

BROODING AND NON-BROODING *DACRYDIUM* (BIVALVIA: MYTILIDAE): A REVIEW OF THE ATLANTIC SPECIES

CARMEN SALAS¹ and SERGE GOFAS²

¹Departamento de Biología Animal, Facultad de Ciencias, Universidad de Málaga, E-29071 Málaga, Spain and

²Muséum National d'Histoire Naturelle, Laboratoire de Biologie des Invertébrés marins et Malacologie,
55 rue Buffon, F-75005 Paris, France

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ABSTRACT

The Atlantic species of the marine bivalve genus *Dacrydium* are reviewed, with particular emphasis on their hinge and protoconch characters. The basic groundplan of a *Dacrydium* comprises a functional primary ligament, a paired series of primary teeth, and a posterior row of secondary teeth separated from the latter by a secondary ligament; this can be transformed into a single series either by loss of the secondary ligament and merging primary and secondary teeth, or by loss of secondary teeth and ligament through paedomorphosis.

Twelve species are recognized, of which eleven are illustrated. One abyssal species is not separable morphologically from the Indian Ocean *D. speculum* Poutiers, 1989 and is new to the Atlantic; four new species (*D. wareni*, *D. dauvini*, *D. filiferum* and *D. balgimi*) are described; a Caribbean form which is hardly distinct from the Eastern Pacific *D. elegantulum* Soot-Ryen, 1955, is described as a new subspecies *D. e. hendersoni*.

The larvae are brooded in *D. hyalinum* (Monterosato, 1875), *D. viviparum* Ockelmann, 1983 and *D. balgimi*. The brooding species have larger larvae (protoconch 210 to 315 µm long) than the non-brooding (protoconch 120 to 150 µm long), and reach a smaller adult size (1.4 to 3 mm instead of 4.5–5 mm). A phylogenetic reconstruction is attempted using parsimony analysis of hinge and shell characters as well as the brooding/non brooding character.

INTRODUCTION

The marine bivalve genus *Dacrydium* was proposed by Torell (1859) with *Modiola vitrea* Holbøll in Møller, 1842 as type-species by monotypy. The first additional species to be described was the Mediterranean *D. hyalinum* (Monterosato, 1875), and there are to date 19 known species of *Dacrydium* from the different ocean basins (Table 1).

Ockelmann (1983) proposed the subfamily Dacrydiinae with *Dacrydium* as the sole included genus. The main definitive character is that the hinge has a primary ligament and primary teeth functional throughout the life of the animal, and in some species an antero-dorsal series of secondary teeth. This hinge morphology is considered homologous with that of the nepionic shell of other mytilids.

The genus has a cosmopolitan distribution, mostly in deep water. The broad distribution and homogeneous morphology makes the recognition of species sometimes very difficult, and raises the question of whether there are actually cosmopolitan deep-sea species, or there is so little morphological differentiation between some species that they cannot be distinguished (Gage & Tyler, 1991: 252–253). The main characters used to distinguish species have been the outlines and shapes of the shells and the gross features of the hinges.

Ockelmann (1983) estimated that there are some 30 extant species of *Dacrydium*; and indicated that 6 undescribed species are in the Zoological Museum, Copenhagen. Allen (1979) showed the outlines of ten unnamed species of *Dacrydium* from the Atlantic and contended that *Dacrydium* must be in process of speciation, however Ockelmann (1983) pointed out that the worldwide representation, from upper shelf to the abyssal zone, indicates a much longer geological history of the subfamily. The oldest known representative of the genus, *D. simulator* Laws, 1936, is found in the Early Pliocene (Opoitian) of New Zealand.

MATERIALS AND METHODS

The study of bivalves from several deep-sea French expeditions: Balgim (Alboran Sea, Strait of Gibrat-

Table 1. The species of *Dacrydium* and their type localities. *D. meridionalis* Smith, 1885 (described from Marion Island), is excluded following its transfer to *Philobrya* by Bernard (1897).

ATLANTIC OCEAN	
<i>D. vitrium</i> (Holbøll in Møller, 1842)	W. Greenland, 73 m
<i>D. hyalinum</i> (Monterosato, 1875)	Palermo, Mediterranean, outer shelf
<i>D. occidentale</i> Smith, 1885	Culebra Island, West Indies, 696 m
<i>D. ockelmanni</i> Mattson & Warén, 1977	W. Norway, 260–290 m
<i>D. angulare</i> Ockelmann, 1983	S. Atlantic Ocean, 1849 m
<i>D. viviparum</i> Ockelmann, 1983	Reykjanes Ridge, 1070–1760 m
INDIAN OCEAN	
<i>D. speculum</i> Poutiers, 1989	SW Ceylon, 3660 m
<i>D. gloriosense</i> Poutiers, 1989	SE of Glorieuses Islands, 3700 m
PACIFIC OCEAN	
<i>D. fabale</i> Hedley, 1904	Wollongong, New South Wales, 180 m
<i>D. pelseeneri</i> Hedley, 1906	Cuvier Island, New Zealand, 200 m
<i>D. pacificum</i> Dall, 1916	Bering Sea, 2562 m
<i>D. rostriferum</i> Bernard, 1978	W. of Cape Flattery (Washington), 2532 m
<i>D. panamensis</i> Knudsen, 1970	Gulf of Panama, 3270–3670 m
<i>D. elegantulum</i> Soot-Ryen, 1953	Galapagos Islands, 45–65 m
<i>D. nipponicum</i> Okutani, 1975	Miyake Island, Japan, 1000–1250 m
<i>D. minimum</i> Okutani & Izumidate, 1992	Sea of Japan, 394–1200 m
<i>D. zebra</i> Hayami & Kase, 1993	Ryukyu Islands, Japan, in subtidal caves
ANTARCTIC	
<i>D. albidum</i> Pelseener, 1903	Drake passage, 400 m
<i>D. modioliforme</i> Thiele, 1912	Gauss sta. [now Australian Antarctic territory]

tar and Ibero-Moroccan Gulf), Eumeli (Cape Verde Basin) and Seamount (from different North Atlantic seamounts) and of the Spanish expedition Fauna I (shelf of Alboran Sea, Strait of Gibraltar and Ibero-Moroccan Gulf), has revealed the presence of 10 species of *Dacrydium* in the Northeast Atlantic, four of which new. A large amount of material of an undescribed Caribbean species is held at the National Museum of Natural History, Washington. The purpose of this paper is to describe them and to assess the possible relationships within the genus.

Most specimens were live collected and the fragile shells are not commonly found as valves in the sediment samples. The technique to open the dry specimens without breaking the shells involves: 1. soaking for one to several hours in a 10% solution of sodium-lauryl-sulphate (a slightly alkaline detergent), 2. bringing to vacuum to let the air push apart the valves and let the liquid in, 3. soaking some more if needed and 4. gently pushing the ventral margin of the shell towards a razor blade, using a fine paintbrush. The cleaning was completed with a brush in the lauryl sulphate solution, then in water, as these shells do not withstand ultrasonic cleaning. A couple of alcohol-preserved specimens were opened as in step (4) and critical point dried.

Specimens were measured as shown on Fig. 1, using the *camera lucida* of a zoom stereomicroscope calibrated on a 20x magnification, with a precision of 0.05 mm. Measurements (length × breadth) of the smallest and of largest specimens in each lot are

given with the lists of material examined.

The larval shell will be called 'protoconch' and the postlarval to adult shell 'teleoconch' throughout, notwithstanding the widespread use of 'prodissoconch' and 'dissoconch' in the literature on bivalves. We consider these parts to be homologous in gastropods and bivalves, and can see no need for a separate terminology.

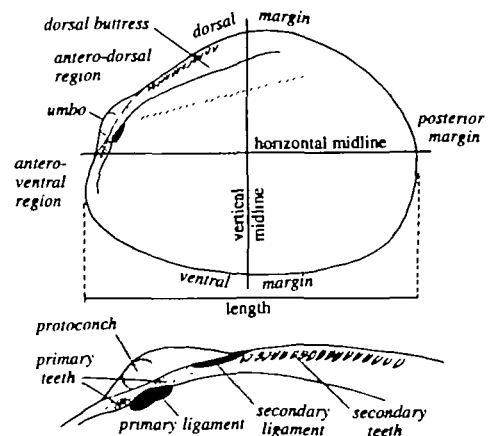


Figure 1. Descriptive terms used for a *Dacrydium* shell.

Abbreviations used in the text:

BMNH:	The Natural History Museum, London
MNHN:	Muséum National d'Histoire Naturelle, Paris
SMNH:	Naturhistoriska Riksmuseet (Swedish Museum of Natural History), Stockholm
USNM:	National Museum of Natural History, Washington
ZMC:	Zoologisk Museum, Copenhagen
sta.:	station
spm.:	specimen, specimens (live taken)
sh.:	shell, shells (empty shell with valves in connection)
v.:	valve, valves

× 2.3 mm); Varangerfjord (70°04'N, 29°03'E, 50 m), 1 spm. (2.5 × 1.7 mm); Narvik (68°31.28'N, 17°30.02'E, 152 m, 1 sh. (1.8 × 1.3 mm)); North Norway, leg. Sneli (68°08'N, 10°10'E, 860 m, 4 spm. (1.9 × 1.4 mm – 3.1 × 2.3 mm)); Snorre oilfield (61°28'N, 02°12'E, 292–340 m), 1 spm. (2.3 × 1.7 mm); Tromsø (69°42'N, 19°00'E, 10–50 m), 2 spm. (3.2 × 2.3 mm); all SMNH. Tromsø, Locard collection, 10 spm. (4.2 × 3.0 mm – 4.7 × 3.4 mm), MNHN.—Iceland: Skjal-fandi, from fishing nets, 36 spm. (2.8 × 2.1 mm – 4.9 × 3.7 mm), SMNH.—Jan Mayen Island: SW coast, 1 spm., 1 v. (4.2 × 3.1 mm), MNHN.

SYSTEMATIC DESCRIPTIONS

Family Mytilidae Rafinesque, 1815
Subfamily Dacrydiinae Ockelmann, 1983

Genus *Dacrydium* Torell, 1859

Description: Shell small, 1–5 mm long, thin, translucent, oblong-modioliform with the umbo at some distance from the anterior end. Protoconch 120 to 350 µm in diameter, with granular-punctate microsculpture and usually a peripheral smooth rim. Teleoconch usually smooth, or with a faint concentric sculpture parallel to the growth lines; in some species with radial threads on the umbonal region. Hinge with a primary internal ligament beneath the umbo, primary teeth (derivatives of provincial teeth according to Ockelmann, 1983) on each side next to the umbo, and in some species a series of secondary teeth posterior to the umbo, united to the primary teeth or separated from them by a secondary ligament. A conspicuous dorsal buttress (called subligamental ridge by Ockelmann, 1983) inside from the umbo to the mid-dorsal side. Two adductor muscle scars, respectively anterior and posterior to the hinge teeth; the anterior smaller.

Dacrydium vitreum (Holbøll in Møller, 1842)
(Figs 2–6)

Modiola vitrea Holbøll in Møller, 1842: 92.

Type locality: West Greenland [Sukkertoppen, 73 m on Møller's manuscript notes, *vide* Schiøtte & Warén, 1992].

Type material: not found in Zoologisk Museum, Copenhagen (Schiøtte & Warén, 1992).

