 88	210	2024–2064	39°43.0′N 39°43.2′N	70°46.0′W- 70°49.5′W	22.2.69	ES
Knorr 35	346	475	39°54.1′N	70°10.7′W	3.12.73	ES
			GUYANA BASIN			
Knorr 25	287	4980–4934	13°16.0′N 13°16.8′N	54°52.2′W- 54°53.1′W	24.2.72	ES
	288	4417–4429	11°02.2′N 11°03.8′N	55°05.5′W- 55°04.8′W	25.2.72	ES
	291	3859–3868	10°06.6′N	55°15.4′W	26.2.72	ES
	306	3392–5073	09°31.1′N	56°24.4′W	2.3.72	ES
J. Charcot	CP02	5073	10°59.0′N	45°15.0′W	14.11.77	CP
Biovema	DS05	5100	10°46.0′N	42°40.3′W	18.11.77	ES
(Vema)	DS11	5867	11°37.5′N 11°37.6′N	32°53.8′W- 32°52.8′W	26.11.77	ES

			BRAZIL BASIN			
Atlantis II 31	142	1624–1796	10°30.0′N	17°51.5′W	5.2.67	ES
	144	2051–2357	10°36.0′N	17°49.0′W	6.2.67	ES
	147	2934	10°38.0′N	17°52.0′W	6.2.67	ES
	155	3730–3783	00°03.0′S	27°48.0′W	13.2.67	ES
	156	3459	00°46.0′S	29°28.0′W	14.2.67	ES
	167	943–1007	07°58.0′S	34°17.0′W	20.2.67	ES
	169	587	08°38.0′S	34°23.0′W	21.2.67	ES
			ARGENTINE BASIN			
Atlantis II 60	239	1661–1669	36°49.0′S	53°15.4′W	11.3.71	ES
	240	2195–2323	36°53.4′S	53°10.2′W	12.3.71	ES
	245	2707	36°55.7′S	53°01.4′W	14.3.71	ES
			WEST EUROPEAN BASIN			
Sarsia	S33/2	1537–183	43°41.0′N	03°36.0′W	13.7.67	ES
	S44	1739	43°40.8′N	03°35.2′W	16.7.67	ES
	S50	1102	43°46.7′N	03°38.0′W	18.7.67	ES
	S61	952	46°20.5′N	04°36.0′W	24.7.67	ES
	S63	1336	46°17.5′N	04°45.2′W	24.7.67	ES
	S66	1472	40°16.3′N	04°44.0′W	25.7.67	ES
Discovery	7601	3100	43°51.8′N	03°43.4′W	4.9.76	AD
Challenger E	80–73	900–2300	'off Rockall'		-.-.73	ES
Chain 106	313	1491–1500	51°32.2′N	12°35.9′W	17.8.72	ES
	318	2560	50°27.3′N	13°20.9′W	19.8.72	ES
	321	2868–2890	50°12.3′N	13°35.8′W	20.8.72	ES
J. Charcot Biacores	245	4270	40°57.0′N	22°16.0′W	14.11.71	CLG
La Perle Biogas I	DS11	2205	47°35.5′N	08°33.7′W	8.8.72	ES
J. Charcot Polygas	DS15	2246	47°35.2′N	08°40.1′W	21.10.72	ES
	DS17	2103	47°32.0′N	08°45.5′W	22.10.72	ES
	DS18	2138	47°32.2′N	08°′N.9′W	22.10.72	ES
	DS20	4226	47°33.0′N	09°36.7′ W	24.10.72	ES
	DS21	4190	47°31.5′N	09°40.7′W	24.10.72	ES
	CV13	4252	47°31.8′N	09°34.2′W	25.10.72	CV
	DS22	4144	47°34.1′N	09°38.4′W	25.10.72	ES
	DS23	4734	46°32.8′N	10°21.0′W	26.10.72	ES
	DS25	2096	44°08.2′N	04°15.7′W	1.11.72	ES
	DS26	2076	44°08.2′N	04°15.0′W	1.11.72	ES
	DS31	2813	47°32.5′N	09°04.2′W	19.4.73	ES
Biogas II	DS32	2138	47°32.2′N	08°05.3′W	19.4.73	ES
Biogas III	DS36	2147	47°32.7′N	08°36.5′W	24.8.73	ES
	DS37	2110	47°31.8′N	08°34.6′W	25.8.73	ES
	DS38	2138	47°32.5′N	08°35.8′W	25.8.73	ES
	DS41	3548	47°28.3′N	09°07.2′W	26.8.73	ES
	DS42	4104	47°32.′N4	09°35.6′W	27.8.73	ES
	DS44	3992	47°33.2′N	09°42.0′W	27.8.73	ES
	DS45	4260	47°33.9′N	09°38.4′W	27.8.73	ES
	DS46	4521	46°28.6′N	10°23.0′W	29.8.74	ES
	DS48	4203	44°29.0′N	04°54.0′W	31.8.73	ES
	DS50	2124	44°08.9′N	04°15.9′W	1.9.73	ES
J. Charcot	DS51	2430	44°11.3′N	04°15.4′W	18.2.74	ES
Biogas IV	DS52	2006	44°06.3′N	04°22.4′W	18.2.74	ES
	DS54	4659	46°31.3′N	10°29.2′W	21.2.74	ES
	DS55	4125	47°34.9′N	09°40.9′W	22.2.74	ES
	KR31	4097	47°37.0′N	09°41.′W6	22.2.74	ES
	DS56	4050	47°32.7′N	09°28.2′W	23.2.74	ES
	DS58	2775	47°34.1′N	09°08.2′W	23.2.74	ES
	DS59	2790	47°31.7′N	09°06.2′W	24.2.74	ES
	DS61	2250	47°34.7′N	08°38.8′W	25.2.74	ES
	CP01	2245	47°34.6′N	08°38.8′W	25.2.74	ES
	DS62	2175	47°32.8′N	08°40.0′W	26.2.74	ES
	DS63	2126	47°32.8′N	08°35.0′W	26.2.74	ES

