Melvicalathis, a new brachiopod genus (Terebratulida: Chlidonophoridae) from deep sea volcanic substrates, and the biogeographic significance of the mid-ocean ridge system*

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Abstract

Brachiopods form a small but significant component of the deep-sea benthos in all oceans. Almost half of the 40 brachiopod species so far described from depths greater than 2000 m are small, short-looped terebratulides assigned to two superfamilies, Terebratuloidea and Cancellothyridoidea. In this study we describe *Melvicalathis*, a new genus of cancellothyridoid brachiopod (Family Chlidonophoridae; Subfamily Eucalathinae) from ocean ridge localities in the south and southeast Pacific Ocean, and cryptic habitats within lava caves in glassy basalt dredged from the Southeast Indian Ridge, Indian Ocean. These small, punctate, strongly-ribbed, highly spiculate brachiopods occur at depths between 2009 m and 4900 m, and appear to be primary colonisers on the inhospitable volcanic rock substrate. The ecology and life-history of *Melvicalathis* and related deep-sea brachiopods are discussed. Brachiopods are rarely reported from the much-studied but localised hydrothermal vent faunas of the mid ocean ridge systems. They are, however, widespread members of a poorly known deep-sea benthos of attached, suspension-feeding epibionts that live along the rarely sampled basalt substrates associated with mid-ocean ridge systems. We suggest that these basalt rocks of the mid-ocean ridge system act as deep-sea "superhighways" for certain groups of deep-sea animals, including brachiopods, along which they may migrate and disperse. Although the mid-ocean ridges form the most extensive, continuous, essentially uniform habitat on Earth, their biogeographic significance may not have been fully appreciated.

Key words: Brachiopoda, Cancellothyridoidea, deep-sea benthos, taxonomy, dispersal, submarine superhighways

Introduction

Brachiopods are now minor contributors to benthic biodiversity in modern oceans, compared to their dominance in the benthos of Paleozoic seas, and abundance in Mesozoic oceans. Of the 5000 described genera (Williams, 1996) and c. 30,000 named brachiopod species, only some 100 genera and 336 species remain today (Logan 2007). However, brachiopods remain a small but significant component of the deep-sea benthos in all oceans, particularly on hard substrates. Twenty-six genera and 40 species, representing four of the five extant brachiopod orders, live at depths greater than 2000 m; sixteen of these species range down to abyssal depths greater than 4000 m (Zezina 1985). Nearly half of all these deep-sea brachiopods are short-looped spe-

cies from two terebratulide superfamilies, Cancellothyridoidea and Terebratuloidea; they are typically small, often strongly ribbed, and highly spiculate. Because of the difficulties associated with sampling hard substrates in the deep oceans (Lewis 1999), few deep-sea brachiopods are available for study, and little is currently known of their ecological requirements. However, their wide distribution and taxonomic diversity make them of considerable interest.

Here we describe a new genus of cancellothyridoid brachiopod, *Melvicalathis*, from basalt substrates at depths between 2009 m and 4900 m in the Indian and Pacific Oceans, and redescribe and figure the type species using new material from four additional localities. We discuss the ecology and life history of these deep-sea brachiopods, including the first evidence for probable semi-continuous reproduction in articulated brachiopods from abyssal environments. Finally, we comment briefly on the significance of the close association between these small brachiopods and the global mid-ocean ridge system for understanding dispersal mechanisms and biogeographic patterns in the deep oceans.

Methods

The study was initiated by the fortuitous discovery by the second author of several small greyish-white, nearly translucent brachiopods during manual picking of selvedge glass from basalts dredged along the Southeast Indian Ridge (SEIR) by the *RV Melville* during a geological and geophysical investigation (Christie *et al.* 1995). These cryptic brachiopods were attached to the under surfaces of small lava tubes collected from two of about 70 dredge stations along sea floor of irregular relief in an axial rift setting (Christie *et al.* 1998). Six brachiopods were detached from the glassy basalt substrate at Station #116, and a single specimen from Station #138 (Fig. 1, Table 1).