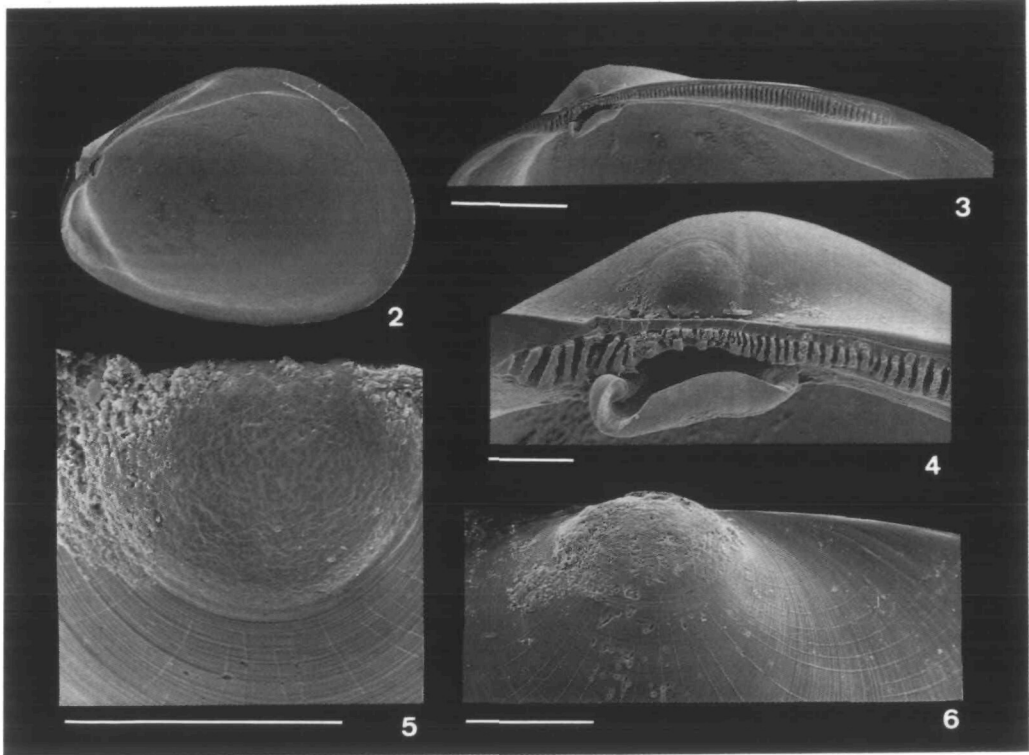
Material examined: Norway: Varangerfjord (70°04'N, 29°03'E, 90 m), 4 spm. (1.6 × 1.2 mm – 3.1

Description: Shell up to 5 mm long, rather stout and convex. Antero-ventral region prominent and broadly rounded; antero-dorsal region gently sloping (approximately 40°) from the dorsal margin; ventral margin slightly convex connecting to a broadly rounded posterior margin. Umbo rather large and blunt, above the horizontal midline, clearly prosogyrous. Protoconch (120 × 100 µm), equilateral, bordered by a very narrow rim. Teleoconch with a microsculpture of fine concentric striae and fine radial threads on the umbonal region.

Hinge with a broad primary ligament on a deep chondrophore beneath the umbo. Crenulated area continuous. A short cluster of 5–7 narrow, slightly diverging teeth anterior to the primary ligament continuing into a very narrow, irregular series of teeth above the anterior part of the ligament. A long series of narrow, parallel teeth from above the ligament (where it overlaps with the anterior series) reaching posteriorly to about two thirds of the length of the dorsal buttress. Dorsal buttress strong and long, reaching beyond the vertical midline of the shell.

Distribution: Northeast America south to Nova Scotia; West and East Greenland, Northern and Eastern Iceland, Jan Mayen, Spitsbergen, Norway south to Lofoten; Barents Sea, White Sea and Kara Sea; 5–2200 m (Mattson & Warén, 1977).

The species is certainly also present in the North Pacific, but its exact range is difficult to establish. The range given by Scarlato (1981: 76) is not reliable, as he obviously included several other species and synonymized *D. nipponicum* without a discussion; however his record for the Bering Sea, substantiated by a figure (Fig. 141, p. 243) can be trusted. Bernard (1983) merely lists 'North Pacific, 53°N to 71°N' without details. There are no formal Japanese records under this name; Okutani and Izumidate (1992:150) reported Scarlato's (1981) citation of *D. vitreum* (i.e. of



Figures 2–6. *Dacrydium vitreum* (Holbøll in Möller, 1842) from Norway, Varanger Fjord, 90 m. **2.** Right valve (length 3.3 mm). **3, 4.** Details of hinge. **5.** Protoconch of the same specimen (diameter 120 μm) **6.** Detail of microsculpture of the early teleoconch of another specimen. Scale bars: **3,** 500 μm ; **4, 5, 6,** 100 μm .

the synonymized *D. nipponicum*) for Japan and described *D. minimum* from a bathyal dredge haul in the Sea of Japan without showing convincing differences separating their new species from *D. vitreum*.

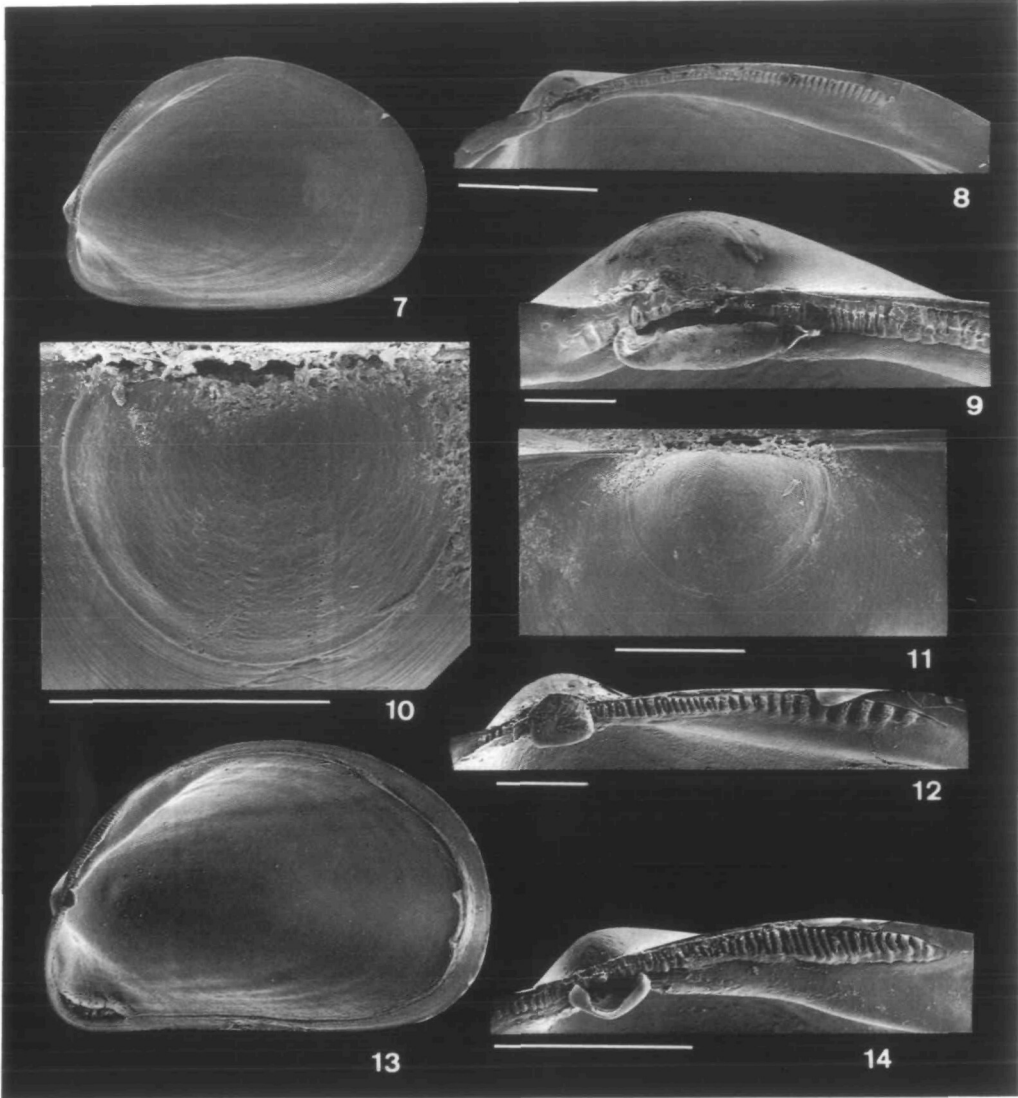
Dacrydium ockelmanni Mattson & Warén,
1977
(Figs 7–14)

Dacrydium ockelmanni Mattson & Warén,
1977: 1–6.

Type locality: Western Norway, outer part of Korsfjorden, NW of Marsteinen lighthouse, 60°08'35"N, 05°00'40"E, 260–290 m; sand and gravel with some shell-sand.

Type material: Holotype (no. 58 633) in the Zoological Museum, Bergen. Paratypes, about 60 specimens and shells, from the type locality, also in Bergen (no. 58 634). Paratypes from the type locality in MNHN; other paratypes in USNM.

Material examined: The paratypes in MNHN and — Norway: Troll West oilfield (60°40–46'N, 03°21–29'E, 324–344 m), 12 spm., 1 v. (1.4 \times 1 mm – 4.0 \times 2.5 mm); Frøy oilfield (59°14.0'N, 03°33.0'E, 100–115 m), 1 spm. (2.0 \times 1.5 mm); Tordis oilfield (61°16'N, 02°07'E, 196–206 m), 3 spm., 1 v. (1.3 \times 0.9 mm – 2.3 \times 1.6 mm); Snorre oilfield (61°28'N, 02°12'E, 292–340 m), 1 spm. (2.4 \times 1.6 mm); SW of Bergen, N of Marsteinen, sta. E003–73 (60°08.1'N, 05°00'E, 300–330 m), 14 spm. (1.7 \times 1.2 mm – 4.0 \times 2.7 mm); NW of Marsteinen, sta. E023–73 (60°08.3'N, 05°00.6'E, 300–400 m), 2 spm. (4.2 \times 2.7 mm – 4.4 \times 2.8 mm); all SMNH. NW of Marsteinen, sta. E067–73 (60°08'35"N, 05°00'40"E, 260–290 m/type locality), 38 spm. (paratypes MNHN, 1.15 \times 0.8 mm – 4.0 \times 2.6 mm).—West Iceland, leg. Larsen, 2 spm. (3.2 \times 2.0 mm – 3.9 \times 2.4 mm; figured in Warén, 1991: fig. 40), SMNH.—Bay of Biscay: Travailleur sta. 10 (43°39'05" N, 3°28'00" W, 1960 m), 6 v. (2.3 \times 1.7 – 4.0 \times 2.6 mm; cited by Locard, 1898: 364–366, as *D. vitreum*); Talisman sta. 18 (43°36'20" N, 2°17'W, 546 m), 1 spm. and 1 v. (3.0 \times 2.1 mm – 4.0 \times 2.8 mm; cited by Locard, 1898: 364–366, as *D. vitreum*); all MNHN.—Mediterranean France: Toulon



Figures 7–12. *Dacrydium ockelmanni* Mattson & Warén, 1977 from Western Norway, Troll West oil field. **7.** Right valve (length 3.4 mm). **8, 9.** Details of hinge. **10.** Protoconch of the same specimen (diameter 140 µm). **11.** Detail of microsculpture of the early teleoconch of another specimen. **12.** Hinge of a juvenile specimen 1.3 mm long. **Figures 13–14.** *Dacrydium ockelmanni* from the Cape Verde Basin, Eumeli sta. CP06. **13.** Right valve (length 3.5 mm). **14.** Detail of hinge. Scale bars: **8, 14,** 500 µm; **9, 10, 11, 12,** 100 µm.

Canyon (42°57.3'N, 6°01.3'E, 500–800 m), leg. Zibrowius, 1 sh., 2 v. (3.25 × 1.85 – 4.25 × 2.55 mm).—Cape Verde Basin: Eumeli 4 sta. CP06 (20°31'N, 18°32'W, 1733 m), 1 spm. (3.5 × 2.25 mm); Eumeli 4 sta. KG 72 (20°34'N, 18°32'W, 1762 m), 1 sh. (2.5 × 1.7 mm); Eumeli 4 sta. KG 73 (20°32'N, 18°33'W, 1760 m), 1 v. (2.5 × 1.7 mm); all MNHN.

Description: Shell up to 4.5 mm long. Antero-ventral region short and rounded; antero-

dorsal region sloping approximately at 45° from the dorsal margin; ventral margin quite straight connecting to a semicircular posterior margin. Umbo moderately large, on the horizontal midline or a little below, slightly prosogyrous. Protoconch (140/145 × 100 µm), equilateral, bordered by a faint smooth rim. Surface of teleoconch without sculpture, except some concentric growth lines.