	DS64	2156	47°29.2′N	08°30.7′W	26.2.74	ES
Biogas V	CP07	2170	′N°09.8′N	04°16.4′W	21.6.74	ES
	DS67	4150	47°31.0′N	09°35.0′W	17.6.74	ES
	DS68	4550	46°26.7′N	10°23.9′W	19.6.74	ES
	DS69	4510	′N°21.9′N	04°52.4′W	20.6.74	ES
Biogas VI	CP08	2177	′N°33.2′N	08°38.5′W	20.10.74	CP
	CP09	2171	47°33.0′N	08°′N.1′W	20.10.74	CP
	DS71	2194	47°34.3′N	08°33.8′W	20.10.74	ES
	DS75	3250	47°28.1′N	09°07.8′W	22.10.74	ES
	DS76	4228	47°34.8′N	09°33.3′W	23.10.74	ES
	CP13	4134	47°34.4′N	09°38.0′W	23.10.74	CP
	CP14	4237	47°32.0′N	09°35.9′W	23.10.74	CP
	KR60	4220	47°32.3′N	09°37.2′W	24.10.74	KR
	KR64	4700	46°30.8′N	10°20.8′W	24.10.74	KR
	DS74	2777	47°33.0′N	09°07.8′W	21.10.74	ES
	DS77	4240	47°31.8′N	09°34.6′W	24.10.74	ES
	DS78	4706	46°31.2′N	10°23.8′W	25.10.74	ES
	CP16	4825	46°27.6′N	10°26.8′W	25.10.74	CP
	DS79	4715	46°30.4′N	10°27.1′W	26.10.74	ES
	CP17	4706	46°30.8′N	10°19.5′W	26.10.74	CP
	CP18	4721	46°30.0′N	10°26.0′W	26.10.74	CP
	DS80	4720	46°29.5′N	10°29.5′W	27.10.74	ES
	DS81	4715	46°28.3′N	10°24.6′W	27.10.74	ES
	CP21	4453	44°21.2′N	04°49.3′W	30.10.74	CP
	DS86	1950	44°04.8′N	04°18.7′W	31.10.74	ES
	CP23	1980	44°04.6′N	04°21.4′W	31.10.74	CP
	DS87	1913	44°05.2′N	04°19.4′W	1.11.74	ES
	CV38	2690	47°30.9′N	08°59.5′W	24.2.74	CV
Thalassa	Z397	511	47°33.8′N	07°12.′W6	22.10.73	GBO
	Z400	1175	47°33.4′N	07°18.1′ W	22.10.73	GBS
	Z413	805	48°03.1′N	08°29.4′W	24.10.73	PBS
	Z417	865	48°12.0′N	09°09.5′W	24.10.73	PBS
	Z427	330	48°27.0′N	09°48.4′W	25.10.73	PBS
	Z435	1050	48°39.7′N	09°53.2′W	26.10.73	PBS
	Z447	1430–1530	48°47.3′N	11°12.0′W-	27.10.73	CP
			48°47.4′N	11°14.3′W		
Incal	DS01	2091	57°59.7′N	10°39.8′W	15.7.76	ES
	CP01	2041	57 57.7′N	10 55.0′W	16.7.76	CP
	DS02	2081	57°58.8′N	10°48.5′W	16.7.76	ES
	CP08	2644	50°14.7′N	13°13.5′W	27.7.76	CP
	CP10	4823	48°25.5′N	15°10.7′W	31.7.76	CP
	DS11	4823	48°18.6′N	15°12.0′W	1.8.76	ES
	CP11	4823	48°20.4′N	15°14.6′W	1.8.76	CP
	WS02	4829	48°19.2′N	15°23.3′W	1.8.76	WS
	OS03	4829	48°19.2′N	15°15.9′W	2.8.76	OS
	OS05	4296	47°31.3′N	09°34.6′W	7.8.76	OS
	KR14	4299	47°29.8′N	09°37.4′W	7.8.76	KR
	WS07	4281	47°30.6′N	09°37.1′W	7.8.76	WS
	DS14	4254	47°32.6′N	09°35.7′W	7.8.76	ES
	DS15	4211	47°33.4′N	09°39.1′W	8.8.76	ES
	DS16	4268	47°29.8′N	09°36.2 ′W	9.8.76	ES
	WS08	4287	47°30.5′N	09°33.7′W	9.8.76	WS
	OS06	4316	46°27.3′N	09°36.2′W	9.8.76	OS
	OS07	4249	47°31.8′N	09°34.3′W	10.8.76	OS
	WS09	4277	47°28.8′N	39°34.0′W	10.8.76	WS
	WS10	4354	47°27.3′N	09°39.9′W	11.8.76	WS
	OS08	4327	47°29.8′N	09°39.2′W	11.8.76	OS
			CANARY BASIN			
Discovery	6696	1564	27°57.0′N	13°36.2′W	15.3.68	ES
	6701	1934	27°45.2′N	14°13.0′W	16.3.68	ES
	6704	2129	27°44.9′N	14°25.0′W	17.3.68	ES