The brachiopods were initially identified as *Eucalathis macroctena* Zezina, 1981, a species originally described from 3 specimens collected from two localities off the west coast of South America. Foster (1989) tentatively assigned another single individual from Eltanin 24 Station #1775 in the south Pacific to this species. Recently, two further examples of similar small, strongly-ribbed brachiopods have been reported from ocean ridges near the Galapagos Islands (Sonne SO 144-3 cruise). We now have records of this cancellothyridoid species from six separate localities in the south and southeast Pacific Ocean and the south Indian Ocean from depths ranging from c. 2000 m down to c. 4900 m, and from sites more than 5000 km apart that span c. 180° of longitude (Fig. 1, Table 1). We also demonstrate that the morphology of these small, strongly-ribbed brachiopods differs sufficiently from typical *Eucalathis* for them to be assigned to a new genus, *Melvicalathis*. In the original description of the species (Zezina 1981), the holotype was illustrated only by line drawings of dorsal and ventral valve interiors, and details of the exterior ribbing were unclear. Further line drawings showing details of the internal morphology are provided. Details of the internal and external morphology of several of the recently collected specimens are illustrated using scanning electron microscopy (SEM). Figured specimens were bleached with sodium hypochlorite (1-2%), rinsed in water, air-dried, mounted on stubs and coated with Au/Pd.

Table 1 summarises locality information for *Melvicalathis macroctena* (Zezina), including cruise name and number, station number, co-ordinates, number of specimens (N), water depths, substrates where known, collection dates, and accession numbers for repositories. The specimens of *Melvicalathis* described in this paper are held in four institutions: P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia (IORAS); Geology Department, University of Auckland, New Zealand (AU); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM), USA; Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB), Germany.

TABLE 1. Locality details for specimens assigned to the new genus *Melvicalathis*. (Cruises: "Academic Kurchatov 4", "Melville", "Eltanin 24", "Sonne SO 144-3").

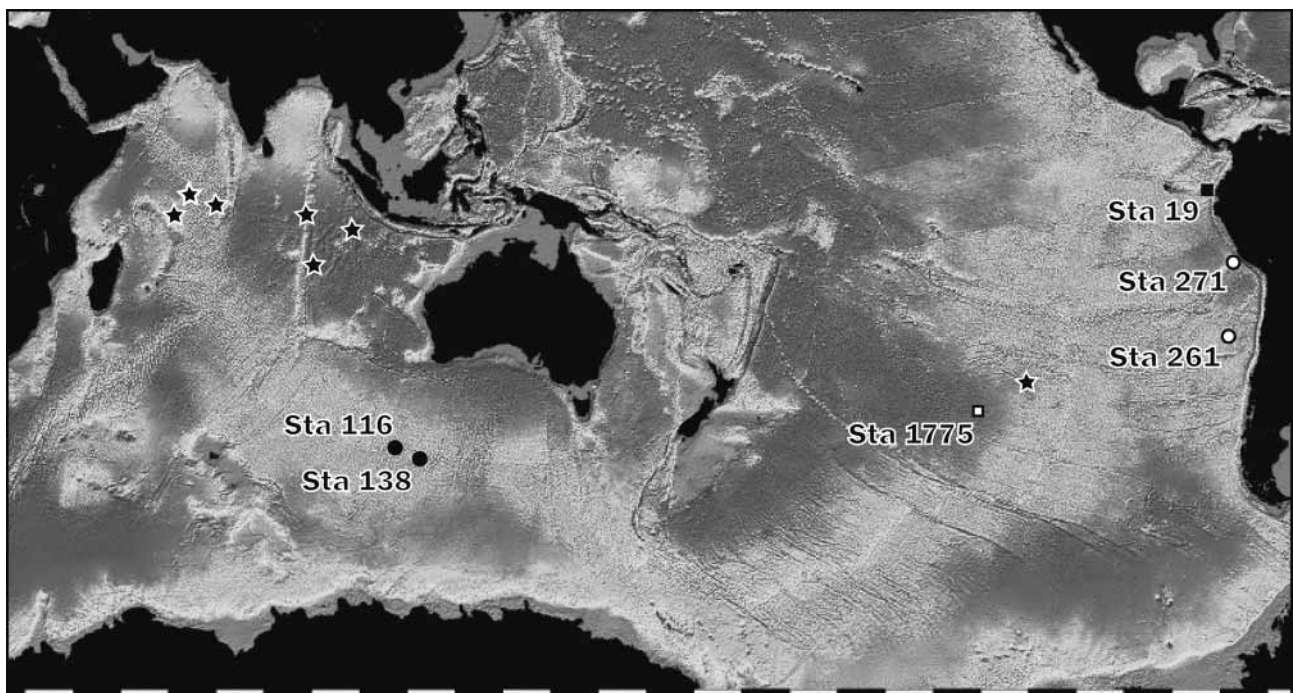| Sta.	Coordinates	Depth (m)	N	Substrate	Date	Notes
Academic Kurchatov 4						
#261	30°24'S 78°59'W	3870	2	?	7.10.1968	Holotype IORAS XI-52-4/2, paratype, broken, IORAS XI-52-4/1
#271	17°42'S 78°59'W	2710-3080	1	Small piece of basalt rock	20.10.1968	Paratype, IORAS XI-52-4/3
Melville						
#116	48°52.7'S 106°30.7'E - 48°52.4'S 106°29.6'E	4770-4900	6	glassy basalt	25.2.1995	AU19070; B320-325, Geology Department, University of Auckland
#138	50°11.7'S 112°52.1'E - 50°11.2' S 112°52.3'E	3820-3870	1	glassy basalt	4.3.1995	AU19071; B326 Geology Department, University of Auckland
Eltanin 24						
#1775	42°01'S 130°02'W - 41°57'S 130°17'W	4831-4851	1	?	14.8.1966	USNM 385106
Sonne SO 144-3						
#19	2°19.94'S 84°25.65W- 2°15.30'S 84°26.18W	2009-2381	2	Manganese encrusted rock	17.11.1999	ZMB Bra 2014, 2015