Hinge with a broad primary ligament on a deep chondrophore beneath the umbo. Crénulated area continuous. A short cluster of 5–7 narrow, slightly diverging teeth anterior to the ligament continuing into a very narrow, hardly denticulated ridge above the anterior part of the ligament. A long series of narrow, parallel teeth from above the ligament (where it overlaps with the anterior series), reaching posteriorly to about two thirds of the dorsal buttress. Dorsal buttress strong, reaching approximately the vertical midline of the shell.

Distribution: Mattson & Warén (1977) reported the species from WSW and SE of Iceland, SW of the Faroes, western Norway, NW of Ireland and Bay of Biscay. The shells from Mediterranean France are most likely Pleistocene fossils, but this occurrence proves that the species has lived in the Mediterranean. The finding of one live specimen in the Cape Verde Basin during the Eumeli expedition, extends the distribution to lower latitudes, in deep water (1733–1768 m depth, whereas in Norway it is found at no more than 500 m depth).

Remarks: This species has been frequently confused with *D. vitreum*, with which it is sympatric and often syntopic in the northern part of its distribution. Until the description of *D. ockelmanni*, all the Atlantic records of *Dacrydium* were referred to *D. vitreum*. *D. ockelmanni* differs from *D. vitreum* in being less plump, having a more slender shape with a shorter but less broadly rounded antero-ventral shell region, smaller and narrower primary ligament, and no radial microsculpture on the early part of the teleoconch.

The continuous posterior series of teeth appears clearly twofold on juvenile specimens, with a narrowing between the derivatives of the primary teeth, and the secondary ones (Fig. 12).

Dacrydium angulare Ockelmann, 1983
(Figs 15–19)

Dacrydium angulare Ockelmann, 1983: 114–118, Figs 46–48, 51.

Type locality: South Atlantic, Cape Basin, 34°35'S, 17°31'E, 1849 m.

Type material: Holotype from Vema sta. 54, and most paratypes in ZMC. Three paratypes in USNM (n° 822398).

Material examined: Cape Verde Basin: Eumeli 2 sta. CP 02 (18°36'N, 20°59'W, 3134 m), 1 spm. (3.0 × 2.05 mm); Eumeli 2 sta. KG 10 (18°30'N, 21°01'W,

3128 m), 2 spm. (0.75 × 0.6 mm – 2.7 × 1.75 mm); Eumeli 2 sta. KG 14 (18°33'N, 21°03'W, 3136 m), 1 v. (2.1 × 1.45 mm); Eumeli 3 sta. KG 53 (18°31'N, 21°03'W, 3119 m), 3 v. (2.75 × 1.75 mm – 4.05 × 2.5 mm); Eumeli 3 sta. KG 56 (21°04'N, 31°08'W, 4570 m), 1 spec. (ca. 2.6 × 1.7 mm, broken); all MNHN.

Description: Shell up to 3 mm long. Antero-ventral region quite acuminate; antero-dorsal margin gently sloping (approximately 40°) from the dorsal margin; ventral margin straight connecting to a semicircular posterior margin. Umbo small and salient, approximately level with the horizontal midline, slightly prosogyrous. Protoconch (165/170 × 145 µm), equilateral, bordered by a narrow smooth rim. Teleoconch with a microsculpture of fine concentric striae and very fine radial threads on the umbonal region.

Hinge with a broad primary ligament on a rather shallow chondrophore beneath the umbo. A short cluster of 5–7 narrow, slightly diverging teeth anterior to the ligament continuing into a very narrow, hardly denticulated ridge above the anterior part of the ligament. A long series of narrow, parallel teeth from above the ligament and reaching posteriorly to less than half the length of the dorsal buttress. Dorsal buttress strong, reaching approximately the vertical midline of the shell.

Distribution: *D. angulare* was first collected off Namibia, South of the Walvis Ridge, in 1849 m depth. This and the deeper, newly reported localities in the Cape Verde Basin in deep water, are under influence of cold Antarctic bottom water.

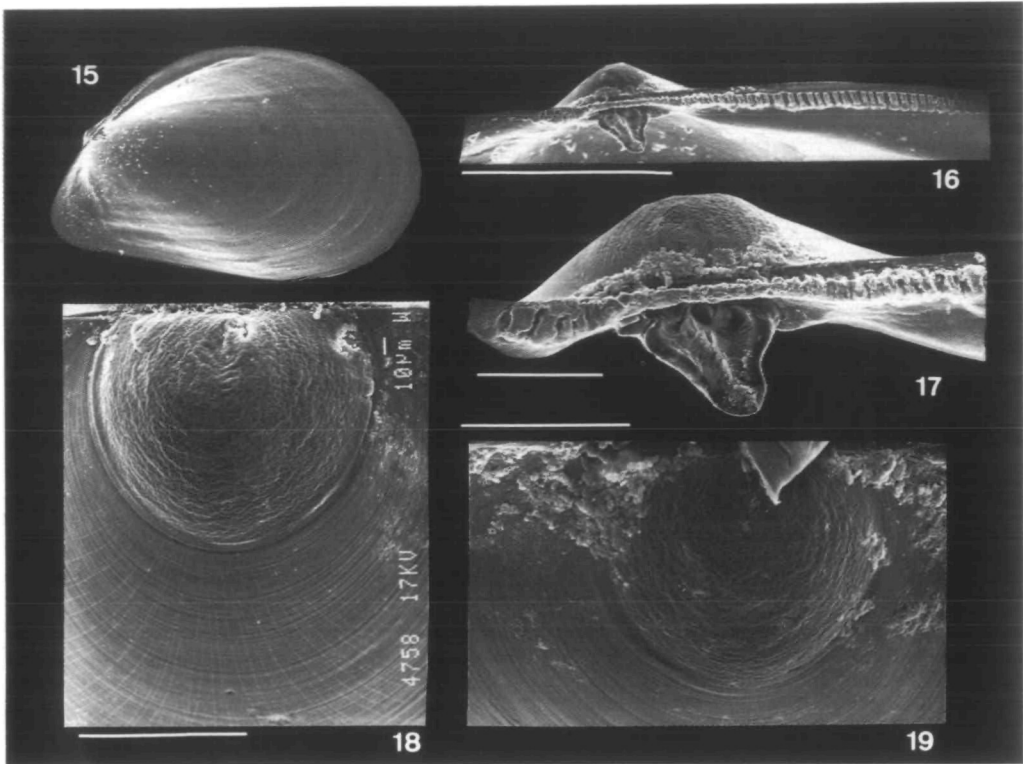
Remarks: Ockelmann (1983) provided so careful and exhaustive a description of this species that the scanning micrographs add little. This species can be easily identified by its shape, with a very acuminate and pointed antero-ventral shell region. It shares with *D. vitreum* and *D. ockelmanni* the hinge morphology with only primary ligament and small number of anterior teeth. Its outline is more similar to that of *D. ockelmanni*, whereas it has radial threads on the umbonal region like *D. vitreum*.

Dacrydium hyalinum (Monterosato, 1875)
(Figs 20–24)

Mytilus (Dacrydium) hyalinum Monterosato, 1875: 10.

Type locality: Off Palermo, Sicily.

Type material: Lectotype (designated by Mattson & Warén, 1977:1), bivalved specimen from the type locality, USNM (n°199198). Para-



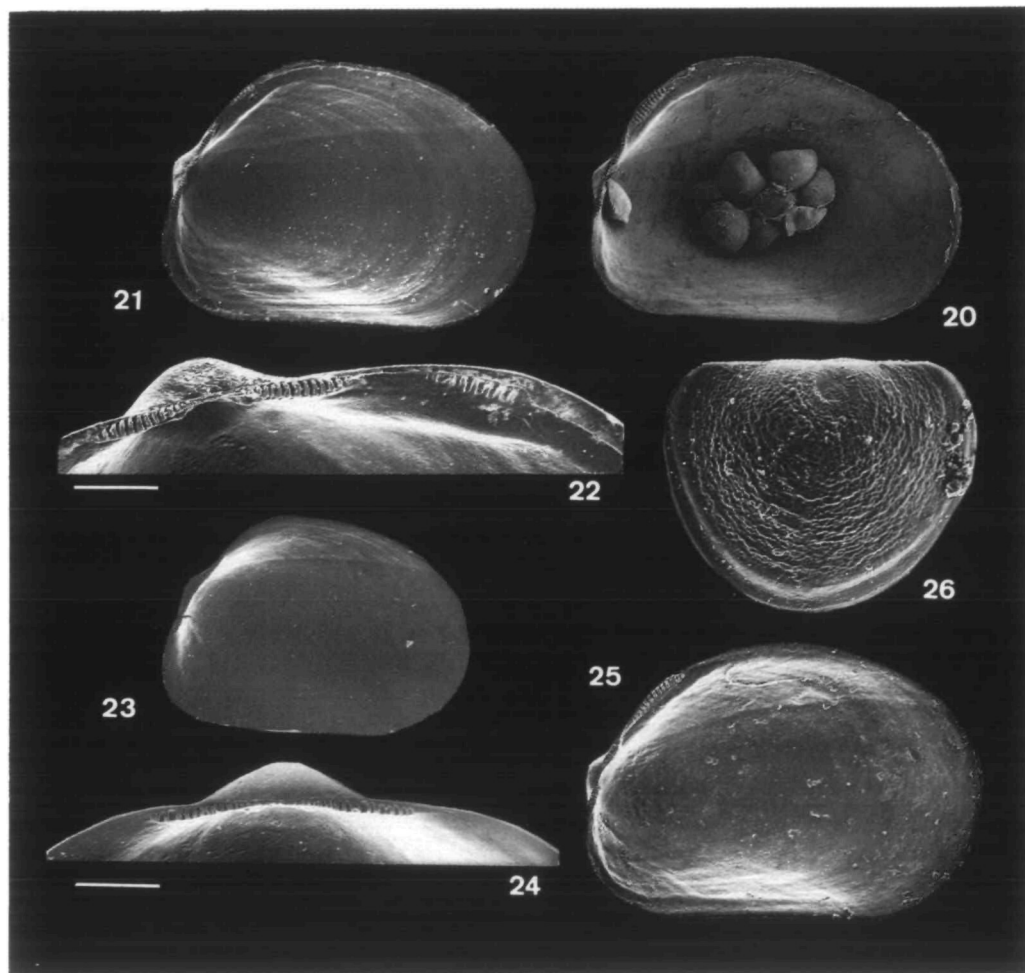
Figures 15–19. *Dacrydium angulare* Ockelmann, 1983 from Cape Verde Basin, Eumeli sta. KG10. **15.** Right valve (length 2.7 mm). **16, 17.** Detail of hinge. **19.** Protoconch of the same specimen (diameter 170 μm). **18.** Protoconch and microsculpture of the early teleoconch of another specimen 0.75 mm long. Scale bars: **16,** 500 μm ; **17, 18, 19,** 100 μm .

lectotypes, four valves and one specimen, from the same lot, in USNM.

Material examined: Sicily: Palermo, Locard collection, 3 spm. obtained from Monterosato (1.3 \times 0.95 mm – 1.7 \times 1.15 mm; the latter Figs 91–93 of Salas, 1996), MNHN; Acitrezza, from MNHN/SMNH workshop 1991 (37°34.4'N, 15°11.7'E, 23–41 m), 2 spm. and 1 v. (1.4 \times 1 mm – 1.9 \times 1.1 mm), SMNH.—France: Banc du Magaud, leg. Picard 1956 (43°03'N, 6°41'E, 135–146 m), MNHN.—Strait of Gibraltar area: Balgim sta. DR49 (35°53'N, 06°33'W, 521 m), 1 spm. (1.1 \times 0.8 mm); sta. DW50 (35°53'N, 06°32'W, 523 m), 1 spm. (1.4 \times 0.9 mm); sta. DW128 (35°35'N, 03°45'W, 480 m), 1 spm. and 1 v. (1.5 \times 1.0 mm – 1.0 \times 0.7 mm); sta. CP135 (35°26'N, 04°14'W, 395 m), 4 spm. (1.4 \times 0.9 mm – 1.9 \times 1.2 mm); sta. DR151 (35°55'N, 05°25'W, 115 m), 2 spm. (0.9 \times 0.65 mm – 1.1 \times 0.75 mm); sta. DR153 (35°56'N, 05°35'W, 4 spm. (1.5 \times 1.0 mm – 2.4 \times 1.6 mm); Strait of Gibraltar, from fishing net, 1 spm. (2.2 \times 1.3 mm); Al Mounir sta. B6D2 (35°53'40"N, 5°34'25"W, 17 spm. (0.9 \times 0.7 mm – 1.6 \times 1.1 mm; corroded by acidic alcohol); all MNHN.