			AZORES MID-ATLANTIC RIDGE			
J. Charcot Bioacores	105	1675	39°35.0′ N	31°23.0′W	20.10.71	DP
	120	2100	39°03.5′N	32°43.5′W	22.10.71	ES
	126	3360	39°19.5′N	33°47.0′W	23.10.71	ES
			SIERRA LEONE BASIN			
Atlantis II	148	3828	10°37.0′N	18°14.0′W	7.2.67	ES
	149	3861	10°30.0′N	18°18.0′W	7.2.67	ES
			ANGOLA BASIN			
J. Charcot Walda	DS13	3985	14°21.5′S	09°46.2′E	? 8.71	ES
Atlantis II42	202	1427–1643 1643	08°56.0′S 08°46.0′S	12°15.0′E- 12°47.0′E	23.5.68	ES
			CAPE BASIN			
J. Charcot Walvis	DS02	5280	33°54.7′S	05°08.3′E	26.12.78	ES
	KG14	4610	33°20.9′S	02°38.0′E	29.12.78	KG
	DS05	4560	33°20.5′S	02°34.9′E	30.12.78	ES
	DS06	4585	33°24.5′S	02°32.9′E	31.12.78	ES
	DS07	5100	26°59.7′S	01°07.1′E	3.1.79	ES
			WEDDELL SEA			
IWSOE	001	728	74°07.0′S	39°38.0′W	6.2.68	ES
	002	412	75°31.5′S	30°08.0′W	25.2.69	AD
	004	793	77°05.5′S	35°04.0′W	26.2.69	AD
	005	1079	77°19.8′S	36°41.3′W	27.2.69	AD
	007	512	77°16.0′S	42°38.0′W	1.3.69	AD
	008	585	77°36.2′S	40°30.0′W	2.3.69	AD
	010	659	77°50.0′S	42°05.2′W	4.3.69	AD
	022	3111	73°28.4′S	30°26.9′W	13.3.69	ES
	023	3697	72°47.6′S	30°29.7′W	14.3.69	AD
	027	4575	64°46.2′S	41°30.1′W	19.3.69	ES

APPENDIX 2. DESCRIBED SPECIES OF THE GENUS *DACRYDIUM*

?Dacrydium sp. Pelseneer, 1911. Probably a juvenile *Amygdalum* (Mattson & Warén, 1977; Ockelmann, 1983).

Dacrydium sp. Salas, 1996
Location of specimens: MNHNP
Dacrydium sp. Salas, 1996: 53, figs, 97–99.
Distribution: Western Mediterranean, 890–2035 m.

Dacrydium sp. a Ockelmann, 1959
Location of specimen: ZMUC.
Dacrydium sp. a Ockelmann, 1959: 50, 195.
Dacydium sp. a Okutani, 1968: 15.
Distribution: Restricted to "depths of Norwegian Sea."

Dacrydium sp. c Ockelmann, 1959
Location of specimen: ZMUC.
Dacrydium sp. c Ockelmann, 1959: 50, 195.
Dacrydium sp. c Okutani, 1968: 15.
Distribution: North Atlantic, WSW and SE Iceland, SW Faroes and W. Norway. Depth range: "intermediate depths."