Description: Shell up to 2.4 mm long. Antero-ventral region hardly to moderately prominent, broadly rounded; antero-dorsal region short and steeply sloping (50° to 60°) from the dorsal margin; ventral margin straight connecting to a semicircular posterior margin. Umbo rather large, blunt, level with the horizontal midline, orthogyrous. Protoconch (210/220 \times 180 μm), slightly inequilateral, bordered by a distinct smooth rim. Teleoconch smooth, or with more or less conspicuous concentric growth lines.

Hinge with a narrow primary ligament, on a rather shallow chondrophore, beneath the umbo. Two clusters of 10–13 narrow, parallel primary teeth are present to both sides of the chondrophore, separated by a toothless interval above the ligament. A secondary ligament at the end of the posterior cluster, followed by a secondary dorsal series of 10–15 broader teeth extending over more than two thirds of the length of the dorsal buttress. Dorsal but-



Figures 20–24. *Dacrydium hyalinum* (Monterosato, 1875) from Banc du Magaud, Mediterranean France. **20.** Right valve of a specimen 1.45 mm long with its 9 brooded larvae. **21.** Specimen 1.25 mm long, with developing secondary teeth. **22.** Detail of hinge. **23.** Specimen 1.0 mm long, with only narrow primary teeth developed. **24.** Detail of hinge. **Figures 25–26.** *Dacrydium hyalinum* from off Palermo, Sicily (specimen sent by Monterosato to Locard). **25.** Right valve (length 1.7 mm). **26.** One of the 12 larvae in protoconch stage found inside the specimen (diameter 217 μm). Scale bars: 100 μm .

tress short and narrow, but prominent, reaching hardly more than the anterior 1/3 of the shell.

Distribution: Western Mediterranean Sea, from Sicily to the Strait of Gibraltar, on hard bottoms in circalittoral and bathyal depths. No records from the Eastern Mediterranean. Occurrences of similar forms on the North Atlantic seamounts are discussed below.

Remarks: Philippi (1844) used the name *Modi-*

ola pygmaea Philippi, 1843 for a Silician Pleistocene species of *Dacrydium*. However, it was originally described from the German Oligocene, and Janssen (1979) considered it a *Modiolula* allied to the Recent *M. phaseolina* (Philippi, 1844). The name *D. hyalinum* as introduced by Monterosato (1875: 10) is virtually a *nomen nudum*, as it is only stated that ‘it has hitherto been confused with *D. vitreum*’ but ‘differs in size and shape’; it can nevertheless be understood by implicit reference to

previous papers (e.g. Monterosato, 1870) where Monterosato more formally compared Mediterranean '*D. vitreum*' to the Nordic ones and gave good descriptive elements. Otherwise, there is no formal description of *D. hyalinum* until Locard (1892: 342–343). Nevertheless, the name is dated from 1875 by most authors, including Locard (1892) and Mattson and Warén (1977), and we can see no reason to abandon this usage.

Examination of a growth series of *Dacrydium hyalinum* shows that the secondary teeth are formed during a short interval of the shell growth, at a size between 1 and 1.2 mm, correlated with the buildup of the dorsal buttress. Just prior to this stage (Figs 23–24), the row of primary teeth has its final length but is still very narrow; it then becomes thicker (i.e. with longer teeth), the secondary ligament starts forming and the secondary teeth are added beyond it by inwards thickening of the dorsal margin (Figs 21–22).

D. hyalinum usually broods 5–10 larvae at a size starting from 1.35 mm, and our own figures agree with those of Ockelmann (1983: 120).

Dacrydium cf. *hyalinum* (Figs 27–32)

Material examined: North Atlantic seamounts: Gorrige Bank, Seamount 1 sta. CP20 (36°34'N, 11°30'W, 305–320 m), 2 spm. (1.25 × 0.9 mm – 1.4 × 0.95 mm), MNHN.—Josephine Bank, Seamount 1 sta. DW61 (36°40'N, 14°16'W, 200–205 m), 4 spm. (1.35 × 0.95 mm), SMNH.—Seine Bank, Seamount 1 sta. DE80 (33°48'N, 14°23'W, 250–256 m), 1 v. (1.5 × 1.05 mm), MNHN.—Ampère Bank, Seamount 1 sta. DE95 (35°05'N, 12°55'W, 197–210 m), 2 spm. (1.1 × 0.75 – 1.2 × 0.85 mm), SMNH; sta. CP99 (35°04'N – 12°55'W, 225–280 m), 5 spm. (1.25 × 0.85 mm – 1.6 × 1.05 mm), MNHN.—Plato Bank, Seamount 2 sta. DW 240 (33°12.3'N, 29°01.9'W, 565 m), 4 spm. (1.9 × 1.25 – 2.35 × 1.45 mm); sta. DW 247 (33°13.7'N, 29°35.3'W, 580 m), 1 spm. (2.05 × 1.35 mm); all MNHN.—Atlantis Bank, Seamount 2 sta. DW 255 (34°04.9'N, 30°15.3'W, 340 m), 1 sh. and 6 v. (1.7 × 1.15 mm – 2.75 × 1.65 mm); sta. DW 258 (33°59.8'N, 30°12.1'W, 420 m), 20 spm. and 7 v. (1.4 × 0.95 – 2.4 × 1.5 mm); sta. TS 270 (34°04.8'N, 30°14.9'W, 330 m), 5 spm., 7 sh. and 25 v. (0.9 × 0.6 mm – 2.0 × 1.3 mm); sta. DW 274 (34°05.1'N, 30°13.6'W, 280 m), 7 spm. and 1 v. (0.95 × 0.7 mm – 2.25 × 1.35 mm); all MNHN.

Remarks: Specimens of *Dacrydium* collected on the shallower part of Gorrige and Ampere seamounts, off SW Portugal and Morocco respectively, are remarkable in that the

secondary teeth are not separated from the primary teeth by any interruption, and thus lack a secondary ligament. This distinctive hinge morphology (Fig. 31, similar to that of juvenile *D. ockelmanni*, see Fig. 12) would suggest that these forms are specifically distinct from *D. hyalinum*, but the same populations contain also specimens with a short, but distinct interval and are then not morphologically separable from some *D. hyalinum* from the strait of Gibraltar. There is also a difference in the number of brooded embryos, which were only two in each of the two specimens opened.

Specimens from the Atlantis Bank (Figs 27–29), conversely, always have primary and secondary teeth well separated. They differ from Mediterranean *D. hyalinum* in being more fragile, more elongate, somewhat larger (2.7 mm whereas Mediterranean specimens rarely reach over 2 mm), and in having smaller and tighter clusters of primary teeth. They also brood a small number of larvae, similar in diameter and aspect to those of *D. hyalinum* and much smaller than those of *D. viviparum*.

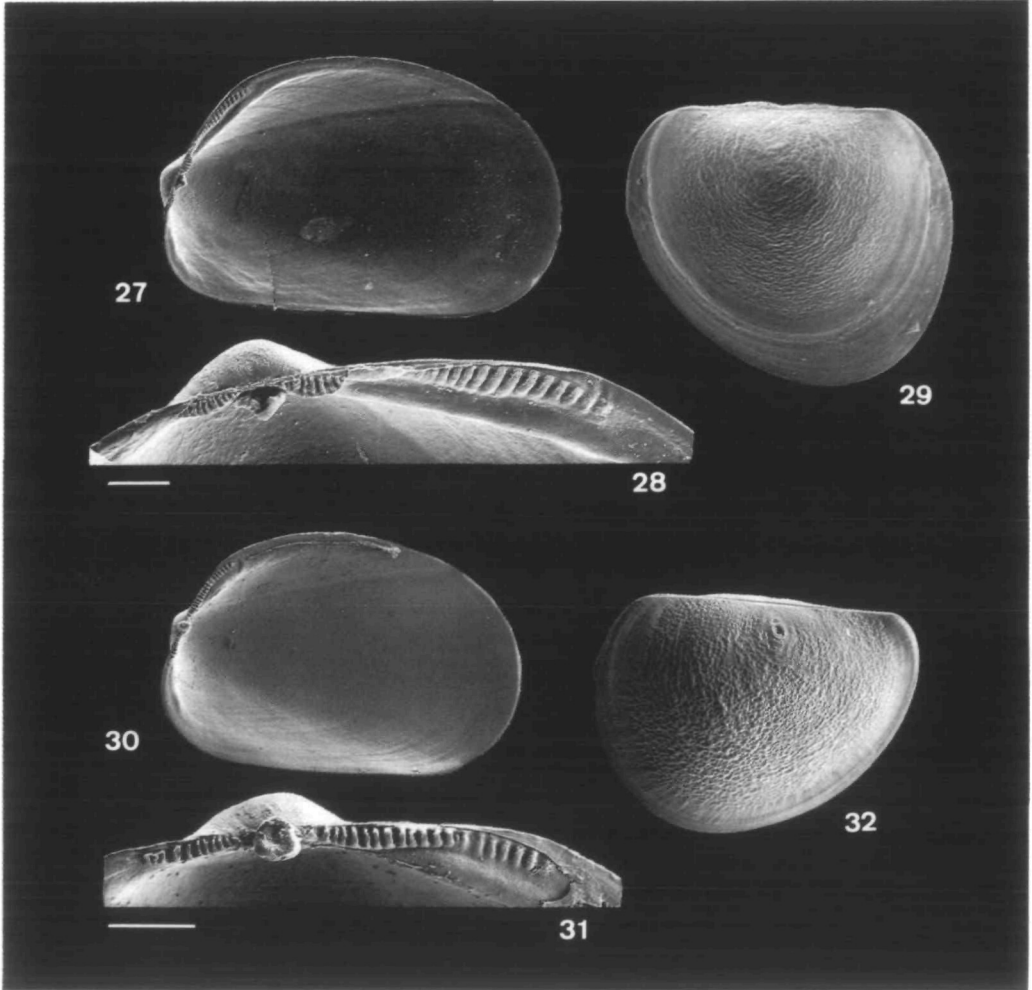
The taxonomic treatment to be given to these seamount forms is quite unclear with existing data. The most likely hypothesis, at least for Ampere and Gorrige Banks, is that they are quite isolated populations related to *D. hyalinum*. This is supported by the observation that such very small species are easily transported as adults and show little endemicity on the seamounts (e.g. the skeneid *Anekes paucistriata* Warén, 1992, 1.5 mm high, was found in the plankton over Gorrige Bank, and is abundant in the benthos on all the North Atlantic seamounts explored; see Warén, 1992: 165–166). A connection with the Mediterranean water is possible, as proved by drifting buoy experiments where floats followed Mediterranean water eddies ('meddies') as far out as the Hyeres Bank in the mid-Atlantic (Richardson, 1996). For the more remote population of the Atlantis Bank, a tenable alternative interpretation is that they are not conspecific and that a brooding form has been derived independently from the deeper, non-brooding *D. wareni* described below.

Dacrydium viviparum Ockelmann, 1983

Dacrydium viviparum Ockelmann, 1983: 118–121; Figs 52–54, 56, 57.

Type locality: Reykjanes Ridge, 60°37'N, 27°52'W, 1505 m.

Type material: Holotype and most of the type series from Ingolf sta. 78, in ZMC. Paratypes: 2



Figures 27–29. *Dacrydium* cf. *hyalinum* from Atlantis Bank, Seamount 2 sta. DW 274. **27.** Right valve (length 1.85 mm). **28.** Detail of hinge. **29.** One of the five incubated larvae, showing incipient postlarval growth (diameter 238 μm). **Figures 30–32.** *Dacrydium* cf. *hyalinum* from Gorringer Bank, Seamount 1 sta. CP 20. **30.** Left valve (1.4 mm). **31.** Detail of hinge. **32.** One of the two incubated larvae found inside the specimen (diameter 214 μm). Scale bars: 100 μm .

shells and 3 valves in BMNH (no. 198335), and 2 shells and 3 valves in USNM (no. 822399).