Dacrydium sp. Poutiers, 1989
Location of specimen: MNHNP.
Dacrydium sp. Poutiers, 1989: 214, 215, fig. 3d.
Distribution: Benthedi Sta. 87, SE Glorieuse Is. 11°44′S 47°35′E. Depth range: 3716 m.

Dacrydium albidum Pelseneer, 1903
Type locality: Southern Ocean, 71°18′S 88°02′W, 200 fm.
Type specimen: IRSNB.
Dacrydium albidum Pelseneer, 1903: 26, pl. VIII, fig. 100.
Dacrydium albidum, Hedley, 1906: 72.
Dacrydium albidum, Thiele, 1912: 21, pl. 17, figs. 10, 10a.
?Dacrydium albidum, Theile, 1912: 226, pl. 17, figs. 9, 9a.
Dacrydium albidum, Lamy, 1937: 70.
Dacrydium albidum, Soot-Ryen, 1951: 20.

Dacrydium albidum, Powell, 1958: 175.
Dacrydium albidum, Powell, 1960: 174.
?Dacrydium albidum, Clarke, 1961: 378.
Dacrydium albidum, Nicol, 1966: 25, pl. 3, figs. 2, 8.
Dacrydium albidum, Okutani, 1968: 15, fig. 1g.
Dacrydium albidum, Egorova, 1982: 64, figs. 271, 272.
Dacrydium albidum, Bernard, 1983: 19.
Dacrydium modioliforme, Bernard, 1983: 19.
Dacrydium albidum, Ockelmann, 1983: 112, 118.
Dacrydium albidum, Poutiers, 1989: 214, 215, fig. 3i.
Dacrydium albidum, Muhlenhardt-Siegal, 1989: 161, pl. 2, fig. 20.
?Dacrydium albidum, Dell, 1990: 33, figs. 55-57.
?Dacrydium modioliforme, Dell, 1990: 34.
Distribution: Southern Ocean, Davis and Ross seas, South Shetland Isles. Depth range: 122-1473 m (possibly to 4758 m-ee Dell (1990) and *D. knudseni* above).

Dacrydium angulare Ockelmann, 1983
Type locality: Cape Basin, Vema Sta. 54, 34°35′S 17°31′E, 1849 m.
Type specimen: Holotype ZMUC; paratypes ZMUC, USNM 822398.
?Dacrydium albidum, Clarke, 1961: 378.
Dacrydium angulare Ockelmann, 1983: 114, figs. 46-48, 51.
Dacrydium angulare, Poutiers, 1989: 214, 215, fig. 3j.
Dacrydium angulare, Salas &: Gofas, 1997: 266, figs. 15-19.
Distribution: South Atlantic. Depth range: 1849 m.

Dacrydium balgimi Salas & Gofas, 1997
Type locality: Off northwestern Morocco, 35°12′N 07°53′W, 2035 m.
Type specimen: Holotype and paratypes MNHNP.
Dacrydium balgimi Salas & Gofas, 1997: 275, figs. 52-57.
Distribution: North Canary Basin. Depth range: 2035 m.

Dacrydium dauvini Salas & Gofas, 1997
Type locality: Atlantis Bank, 34°05.1′N 30°13.6′W, 260 m.
Type specimen: Holotype and paratypes MNHNP; paratypes SMNH.
Dacrydium dauvini Salas & Gofas, 1997: 273, figs. 44-48.
Distribution: Atlantis Bank, Canaries Basin. Depth range: 280-330 m.

Dacrydium filiferum Salas & Gofas, 1997
Type locality: Atlantis Bank, 34°04.8′N 30°14.9W, 330 m.
Type specimen: Holotype and paratypes MNHNP.
Dacrydium filiferum Salas & Gofas, 1997: 275, figs. 49-51.
Distribution: Atlantis Bank, Canaries Basin. Depth range: 330-340 m.

Dacrydium elegantulum elegantulum Soot-Ryen, 1955
Type locality: Bahía de Gardner, Islas Galapagos, Sta. BS 453, 35 fms.
Type specimen: Holotype AHF.
Dacrydium (Quendreda) elegantulum Soot-Ryen, 1955: 87, pl. 8, fig. 41.
Dacrydium elegantulum, Bernard, 1978: 62.
Dacrydium (Quendreda) elegantulum, Bernard, 1983: 19.
Dacrydium elegantulum Ockelmann, 1983: 112, 113.
Distribution Bahía de Gardner, Islas Galapagos; Baja California; off Redondo Beach, California. Depth range: 45-64 m.