Distribution: Only known from the Reykjanes Ridge (Ockelmann, 1983).

Remarks: This species was not present in our material. According to Ockelmann's (1983) description and figures, *D. viviparum* resembles *D. hyalinum* in having a similar oblong-modioliform shape, a short and steep antero-dorsal region, a hinge with both pri-

mary and secondary ligaments and protoconch with granular-punctate sculpture. The principal shell difference is the size of the protoconch, which in *D. viviparum* is ca. 270 μm long instead of 220 μm in *D. hyalinum* and related seamount populations.

Dacrydium occidentale Smith, 1885
(Figs 33–35)

Dacrydium occidentale Smith, 1885: 282; pl. 17, fig. 1–1a

Type locality: off Culebra Island, West Indies, 390 fathoms (710 m).

Type material: A shell (the figured syntype; no holotype designated) 4.5 mm long, from Challenger Expedition, sta. 24, destroyed by the acidic glass, in BMNH.

Material examined: Florida, off Fowey Rocks, 'in the Gulf Stream', 465 fathoms (846 m), 1 spec., leg. Rush (4.2 × 2.5 mm), USNM (no. 83106).—Virgin Islands, 200–300 fathoms (364–546 m), 1 juvenile specimen, leg. Goes, 1869 (1.75 × 1.15 mm), SMNH.

Description: Shell up to 4.5 mm long. Antero-ventral region very small, resulting in a quite narrowing anterior profile; antero-dorsal region slightly curved, sloping ca. 45° and very evenly connecting the broadly rounded dorsal margin; ventral margin concave, connecting to a rounded posterior margin. Umbo small, well below the horizontal midline, orthogyrous. Protoconch approximately 170 μm in maximum diameter. Teleoconch smooth except for concentric growth striae, with a quite thick periostracum.

Hinge with a broad primary ligament on a rather shallow chondrophore beneath the umbo. Two short clusters of 8–9 narrow, slightly diverging primary teeth on both sides of the chondrophore, separated by a narrow toothless interval above the ligament. A secondary ligament at the end of the posterior cluster, followed by a long secondary dorsal series of ca. 40 teeth increasing gradually in length towards the posterior part and extending over half the length of the dorsal buttress. Dorsal buttress prominent, reaching approximately the anterior 1/3 of the shell.

Remarks: A redescription of this species was needed as Smith (1885) only figured the outside and hinge characters later proved to be critical. The specimen in Fig. 33 matches Smith's figure for both size and outline, and may confidently be considered as conspecific. We also examined a very small specimen from off Virgin Islands, collected near the type locality in comparable depths, but its identification is only tentative.

It is by mistake that *D. occidentale* is placed in the synonymy of *D. vitreum* by Bernard (1983: 19).

***Dacrydium wareni* new species**
(Figs 36–43)

Dacrydium cf. *hyalinum*: Salas, 1996: 53, figs. 94–96 and 97–99.

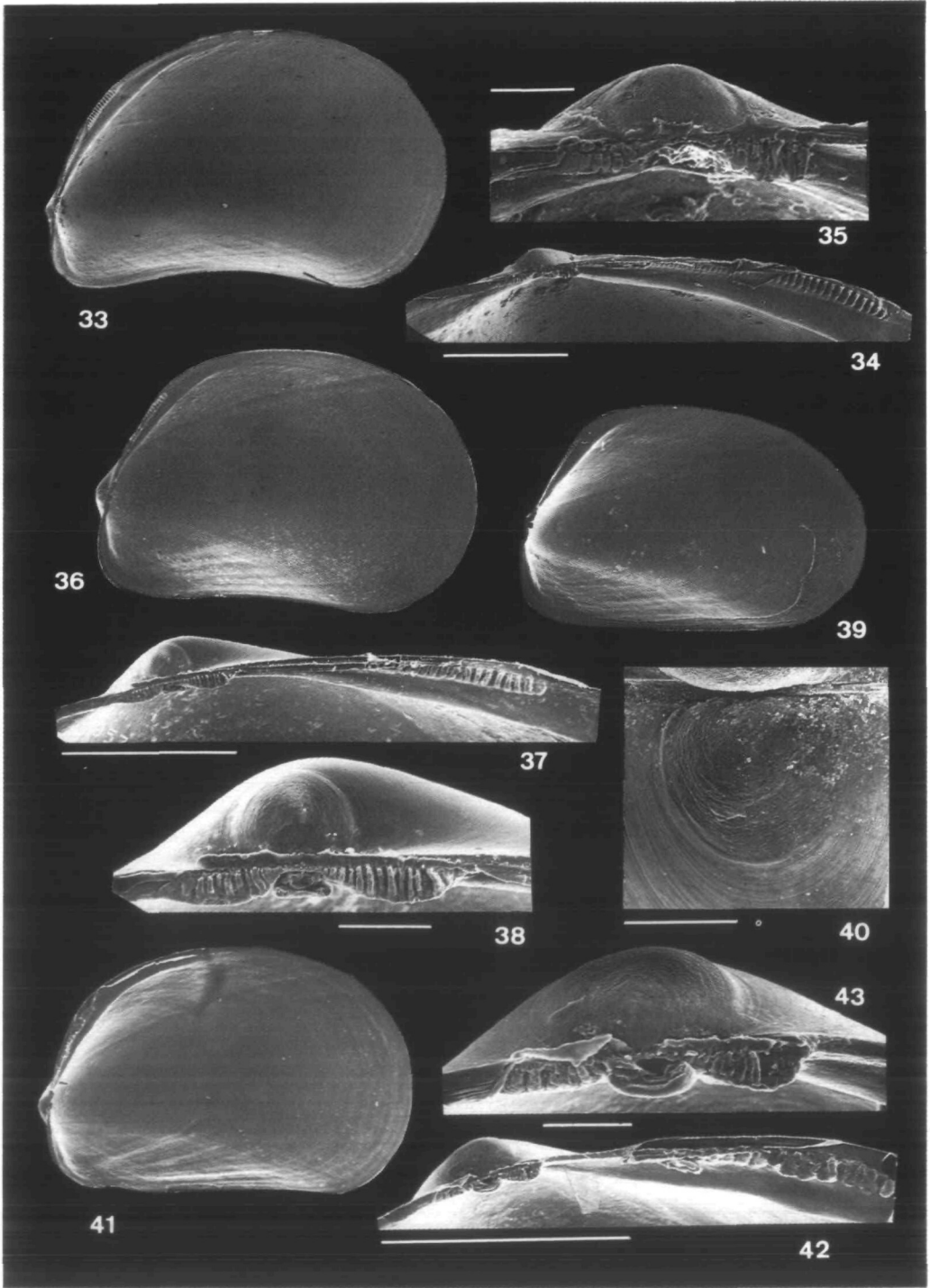
Type locality: Off Northwestern Morocco, 35°31'N, 07°42'W, 1510 m.

Type material: Holotype (spm., 3.9 × 2.65 mm) and 9 paratypes (spm., 3.2 × 2.1 mm – 4.0 × 2.7 mm) from the type locality, Balgim sta. CP63, in MNHN. Paratypes, Balgim sta. CP92 (34°24'N, 07°30'W, 1182 m), 11 spm. (1.0 × 0.7 mm – 4.9 × 3.1 mm; Salas, 1996, Figs 94–96), in SMNH.

Material examined (all MNHN except where stated): The type material and—Off Northwestern Spain: Travailleur sta. 1 (43°00'40"N, 9°37'40"W, 2018 m), 2 sh. (3.5 × 4.6 mm; cited by Locard, 1898: 364–366, as *D. vitreum*); Seamount 1 sta. DW 108 (42°51'N, 11°53'W, 1110–1125 m), 1 v. (4.45 × 2.9 mm); sta. DW111 (42°40'N, 11°36'W, 675–685 m), 6 spm. (2.65 × 1.8 mm – 4.75 × 1.8 mm); sta. DW116 (42°52'N, 11°51'W, 985–1000 m), 2 spm. and 9 v. (2.65 × 1.85 mm – 4.55 × 2.8 mm), SMNH; sta. CP117 (42°43'N, 11°45'W, 770 m), 11 spm. (1.75 × 1.2 mm – 3.9 × 2.6 mm), SMNH.—Off Northwestern Morocco: Balgim sta. CP62 (35°31'N, 07°26'W, 1250 m), 10 spm. (3.4 × 2.3 mm – 4.5 × 2.8 mm); sta. DW88 (34°20'N – 07°19'W, 740 m), 1 spm. (2.1 × 1.4 mm); sta. CP90 (34°21'N, 07°24'W, 890 m), 1 spm. (3.5 × 2.1 mm; Salas, 1996, figs 97–99); sta. DW 94 (34°25'N, 07°28'W, 1175 m), 1 spm. (1.1 × 0.8 mm); sta. CP95 (34°24'N, 07°39'W, 1378 m), 17 spm. (1.9 × 1.3 mm – 4.5 × 3.0 mm); sta. DW96 (34°23'N, 07°40'W, 1255 m), 1 spm. (3.7 × 2.4 mm); sta. CP108 (36°11'N, 08°06'W, 1527 m), 2 spm. (1.3 × 0.95 mm – 3.5 × 2.2 mm).—North Atlantic seamounts: Josephine Bank, Seamount 1 sta. DE48 (36°48'N, 14°32'W, 1350–1360 m); Lion Bank, Seamount 1 sta. DW63 (35°15'N, 15°35'W, 630 m); Hyères Bank, Seamount 2 sta. DW 182 (31°23.2'N, 28°53.5'W, 480 m), 18 spm. and 2 v. (2.35 × 1.5 mm – 3.45 × 2.2 mm); Irving Bank, Seamount 2 sta. DW237 (32°15.9'N, 27°31.8'W, 670 m), 1 spm. (2.35 × 1.55 mm); sta. DW 238 (32°17.3'N, 27°32.3'W, 890 m), 1 v. (4.0 × 2.6 mm); Plato Bank, Seamount 2 sta. DW 242 (33°11.8'N, 28°57.0'W, 710 m), 2 v. (3.65 × 2.15 – 4.0 × 2.15 mm).

Description: Shell up to 4.9 mm long, thin, translucent, oblong-modioliform in shape. Antero-ventral region hardly projecting forwards from the umbo, and quite rounded; antero-dorsal region sloping quite abruptly (45° to 50°) from the dorsal margin and making a blunt angle with it; ventral margin slightly concave connecting to a semicircular posterior margin. Umbo small, slightly below the horizontal midline, orthogyrous. Protoconch small (160/170 × 145 μm), equilateral, bordered by a very narrow, indistinct smooth rim. Teleoconch smooth and glossy externally, with growth lines hardly distinct; a faint radial fold running dorsally from the umbo to the posterior part of the dorsal margin. Periostracum thin, brown-greenish.

Hinge with a rather small primary ligament



Figures 33–35. *Dacrydium occidentale* Smith, 1885 from off Florida. **33.** Right valve (length 4.2 mm). **34, 35.** Details of hinge. **Figures 36–40.** *Dacrydium wareni* n. sp. from off Morocco. **36.** Right valve of the holotype from Balgim sta. CP 63 (length 3.9 mm). **37, 38.** Detail of hinge. **39.** Right valve of a paratype from Balgim sta. CP 92 (length 3.0 mm). **40.** Protoconch of another paratype from Balgim sta. CP 92. **Figures 41–43.** *Dacrydium wareni* n. sp. from Hyeres Bank, Seamount 2 sta. DW182. **41.** Right valve (length 2.75 mm). **42, 43.** Detail of hinge. Scale bars: **34, 37, 42, 500** μm ; **35, 38, 40, 43, 100** μm .

beneath the umbo, in a narrow chondrophore. Two clusters of 12–14 narrow, parallel primary teeth on both sides of the primary ligament, separated by a very narrow toothless interval above the ligament. A relatively long secondary ligament at the end of the posterior cluster, followed by a secondary dorsal series of 20–25 teeth increasing gradually in length towards the posterior part and extending over two thirds of the length of the dorsal buttress. Dorsal buttress prominent, reaching approximately the anterior 1/4 of the shell and strongly sloping forwards.

Two elongated and ill-defined adductor muscle scars; the anterior one under the end of the anterior ridge, the posterior one behind the end of the dorsal buttress.

Distribution: This species appears widely distributed in the Northeastern Atlantic, on the West European continental margin from NW Iberian Peninsula to Morocco, and on the Lusitanian and Mid-Atlantic seamounts, mainly between 700–1500 m depth.

Remarks: The absence of any brooded larva among approximately one hundred live-taken specimens contrasts with the occurrence of embryos in nearly every other specimen in *D. hyalinum* and conclusively indicates a non-brooding reproductive biology. This is reflected in the diameter of the protoconch which is markedly smaller than in *D. hyalinum*. The shells of *D. wareni* also differ from the latter in being much more fragile, with a more delicate hinge and smaller umbo.

This species most resembles *D. occidentale* with which it shares a similar hinge type, protoconch, and size of teleoconch. Large specimens of *D. wareni* may have an elongate outline with concave ventral margin and are then very similar to the Caribbean species. The most convincing difference is in the number of secondary teeth, which is almost twice as much in *D. occidentale* as in a *D. wareni* of comparable size; the antero-ventral region is generally more developed, and the antero-dorsal region more steeply sloping in *D. wareni* than in *D. occidentale*.

Soot-Ryen's (1966) description and figure of

Dacrydium sp. from the Michael Sars Expedition, sta. 24 (35°34'N, 07°35'W, 1615 m), are likely to be *D. wareni*, considering also the hydrological characteristics at the depth, and not *D. hyalinum* as Mattson & Warén (1977) suggested.

Dacrydium dauvini new species (Figs 44–48)

Type locality: Atlantis Bank, 34°05.1'N, 30°13.6'W, 280 m, on bioclastic sand.

Type material: Holotype (sh., 1.25 × 0.85 mm) and 2 paratypes (1 sh. and 1 v., 1.15 × 0.75 mm) from the type locality, Seamount 2 sta. DW 274, MNHN. Paratypes (10 sh., 1.2 × 0.8 to 1.35 × 0.9 mm) from Seamount 2 sta. TS 270 (34°04.8'N, 30°14.9'W, 330 m), 5 MNHN, 5 SMNH.

Description: Shell up to 1.35 mm long, oblong, translucent. Antero-ventral margin broadly rounded, hardly projecting forwards from the umbo; antero-dorsal region very short and very steeply sloping (70°–80°) from the dorsal margin with which it makes a blunt angle; ventral margin nearly straight, quite short, connecting to a broadly rounded posterior margin. Umbo large and little prominent, level to the horizontal midline, orthogyrus. Protoconch relatively small (170 × 145 μm), very slightly inequilateral, bordered by a conspicuous smooth rim. Teleoconch sculpture of concentric growth lines, some of which make irregularly spaced elevated concentric lines. Two characteristic radial folds, a faint one running from the umbo to the posterior part of the dorsal margin, and a stronger one just beneath the anterior part of the dorsal margin.

Hinge nearly symmetrical, with a large primary ligament beneath the umbo and on a rather shallow chondrophore. Two clusters of primary teeth, 11–13 in the antero-ventral side and 13–15 on the antero-dorsal, separated by a narrow, hardly crenulated rim above the chondrophore. Dorsal buttress very short, meeting the incipient dorsal fold at its anterior termination.

Distribution: The species is known only from



Figures 44–48. *Dacrydium dauvini* n. sp. from Atlantis Bank. **44.** Right valve of the holotype from Seamount 2 sta. DW 274 (length 1.25 mm). **45.** Detail of hinge. **46.** Paratype from Seamount 2 sta. TS 270 (length 1.2 mm). **47, 48.** Protoconch and microsculpture of early teleoconch of another paratype from DW 274, 1.25 mm long (diameter of protoconch 170 μm). **Figures 49–51.** *Dacrydium filiferum* n. sp. from Atlantis Bank. **49.** Right valve of the holotype from Seamount 2 sta. TS 270 (length 1.1 mm). **50.** Detail of hinge. **51.** Protoconch and microsculpture of early teleoconch of another paratype 1.2 mm long (diameter of protoconch 200 μm). Scale bars: 100 μm .

Atlantis Bank, where it coexists with *D. filiferum* n. sp. and *D. cf. hyalinum*.

Remarks: The extremely short hinge line, sloping steeply forwards, gives a characteristic outline resembling the shells of *Limatula*. The strong radial folds, perhaps a mechanical alternative to a long dorsal buttress, also make it very different from any described species. The hinge has no secondary teeth, whereas these are already formed in a *D. hyalinum* of comparable size (see Figs 21–22).

Since no living animals have been taken, nothing is known of its biology; the size of the protoconch is intermediate between known brooders and non-brooders and gives no clue on its reproductive biology.

The species is named after Jean-Claude Dauvin, who insisted on bringing to the Seamount 2 expedition the suprabenthic sled which collected most of the specimens.

Dacrydium filiferum new species (Figs 49–51)

Type locality: Atlantis Bank, 34°04.8'N, 30°14.9'W, 330 m, on bioclastic sand.

Type material: Holotype (sh., 1.1 \times 0.75 mm) and paratypes (3 sh., 1.2 \times 0.8 to 1.3 \times 0.85 mm) from the type locality, Seamount 2 sta. TS 270, MNHN. Paratype (1 v., 1.15 \times 0.8 mm), from Seamount 2 sta. DW 255 (34°04.9'N, 30°15.3'W, 340 m), MNHN.

Description: Shell up to 1.3 mm long, oblong, translucent. Antero-ventral region large, broadly rounded, reaching a little forwards from the umbo; antero-dorsal region very short, sloping abruptly (ca. 70°) from the dorsal margin and making a quite abrupt angle with it; ventral margin slightly convex, connecting to a broadly rounded posterior margin. Umbo large and quite flat, well above the horizontal midline, orthogyrous. Protoconch (200 \times 165 μm), very slightly inequilateral, bordered by a conspicuous smooth rim. Sculpture of the teleoconch of concentric growth lines, some of which make irregularly spaced elevated concentric lines, and of very tenuous, diverging radial threads. There are two charac-

teristic radial folds, a faint one running from the umbo to the posterior part of the dorsal margin, and another just beneath the anterior part of the dorsal margin.

Hinge symmetrical, with a large primary ligament beneath the umbo and on a rather shallow chondrophore. Two clusters of 11–15 primary teeth on both sides of the chondrophore, separated by a narrow, hardly crenulated interval above the ligament. Dorsal buttress very short, meeting the incipient dorsal fold at its anterior termination.

Distribution: The species is known only from Atlantic Bank.

Remarks: This species resembles *D. dauvini* in shape and size, and in the presence of two dorsal folds along the shell. The outline of *D. filiferum* is more 'modioliform', with the umbo larger and flatter, in a position more dorsal on the hinge line. The antero-ventral region is larger, more prominent anteriorly and convex; the ventral margin is more convex. *D. filiferum* has a characteristic microsculpture of radial threads on the umbonal region and extending over most of the shell, which is not present in *D. dauvini*; this has been seen to be a reliable specific character separating e.g. *D. vitreum* from *D. ockelmanni*.

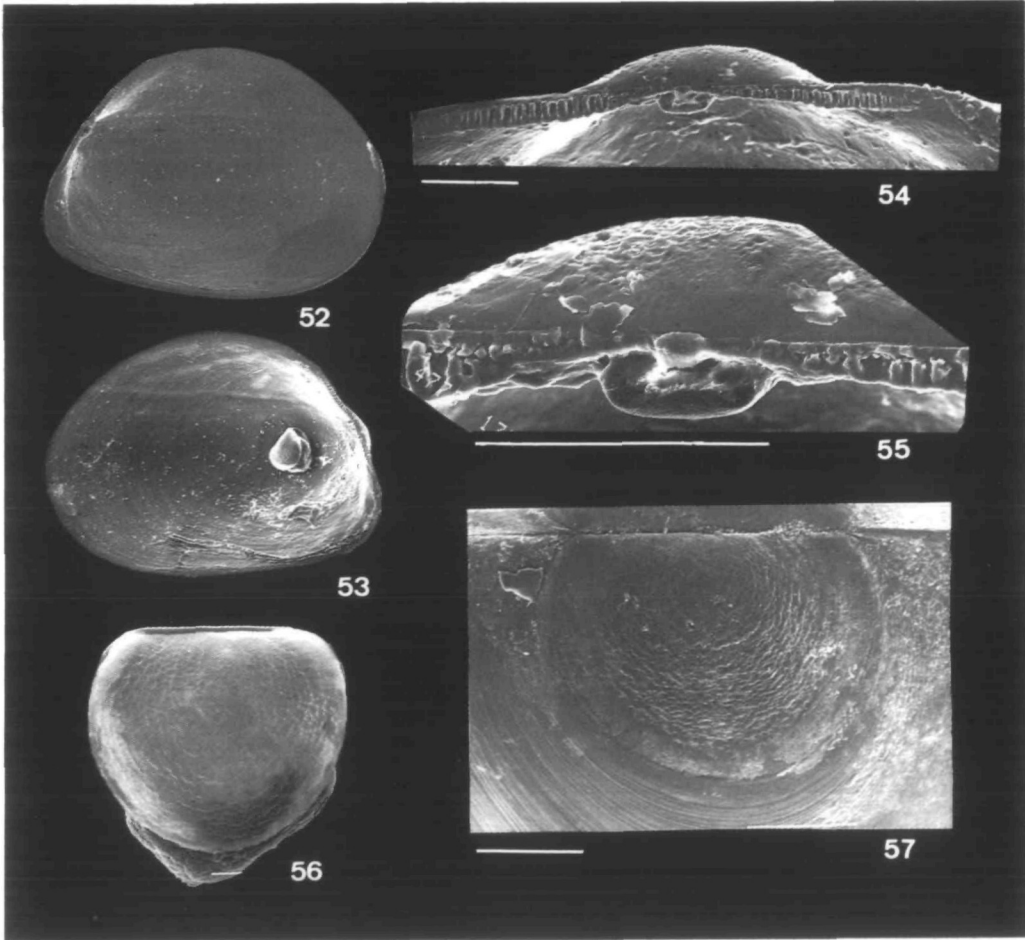
No living specimens have been taken, but the size of the protoconch may suggest larval incubation.

Dacrydium balgimi new species (Figs 52–57)

Type locality: Off Northwestern Morocco, 35°12'M. 07°53'W, 2035 m, ooze, corals.

Type material: Holotype (spm. 1.4 \times 1.1 mm), with one incubating larva in protoconch stage; paratypes, 2 spm. (1.0 \times 0.75 mm – 1.15 \times 1.9 mm), all from Balgim sta. CP68, in MNHN.

Description: Shell up to 1.4 mm long, thin. Antero-ventral region broadly rounded; antero-dorsal region sloping ca. 50° and gradually continuing into a broadly rounded dorsal margin; ventral margin very slightly convex, connecting to a semicircular posterior margin.



Figures 52–57. *Dacrydium balgimi* n. sp. from Ibero-Moroccan Gulf, Balgim sta. CP68. **52, 53.** Right and left valves of the holotype (length 1.4 mm). **54, 55.** Detail of hinge. **56.** Single immature larva found inside the holotype (diameter 180 μm). **57.** Protoconch and microsculpture of early teleoconch of a paratype 1.15 mm long (diameter of protoconch 315 μm). Scale bars: 100 μm .