Dacrydium elegantulum hendersoni Salas & Gofas, 1997
Type locality: Florida, off Sand Key, 100 fm.
Type specimen: Holotype and paratypes. USNM 459094; paratypes USNM 459098.
Dacrydium elegantulum hendersoni Salas & Gofas, 1997: 278, figs. 61-65.
Distribution: off Sand Key, Florida. Depth range: 155-200 m.

Dacrydium fabale Hedley, 1904
Type locality: 16 m. E of Wollongong, New South Wales, 100 fm. Type specimen: Holotype AMS.
Dacrydium fabale Hedley, 1904: 199, pl. X, fig. 39.
Ouendreda fabale, Iredale, 1936: 271.
Dacrydium fabale, Lamy, 1937: 70.
Dacrydium (Quendreda) fabale, Soot-Ryen, 1955: 87, pl. 8, fig. 41.
Dacrydium fabale, Ockelmann, 1983: 112, 113.
Distribution: off New South Wales. Depth range: 182 m.

Dacrydium gloriosense Poutiers, 1989
Type locality: Benthidi Sta. 87, 11° 44′S 47°35′E, 3716 m.
Type specimen: Holotype MNHNP.

Dacrydium gloriosense Poutiers, 1989: 210, 212, 215, figs. 2a–c, 3g.
Distribution: SE of the Glorieuse Isles. Depth range: 3700–3718 m.

Dacrydium hyalinum (Monterosato, 1875)
Type locality: Off Palermo, Sicily.
Type specimen: Lectotype USNM 199198, paralectotypes from the same lot USNM.
Dacrydium sp. Monterosato, 1870: 43–46.
Dacrydium hyalinum Hidalgo, 1870: 128, *nomen nudum.*
Mytilus vitreus, Jeffreys, 1870: 68.
Dacrydium vitreum, Monterosato, 1872: 18.
Mytilus (Dacrydium) hyalinus Monterosato, 1875: 10.
Dacrydium hyalinum, Monterosato, 1878: 66.
Dacrydium vitreum, Jeffreys, 1883: 394.
Dacrydium hyalinum, Clessin, 1889: 156.
Dacrydium hyalinum, Locard, 1891: 342.
Dacrydium hyalinum, Locard, 1896: 205.
Dacrydium vitreum var. *hyalina,* Lamy, 1937: 68.
?Dacrydium sp. Soot-Ryen, 1966: 8. See Okutani (1968: fig. 1f) and Mattson & Warén (1977).
Dacrydium hyalinum, Okutani, 1968: 15.
Dacrydium hyalinum, Mattson & Waren, 1977: p. 1, figs. 3, 9.
Dacrydium hyalinum, Ockelmann, 1983: 112, 113, 120.
Dacrydium hyalinum, Nordsieck, 1989: 30.
Dacrydium hyalinum, Salas, 1996: 53, figs. 91–93.
Dacrydium hyalinum, Salas & Gofas, 1997: 266, figs. 20–24.
Distribution: Off Palermo and possibly lusitanean (35°34′N 07°35′W. See Soot-Ryen (1966) and Mattson & Warén (1977). Depth range: 76–1615 m.

?Dacrydium meridionale Smith, 1885. Probably a phylobryid. See Bernard (1897), Melville & Standen (1907), Lamy (1937), Powell (1960), Okutani (1968), and Poutiers (1989).

Dacrydium minimum Okutani & Izumidate, 1992
Type locality: Yamatotai Bank, Sea of Japan, 39°45.77′N 135°00.00′E, 1200 m.
Type specimen: Holotype NSMT Mo-69662; paratype NSTM Mo-69663.
Dacrydium minimum Okutani & Izumidate, 1992: 149, figs 1–3.
Distribution: Sea of Japan. Depth range: 394–1200 m.

?Dacrydium modioliforme Theile, 1912
Type locality: Gauss Station, Davis Sea, 400 m.
Type specimen: ?ZMHU
Dacrydium modioliforme Theile, 1912: 226–227, fig. 10, 10a. But see Nicol (1966), Knudsen (1970), Poutiers (1989), and Dell (1990). Probably synonymous with *D. albidum* See also *D. knudseni.*
?Dacrydium modioliforme, Thiele & Jaeckel, 1931: 170.
Dacrydium modioliforme, Lamy, 1937: 70.
Dacrydium modioliforme, Soot-Ryen, 1951: 20.
Dacrydium modioliforme, Powell, 1960: 174.
Dacrydium modioliforme, Nicol, 1966: 26.
Dacrydium modioliforme, Okutani, 1968: 15.
Dacrydium modioliforme, Knudsen, 1970: 92, 178.
Dacrydium modioliforme, Bernard, 1978: 63.
Dacrydium modioliforme, Poitiers, 1989: 214.
?Dacrydium modioliforme, Dell, 1990: 34.
Distribution: Southern Ocean. Depth range: 400–?4758 m.