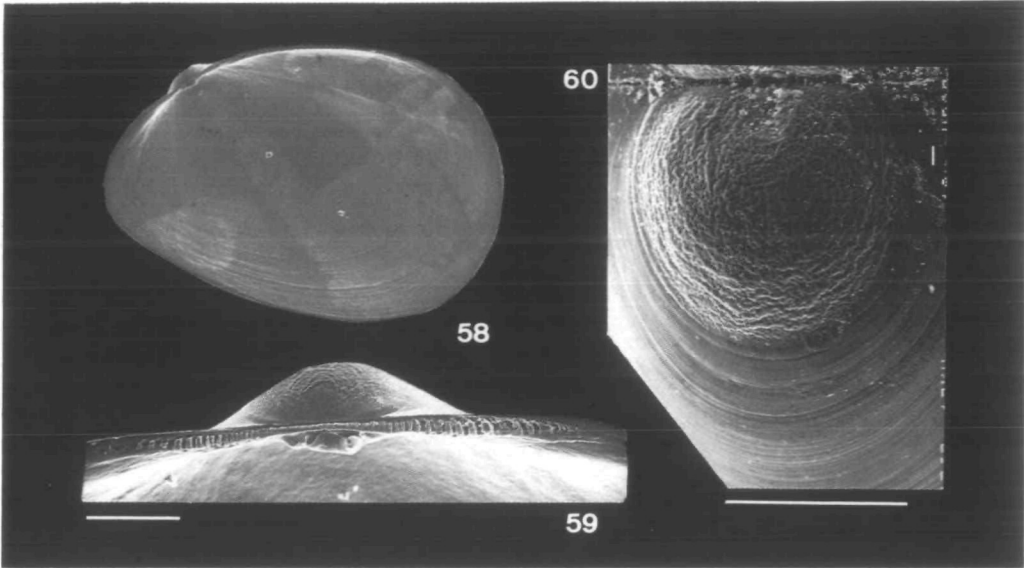
Umbo very large and flat, level with the horizontal midline. Protoconch (315 \times 230 μm), very slightly inequilateral, bordered by a very broad, flat smooth area. Teleoconch with only irregular growth lines. A very weak, but sharp fold running from the umbo to the posterior end of the dorsal margin.

Hinge nearly symmetrical, with a large primary ligament beneath the umbo on a rather shallow chondrophore. Two clusters of ca. 15 primary teeth on each side of the ligament, separated by a narrow toothless interval above the chondrophore. Dorsal buttress very short and poorly defined.

Distribution: The species is known only from the type locality.

Remarks: *D. balgimi* differs from the other described *Dacrydium* by its very large and hardly prominent umbo, and largest known protoconch in the genus. It lacks secondary teeth at a size where other species have completed their adult hinge morphology, and for this reason may be considered neotenous.

The holotype was brooding a single, immature (180 μm diameter) larva, which proves sexual maturity at a shell size of 1.4 mm, but this does not preclude that the species may



Figures 58–60. *Dacrydium* cf. *speculum* from Cape Verde Basin, Eumeli sta. KG07. 58. Right valve (length 1.85 mm). 59. Detail of hinge. 60. Detail of protoconch and microsculpture of early teleoconch of another specimen 1.3 mm long (diameter of protoconch 155 μ m). Scale bars: 100 μ m.

grow somewhat larger.

The hinge of this species shows at high magnification the remains of some minute teeth, formed earlier than the paired 'primary' set, and which may be the true provincial teeth.

The locality where this species was collected also yielded deep-water corals, which may indicate an affinity for deep hard bottoms.

Dacrydium cf. *speculum* Poutiers, 1989
(Figs 58–60)

Dacrydium speculum Poutiers, 1989: 210–210; Figs 1a–c, 3a.

Type locality: off SW Ceylon, 5°37'S, 78°24'E, 3660 m.

Type material: Holotype (spm., 1.15 \times 0.85 mm) and paratype (1 v., mounted on a SEM plot and badly damaged) from Safar II Expedition, sta. 2 SIPAN 19, in MNHN.

Material examined: Cape Verde Basin: Eumeli 2 sta. KG 07 (21°03'N, 31°11'W, 4580 m), 2 spm., 1 v. (1.3 \times 0.95 mm – 1.85 \times 1.27 mm), MNHN.

Description: Shell up to 1.85 mm long, extremely fragile. Antero-ventral region quite large and prominent; antero-dorsal region very gently sloping and very gradually connecting to the broadly rounded dorsal margin; maximum elevation well behind the vertical mid-

line; ventral margin slightly convex, connecting to a very broadly rounded, somewhat truncated, posterior margin. Umbo large and blunt, well above the horizontal midline. Protoconch (155 \times 155 μ m) equilateral, bordered by a narrow smooth rim. Teleoconch smooth, except for inconspicuous growth lines.

Hinge with a small but quite broad primary ligament on a shallow chondrophore beneath the umbo. Two clusters of 18–20 small primary teeth on each side, separated by a narrow toothless interval above the umbo. Posterior cluster slightly longer, occupying most of the length of the dorsal buttress which is inconspicuous and reaches hardly the 1/3 of the shell length.

Distribution: *Dacrydium speculum* was described from the Indian Ocean, and its presence in deep water from the Atlantic Cape Verde Basin is perhaps questionable. It may however be considered because it is an abyssal species, and that there are several other cases of possible cosmopolitan species. Examples (Knudsen, 1970) are *Bentharca asperula* (Dall, 1881) and *Abra profundorum* (Smith, 1885). The question of whether this cosmopolitanism is real, or if morphological differentiation is too slight to allow recognition of species is beyond the scope of this paper.

Remarks: This *Dacrydium* is very characteristic and different from the other Atlantic species by its globular, rounded-modioliform shape, with the antero-ventral shell region rather convex and somewhat prominent. It is also remarkable in the shape of the protoconch, which is circular and equilateral in outline. Our description is based on the specimens from Cape Verde Basin, which differ from the holotype in being slightly larger and having a more rounded antero-ventral region.

Dacrydium elegantulum hendersoni
new subspecies
(Figs 61–65)

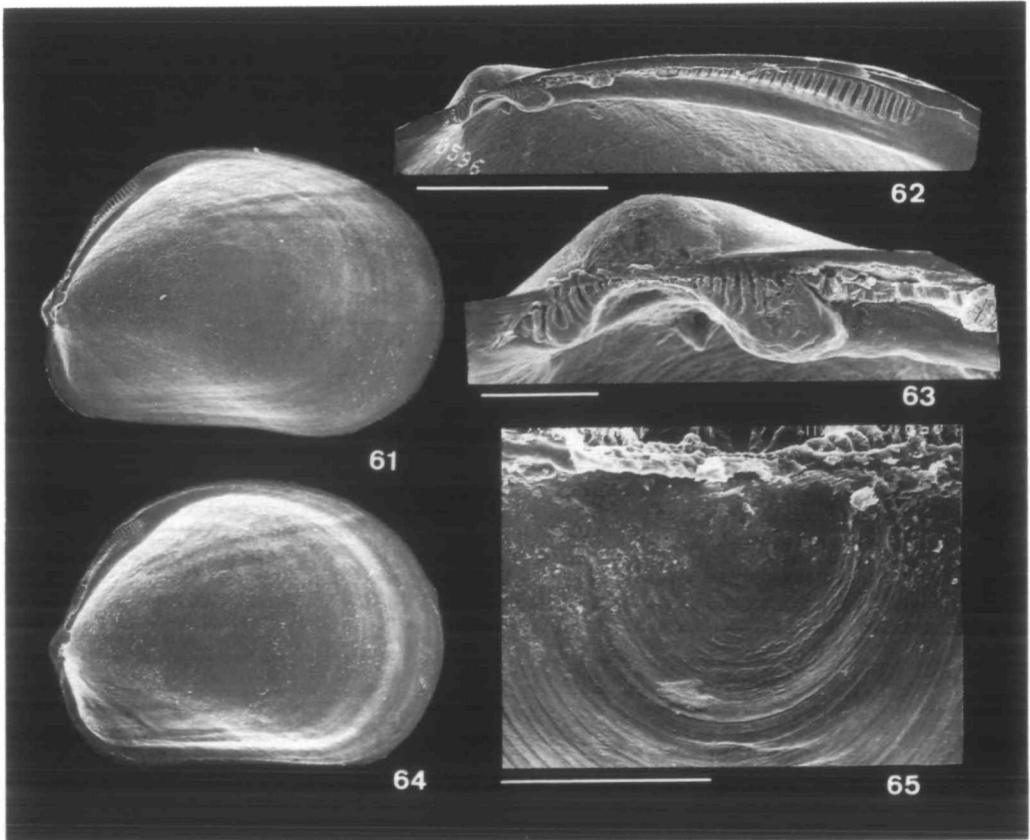
Type locality: Florida, off Sand Key, 100 fathoms (182 m).

Type material: Holotype (spm., 2.8 × 2.35 mm) and paratypes (5 spm., 30 v.; 2.7 × 2.1 – 3.4 × 2.55 mm) from off Sand Key, Florida, Eolis sta.

324, 182 m, Henderson leg., USNM 459094.— Paratypes (11 spm. and 11 v., 2.9 × 2.25 mm – 3.45 × 2.5 mm) from off Sand Key, Eolis sta. 164, 168 m, USNM 459102; (11 spm. and 20 v.; 2.35 × 1.85 mm – 3.6 × 2.65 mm) from off Sand Key, Eolis sta. 323, 200 m, USNM 459099; (6 spm. and 11 v.; 2.1 × 1.7 mm – 3.6 × 2.55 mm), from off Sand Key, Eolis sta. 338, 155 m, USNM 459098.

Material examined: The type material and—South-western Florida: off Sand Key, 136–218 m, 5 spm., 30 v.; off Fowey Light, 85–200 m, 26 spm. and 184 v.; Triumph Reef, 128–164 m, 27 spm., 14 v.; Ragged Key, 136–164 m, 12 v.; Ajax Reef, 128–182 m, 21 v.; Key West, 136–200 m, 45 spm., 58 v.; Western Dry Rocks, 164–200 m, 2 spm., 13 v.; Caesar's Creek, 164 m, 2 spm., 7 v.; all USNM, leg. Henderson. Debray Beach (18 miles East), 500–546 m, 2 spm, USNM.

Description: Shell up to 4 mm long, rather stout. Antero ventral region broadly rounded,



Figures 61–65. *Dacrydium elegantulum hendersoni* n. ssp. from off Florida, Eolis sta. 324. **61.** Right valve of the holotype (length 2.8 mm). **62, 63.** Detail of hinge. **64.** Right valve of a paratype (length 3.0 mm). **65.** Protoconch of another paratype (diameter 145 μ m). Scale bars: **62,** 500 μ m; **63, 65,** 100 μ m.

not projecting forwards from the umbo or receding slightly beyond it; antero-dorsal region sloping ca. 45° from the dorsal margin and forming a very blunt angle with it; ventral margin straight or slightly concave, abruptly connecting to a broadly semicircular posterior margin. Umbo rather small, blunt, well below the horizontal midline, very slightly prosocline. Protoconch (145 × 115 µm) slightly inequilateral, bordered by a very narrow, indistinct rim. Teleoconch with quite distinct growth lines, and with broad irregular opaque whitish streaks seen from both sides by transparency.

Hinge with a narrow primary ligament, on a deep chondrophore, beneath the umbo. Two clusters of 5–10 irregular, diverging teeth on both sides of the chondrophore, the posterior one larger and borne on a prominent club-shaped thickening. A secondary ligament at the end of the posterior cluster, followed by a secondary dorsal series of 25–30 teeth, distinctly increasing in length towards the posterior end, extending over most of the length of the dorsal buttress. Dorsal buttress quite narrow, somewhat arched, reaching approximately the anterior 1/3 of the shell length.

Remarks: This form most resembles the Eastern Pacific *D. elegantulum* Soot-Ryen, 1955, of which it seems to be the Atlantic counterpart. The nominal subspecies is known with certainty only from the Galapagos Islands, and the records from California given by Soot-Ryen are questionable (E. Coan, pers. comm.).

The thickened clusters of primary teeth are the 'tooth-like thickenings . . . on both sides of the deep-set resilifer' mentioned by Soot-Ryen (1955: 87). The only noticeable difference is that the white rays on the shell are less vivid than on Soot-Ryen's holotype from Galapagos. The question of how Central American species or subspecies pairs should be treated has no general answer, as the time of separation by the Isthmus of Panama (approximately 3.5 m.y. ago: Coates & al., 1992) is well within the average time span of a molluscan species.

D. elegantulum hendersoni seems to be quite common on the continental shelf of Florida and, in view of its similarity in size and outline, certainly accounts for the Caribbean records of '*Dacrydium vitreum*' (e.g. Abbott, 1974).