Dacrydium nipponicum Okutani, 1975
Type locality: Soyo-Maru Sta. B2 (11-XII-1967) 34°22.2′N 139°41.9′E. 1080–1205 m.
Type specimen: Holotype and paratypes TRFRL.
Dacrydium pacificum (*non* Dall 1916), Okutani, 1968: 14, fig. 1a.
Dacrydium nipponicum Okutani, 1975: 68, fig. 1, pl. III, fig. 2.
Dacrydium nipponicum, Bernard, 1978: 62.
Dacrydium nipponicum, Ockelmann, 1983: 112.
Dacrydium nipponicum, Poutiers, 1989: 214, 215, fig. 3k.
Dacrydium nipponicum, Hayami & Kase, 1993: 47.
Dacrydium nipponicum, Salas & Gofas, 1997: 263.
Distribution: Off Miyake Isle, Sea of Japan. Depth range: 1000–1250 m.

Dacrydium occidentale Smith, 1885
Type locality: Challenger Sta. 24, off Culebra Isle, 18°38.5′N 65°05.5′W, 390 fm.
Type specimen: Syntype, BMNH: type material completely destroyed by Bynes' disease; no other material exists.
Dacrydium occidentale Smith, 1885: 282, pl. XVII, fig. 1, 1a.
Dacrydium occidentale, Lamy, 1937: 69.

Dacrydium occidentale, Okutani, 1968: 15 fig. 1b.
Dacrydium occidentale, Nordsieck, 1969: 30, pl. IV, figs. 20. 12.
Dacrydium occidentale, Bernard, 1978: 63.
Dacrydium occidentale, Ockelmann, 1983: 112.
Dacrydium occidentale, Poutiers, 1989: 214, 215, fig. 3e.
Dacrydium occidentale, Kayami & Kase, 1993: 47.
?*Dacrydium occidentale,* Salas & Gofas, 1997: 270, figs. 33–35.
Distribution: West Indies. Depth range: 702 m.

Dacrydium ockelmanni Mattson & Warén, 1977
Type locality: W. Norway, Korsfjorden, 60°08.35′N 05°00.40′E, 260–290 m.
Type material: Holotype ZMUB 58633, paratypes 58634. Other paratypes MNHN and USNM.
?*Dacrydium* sp. Lande, 1975: 10, 12.
Dacrydium ockelmanni Mattson & Warén, 1977: 2, figs. 4–6, 10–13.
Dacrydium ockelmanni, Ockelmann, 1983: 112, 113, 116.
Dacrydium ockelmanni, Høisaeter, 1986: 115.
Dacrydium ockelmanni, Smith & Heppell, 1991: 60.
Dacrydium ockelmanni, Warén, 1991: 114, 115, fig. 40A–C.
Dacrydium ockelmanni, Salas & Gofas, 1997: 264, figs. 7–14.
Distribution: Bay of Biscay, NW of Ireland, WSW and SE of Iceland, SW of Faroes, off W Norway. Depth range: 145–600 m.

Dacrydium pacificum Dall, 1916
Type locality: Albatross Sta. 3604, 54°54′N 168°59′W, 1401 fm.
Type material: Syntypes USNM 214092, SBMNH 34061, paratypes ZMUC.
Dacrydium pacificum Dall, 1916: 405.
Dacrydium pacificum, Dall, 1921: 22.
Dacrydium pacificum, Oldroyd, 1924: 72.
Dacrydium pacificum, Lamy, 1937: 69.
Dacrydium pacificum, Clarke, 1962: 58.
Dacrydium pacificum, Boss et al., 1968, p. 335.
Dacrydium pacificum, Knudsen, 1970: 89, fig. 52C–E.
Dacrydium pacificum, La Rocque, 1973: 38.
Dacrydium pacificum, Abbott, 1974: 437.
Dacrydium pacificum, Okutani, 1975: 69.
Dacrydium pacificum, Bernard, 1978: 62.
Dacrydium pacificum, Bernard, 1983: 19.
Dacrydium pacificum, Ockelmann, 1983: 112.
Dacrydium pacificum, Poutiers, 1989: 212, 215, fig. 3b.
Dacrydium pacificum, Scott et al., 1990: 11.
Distribution NE Pacific and SE Bering Sea. Depth range: 2562 m.

Dacrydium panamensis Knudsen, 1970
Type locality: Galathea Sta. 726, 05°49′N 78°52′W, 3270–3670 m.
Type specimen: Holotype ZMUC.
Dacrydium sp. Wolff, 1961: 150, fig. 19.
Dacrydium sp. Okutani, 1968: 15, fig. 1e.
Dacrydium panamensis Knudsen, 1970: 91, figs. 53, 54.
Dacrydium panamensis, Abbott, 1974: 437.
Dacrydium panamensis, Bernard, 1978: 62, 63.
Dacrydium panamensis, Bernard, 1983: 19.
Dacrydium panamensis, Ockelmann, 1983: 112.
Dacrydium panamensis, Poutiers, 1989: 212, 215, fig. 3h.
Dacrydium panamensis, Dell, 1990: 34.
Distribution: East Pacific, Gulf of Panama. Depth range: 3270–3670 m.

Dacrydium pelseneeri Hedley, 1906
Type locality: 'continental shelf', New Zealand. Type specimen: ?NMNZ.
Dacrydium pelseneeri Hedley, 1906: 72, pl. II, fig. 8.
Dacrydium pelseneeri, Lamy, 1937: 70.
Dacrydium pelseneeri, Soot-Ryen, 1955: 87.
Dacrydium pelseneeri, Ockelmann, 1983: 112.
Distribution: Depth range, shelf depths.

Dacrydium radians Suter, 1908. Gatliff & Gabriell (1916) and Lamy (1937–71), indicate probably a senior synonym of *Modiolaria rhyllensis* Gatliff & Gabriell, 1912.

Dacrydium rostriferum Bernard, 1978
Type locality: West of Cape Flattery, 48°26.6′N 126°54.5′W, 2532 m.
Type specimen: Holotype LACMNH 1880, Paratypes USNM 771804, NSMT .55441, California Academy of Sciences 59409, Oregon State University Biological Institution 01501.
Dacrydium (Dacrydium) rostriferum Bernard, 1978: 62, figs. 1, 12.
Dacrydium rostriferum, Bernard, 1983: 19.
Dacrydium rostriferum, Ockelmann, 1983: 112.
Dacrydium rostriferum, Poutiers, 1989: 214, 215, fig. 3f.
Dacrydium rostriferum, Hayami & Kase, 1993: 47.

Distribution: Off the coast of Washington, USA, between 44°38′N 125°35′W and 48°22′N 126°54′W. Depth range: 2530-2865 m.

Dacrydium speculum Poutiers, 1989
Type locality: off SW Sri Lanka, Safari II Sta. 2 SIPAN 19, SW of Sri Lanka, 05°37′N 78°24′E, 3660 m.
Type specimen: Holotype MNHNP.
Dacrydium speculum Poutiers, 1989: 210, 212, 214, 215, figs. 1a-c, 3a.
?*Dacrydium* cf. *speculum* Salas & Gofas, 1997: 277, figs. 58-60.
Distribution SW of Sri Lanka; ?Cape Verde Basin (Salas & Gofas, 1997). Depth range: 3660 m, (4580 m if present in Cape Verde Basin).