PARSIMONY ANALYSIS

The twelve Atlantic species of *Dacrydium* show a variety of character states in the mor-

phology of the shell, and particularly of the hinge, which may tentatively be used for investigating phylogenetic relationships among the species. As an outgroup, we used *Modiolula phaseolina* (Philippi, 1844) which in juvenile stage resembles very much *Dacrydium hyalinum*, but later loses its primary ligament and fuses primary teeth into a small continuous cluster.

Characters which have been considered as appropriate for coding are shown in Table 2, and were introduced in the matrix with equal weight and unordered. The matrix has been run under the branch and bound option of the PAUP 3.1.1. software package (Swofford, 1993), with zero-length branches collapsed. A single tree was found (fig. 66), with 10 steps and a consistency index CI = 0.7.

DISCUSSION

Phylogeny

The parsimony reconstruction gives some clues to the phylogenetic relationships among the species included. All the species of *Dacrydium* share a persistent primary ligament, a character state which is definitive of the genus.

The first branching in the reconstruction separates *D. elegantulum hendersoni* from the remaining species. This species shares most character states (including the occurrence of colour patterns on the shell) with the outgroup, and thus may be considered as the most plesiomorphic. We consider the absence of colour patterns as a derived state.

The branch including *D. vitreum*, *D. angulare* and *D. ockelmanni* is defined by a loss of the secondary ligament, leading to a hinge where the primary and secondary teeth form a continuous series posterior to the umbo. These three species retain non-incubating development, and *D. angulare* and *D. vitreum* also share the radial microsculpture. This group appears well supported and is likely to be monophyletic.

Another branch includes *D. wareni*, *D. hyalinum*, *D. viviparum* on the one hand, and all the species lacking the secondary teeth on the other hand. The position of *D. occidentale* is not resolved, because this species retains mostly plesiomorphic character states.

The placement of the four species with only primary teeth developed is questionable. The grouping of *D. cf. speculum*, *D. dauvini* and *D.*

Table 2. Matrix of characters used for the parsimony analysis. Character 0: primary ligament lost in adult = 0, persistent = 1; character 1: unpigmented shell = 0, pigmented with patterns = 1; character 2: secondary ligament absent = 0, present = 1; character 3: secondary teeth absent = 0, present = 1; character 4: radial microsculpture absent = 0, present = 1; character 5: slope of antero-dorsal region > 45° = 0, < 45° = 1; character 6: non-incubating = 0, incubating = 1.

Characters	(0)	(1)	(2)	(3)	(4)	(5)	(6)
<i>M. phaseolina</i>	0	1	1	1	0	1	0
<i>D. vitreum</i>	1	0	0	1	1	1	0
<i>D. ockelmanni</i>	1	0	0	1	0	1	0
<i>D. angulare</i>	1	0	0	1	1	1	0
<i>D. hyalinum</i>	1	0	1	1	0	0	1
<i>D. cf. hyalinum</i>	1	0	0	1	0	0	1
<i>D. balgimi</i>	1	0	0	0	0	1	1
<i>D. dauvini</i>	1	0	0	0	0	0	?
<i>D. filiferum</i>	1	0	0	0	1	0	?
<i>D. wareni</i>	1	0	1	1	0	0	0
<i>D. speculum</i>	1	0	0	0	0	1	?
<i>D. viviparum</i>	1	0	1	1	0	0	1
<i>D. occidentale</i>	1	0	1	1	0	1	0
<i>D. e. hendersoni</i>	1	1	1	1	0	1	0

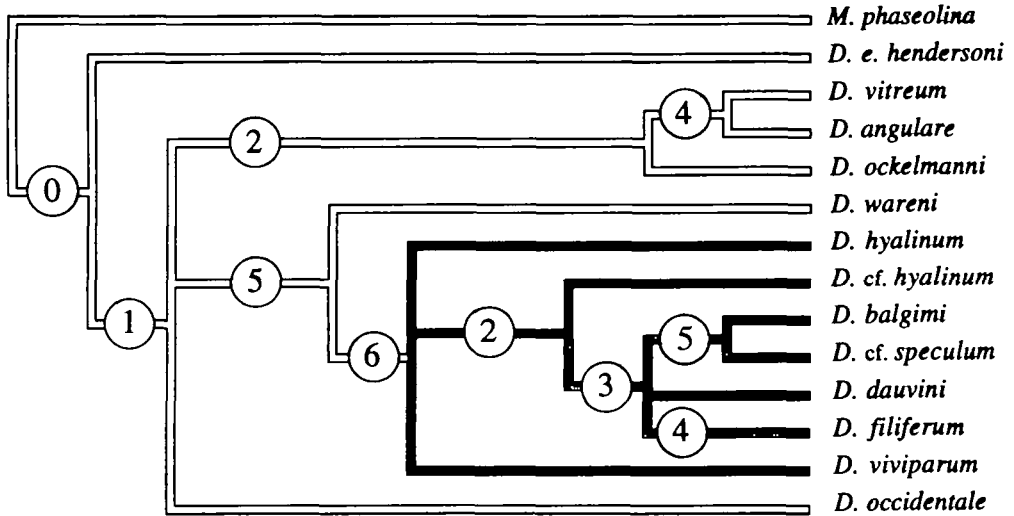


Figure 66. Most parsimonious reconstruction obtained under PAUP using the character matrix of Table 2. Black branches indicate the brooding species, white branches the non-brooding ones, and shaded branches those for which the larval development is not known. Steps: (0) primary ligament persistent; (1) loss of colour patterns; (2) loss of secondary ligament; (3) loss of secondary teeth; (4) radial microsculpture present; (5) antero-dorsal angle steepening to > 45°, and reversal 5-; (6) adquisition of brooding. Note the convergences for characters (2) and (4).

filiferum with the incubating species is the most parsimonious reconstruction, but is not supported by positive data on brooding. The latter species shares the radial microsculpture

with members of the other group, and its grouping with *D. vitreum* would involve only one step more in the tree (a convergence for the loss of secondary ligament and secondary

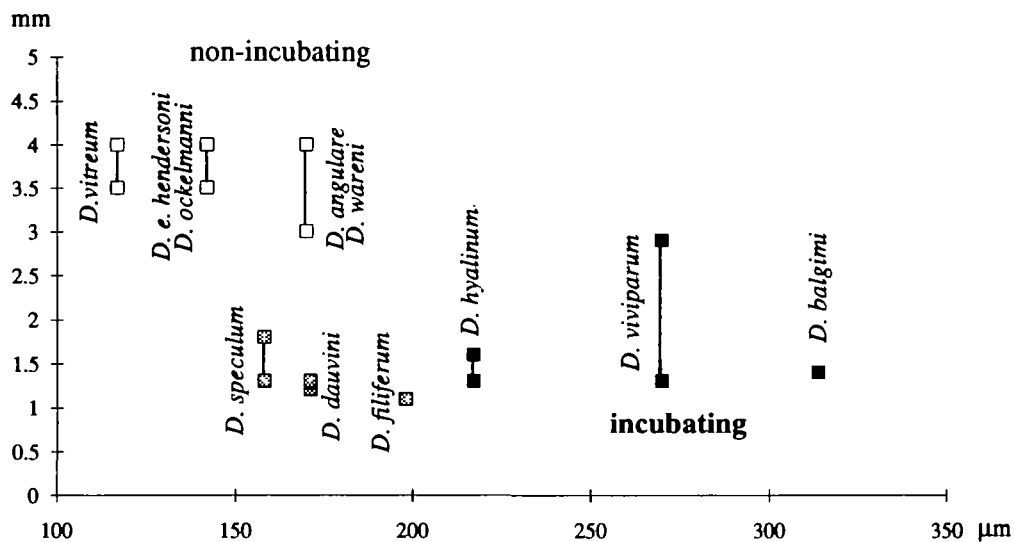


Figure 67. Plot of shell length (vertical axis) versus maximum diameter of protoconch (horizontal axis) for the Atlantic *Dacrydium* species. Black symbols denote the incubating species, white symbols the non-incubating, grey symbols those for which there are no data.

teeth, but not for the microsculpture). Obviously, the loss of the secondary teeth is not a very reliable character for inferring phylogenetic relationships, because species with such a simplified hinge may be paedomorphic derivatives of virtually any *Dacrydium* species.

The remaining species in the branch, which share a reniform outline, steep and short cardinal line, are likely to form a monophyletic group. It is rooted on the non-incubating *D. wareni*, from which the very similar incubating species *D. hyalinum* and *D. viviparum* are inferred as derived. The loss of the secondary ligament in the Gorringe and Ampere populations of *D. cf. hyalinum* implies a convergence with the *D. vitreum* branch.

The genus-group taxon *Quendreda* Iredale 1936 (type species by original designation: *Dacrydium fabale* Hedley, 1904) was characterized by the 'grooved teeth' surrounding the primary ligament which must be understood as the two thickened clusters of primary teeth usually seen in the *D. hyalinum* group. We consider this character state as plesiomorphic and thus unacceptable as definitive of a taxon. Anyway, we prefer not to use formal subgenera because of the uncertainty in the position of species with most paedomorphic hinge.

Brooding

Brooding has been recognized in *D. hyalinum* and the similar seamount forms, in *D. balgimi* and was reported by Ockelmann (1983) in *D. viviparum*. *Dacrydium* is the only genus of the Mytilidae where this is documented. The brooding species display developing larvae in virtually every other specimen, and for this reason we consider that the absence of any larva inside the ca. 100 specimens examined of *D. wareni* or *D. elegantulum hendersoni* is conclusive evidence of non-brooding.

Among deep-sea bivalves, brooding is not particularly common. The only comparable case known to us is that of *Microgloma*, a very small Atlantic protobranch (Warén, pers. comm.; see Salas, 1996: 42–43 for figures of adults and protoconchs). Brood protection is otherwise found in many small bivalves, mainly littoral or shelf species, in unrelated families (see Sastry, 1979: 258–260 for a review).

The acquisition of brooding may be a size-related trend. With the exception of *D. viviparum* which reaches nearly 3 mm in length, the adult size of brooding species is smaller than that of the non-brooding. The small brooding species grow larger larvae (Fig. 67), leading to the apparent paradox that the least space there is, the more is used.

This is better understood when considering that the reduction in volume with smaller size is quite drastic: the volume (assimilated to an ellipsoid) inside a shell 1.5 mm long is about 20 times less than that inside a shell 4 mm long, that of a larva 240 μm long about 3 times that of a larva 150 μm long. With this example, the number of offspring would be some 60 times less in an adult *D. hyalinum* than in *D. ockelmanni* assuming a proportional resource allocation; thus, more protection of the offspring is needed to ensure successful recruitment.

The question of whether brooding has evolved only once, or is a recurrent trend in the genus, is important but cannot be solved. The incubating forms such as *D. viviparum* and the seamount populations referred to *D. cf. hyalinum* can be viewed as isolates in the lineage that includes the Mediterranean *D. hyalinum*, but alternatively could be separate offshoots from a widespread *D. wareni* type, evolving brooding where advantageous in the shallower part of the seamounts.

Hinge morphology

The various hinge morphologies seen in *Dacrydium* can be derived from a basic groundplan resembling *D. hyalinum* or *D. wareni*, with a pair of clusters of primary teeth, a secondary ligament and a posterior row of secondary teeth. The morphology seen in the *D. vitreum* group, with a continuous dorsal series, is derived from this by suppression of the secondary ligament and merging of teeth into a single, functional series. The primary and secondary teeth can still be recognized on juvenile specimens (Fig. 12), but later form a perfect continuum. A similar evolution has led to the hinge morphology in the populations from Gorringer and Ampere Bank of *D. cf. hyalinum*, with primary and secondary teeth separated by a narrowing of the series. Other characters in the species (outline, brooding, slope of dorsal buttress) indicate that this is more related to *D. hyalinum* and thus that this fusing of the teeth has evolved twice.

The hinge with only primary teeth in the adult stage may be remotely 'primitive' according to an ontogenetic criterion, but must be viewed as a secondary loss and thus a derived condition within the group of species considered here. It is a pedomorphic trait, found also in juveniles of the other species of *Dacrydium*. We are not certain that the primary teeth of the adult shell are really derivatives of

the provincial teeth as assumed by Ockelmann (1983): the hinge of some specimens show some very minute teeth formed earlier (see fig. 55) which may be the actual provincial teeth.

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