Dacrydium vitreum (Møller, 1842)
Type locality: Sukkertoppen, West Greenland, 73 m.
Type specimen: originally ZMUC, probably lost (Warén, 1991).
Modiola? vitrea Holböll MS, in Møller, 1842: 92
Dacrydium vitreum, Torell, 1859: 138, pl. i, fig. 2a, b.
?*Dacrydium vitreum,* Hidalgo, 1870: 128.
Modiolaria (Dacrydium) vitrea, Mörch, in Jones, 1875: 133
Dacrydium vitreum, Jeffreys, 1876: 429.
Dacrydium vitreum, Friele, 1878: 222.
Dacrydium vitreum, Sars, 1878 (in part): 28, pl. 3, fig. 2a, b.
Dacrydium vitreum, Jeffreys, 1879: 569.
Dacrydium vitreum, Verrill, 1882: 579, pl. 44, fig. 8.
Dacrydium vitreum, Verrill, 1884: 281.
?*Dacrydium vitreum,* Smith, 1885: 282.
?*Dacrydium vitreum,* Dautzenberg, 1889: 77.
Dacrydium vitreum, Clessin, 1889: 155, pl. 6, figs. 16, 17.
Dacrydium vitreum, Dall, 1889: 38.
Dacrydium vitreum, Posselt, 1895 (in part): 66.
Dacrydium vitreum, Locard, 1896: 205.
Dacrydium vitreum, Dautzenberg, 1897: 199.
?*Dacrydium vitreum,* Bernard, 1898: 71.
Dacrydium vitreum, Locard, 1898: 364.
Dacrydium vitreum, Posselt & Jensen (in part), 1898: 21.
Dacrydium vitreum, Locard, 1899: 170.
Dacrydium vitreum, Friele & Grieg, 1901: 24.
Dacrydium vitreum, Whiteaves, 1901: 121.
Dacrydium vitreum, Jensen, 1905: 325.
?*Dacrydium vitreum,* Dautzenberg & Fisher, 1912: 373.
Dacrydium vitreum, Jensen (in part), 1912: 54.
Dacrydium vitreum, Johnson, 1915: 34.
Dacrydium vitreum, Odhner, 1915: 82.
Dacrydium vitreum, Grieg, 1916: 8.
?*Dacrydium vitreum,* Dautzenberg, 1927: 275.
Dacrydium vitreum, Thorson, 1934: 6.
Dacrydium vitreum, Johnson, 1934: 28.
Dacrydium vitreum, Theile, 1935: 798.
Dacrydium vitreum, Lamy, 1937: 66.
Dacrydium vitreum, La Rocque, 1953: 38.
Dacrydium vitreum, Ockelmann, 1959: 48, pl. 1, fig. 19.
Dacrydium vitreum, Scarlato, 1960: 61, pl. 1, fig. 3.
Dacrydium vitreum, Soot-Ryen, 1966: 8.
Dacrydium vitreum, Okutani, 1968: 14, 15, fig. 1d.
Dacrydium vitreum, Knudsen, 1970: 90, 92, fig. 52A, B.
Dacrydium vitreum, Abbott, 1974: 436, fig. 5102.
Dacrydium vitreum, Mattson & Warén, 1977: 1-3, figs. 1, 2, 7.
Dacrydium vitreum, Bernard, 1978: 62.
Dacrydium vitreum, Scarlato, 1981: 242, fig. 141.
Dacrydium vitreum, Bernard, 1983: 19.
Dacrydium vitreum, Ockelmann, 1983: 112, 113, 115, fig. 49.
Dacrydium vitreum, Høisaeter, 1986: 115.
Dacrydium vitreum, Nordsieck, 1989: 29, pl. IV, fig. 20.10.
Dacrydium vitreum, Poutiers, 1989: 212, 215, fig. 3c.
Dacrydium vitreum, Smith & Heppell, 1991: 60.
Dacrydium vitreum, Warén, 1991: 114, 115, fig. 40D-F.
Mytilus vitrea (= Dacrydium vitreum), Schiøtte & Warén, 1992: 14.
Dacrydium vitreum, Salas & Gofas, 1997: 263, figs. 2-6.
Distribution: W and E Greenland, Baffinland, off Nova Scotia, N and E of Iceland, Jan Mayen, Spitsbergen, W. Norway south to Lofoten Isles, Barents, White and Kara Seas, Bering Sea, North of Gulf of Alaska, Kamchatka, Sea of Okhotsk. Depth range: 5-2258 m, but most frequently found 5-200 m.

Dacrydium viviparum Ockelmann, 1983
Type locality: Ingolf Stas 78, 80, 90, 64°45′N 29°06′W south to 60°37′N 27°52′W, 1070-1505 m.

Type specimen: Holotype MZUC, paratypes BMNH 198335, USNM 822399.
?*Dacrydium vitreum* var. *elongata* Locard, 1898: 364.
Dacrydium vitreum, Jensen, 1912 (in part): 56-65.
Dacrydium sp. b Ockelmann, 1959: 50.
Dacrydium sp. b Okutani, 1968: 15.
Dacrydium viviparum Ockelmann, 1983: 118, 120, figs. 52-54, 56, 57.
Dacrydium viviparum, Warén, 1991: 115.
Dacrydium viviparum, Hayami & Kase, 1993: 48.
?*Dacrydium* cf. *hyalinum,* Salas & Gofas, 1997: 269, figs. 27-32.
Dacrydium viviparum, Salas & Gofas, 1997: 269.
Distribution: West European, Canary and North America Basins and possibly the Mediterranean. Depth range: 952-2430 m.

Dacrydium wareni Salas & Gofas 1997
Type locality: Off northwestern Morocco, 35°31′N 07°42′W, 1510m.
Type specimen: Holotype MNHMP; paratypes SMNH.
Dacrydium cf. *hyalinum,* Salas 1996: 53, figs. 94-96.
Dacrydium wareni Salas & Gofas 1997: 271, figs. 36-43.
Distribution: Mediterranean off Morocco, Gulf of Sirte (JAA pers. obs.); off northwestern Spain, West European and Canary Basin. Depth range: 395-2018 m.

Dacrydium zebra Hayami & Kase, 1993
Type locality: "Devil's Palace," Shimoji Islet, Miyako Islands, 24°49.6′N 125°08.2E, 25 m.
Type specimen: Holotype UMUT, RM19432a; paratypes UMUT RM19432-41.
Dacrydium sp. Kase & Hayami, 1992: 448.
Dacridium sp. Hayami & Kase, 1993a: 3, fig. 7.
Dacrydium Zebra Hayami & Kase, 1993b: 46, figs. 148-158.
Distribution: Submarine caves, Sea of Japan. Depth range: 12-40 m.