FIGURE 1. The mid-ocean ridge systems and geographic distributions of *Melvicalathis macroctena* (Zezina, 1981), and species of the related chlidonophorid brachiopod, *Bathynanus* (star symbols). Note the concentration along areas of probable hard rock substrates. The two stations of "*Academic Kurchatov*" (type locality) are adjacent to and on the Nazca Ridge. Key to symbols: ○ "*Academic Kurchatov*", ● RV "*Melville*", ■ FS "*SONNE*", □ "*Eltanin*" Cruise.

Taxonomy

Order Terebratulida Waagen, 1883
Superfamily Cancellothyridoidea Thomson, 1926
Family Chlidonophoridae Muir-Wood, 1959
Subfamily Eucalathinae Muir-Wood, 1965
Melvicalathis **Lee, Lüter & Zezina, new genus**
(Figures 2–6)

Diagnosis. Costae broad, triangular in cross-section; foramen hypothyrid, beak very attrite; transverse band of loop medially directed towards dorsal valve; loop may be incomplete.

Etymology. The generic name is based on the name of the *RV Melville* which collected most of the specimens on which this investigation is based, and "*calathis*", a suffix indicating close relationship with other brachiopod genera in the subfamily Eucalathinae.

Type species. Eucalathis macroctena Zezina, 1981

Type locality. Academik Kurchatov Station #261, southeast Pacific Ocean (30°24'S, 78°59'W) at a depth of 3870 m, collected by Sigsby Trawl, 7 October 1968 (Zezina 1981: 159, fig. 20).

Material.

Holotype. Accession number XI-52-4/2, living specimen (adult female, length 3.7 mm; width 3.8 mm).

Paratypes. Paratype 1, accession number XI-52-4/1, collected with the holotype, and broken during preparation. Paratype 2, accession number XI-52-4/3, Station #271, 17°42'S, 78°9'W, 2710 m, attached to basalt rock, 20 October 1968. The holotype and 2 paratypes are held in P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia.

Other material examined. Six specimens collected by *RV Melville* Station #116, Southeast Indian Ridge (48° 52.7' S, 106° 30.7 'E–48° 52.4'S, 106° 29.6' 'E), 25 February, 1995; one specimen collected from *RV Melville* Station #138, Southeast Indian Ridge (50° 11.7' S, 112° 52.1'E–50° 11.2' S, 112° 52.3'E), 4 March, 1995. These specimens are held in the reference collection, Department of Geology, University of Auckland.

One specimen collected live from *Eltanin* cruise 24, USC1775, 42° 01"S, 130° 02"W–41°57"S, 130°17"W, southeast Pacific Ocean, at depths of 4831–4851 m, 14 August, 1966, collected by 10' Blake Trawl (Foster 1989; figs 12, 13). This specimen is held in the United States National Museum, Washington DC.

Two specimens collected live from *Sonne* SO 144-3 cruise, Galapagos Spreading Centre, east Pacific (2°19.94'S, 84°25.65W–2°15.30'S 84°26.18W), at depths of 2009–2381 m, on 17 November, 1999. These specimens are held in the Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.

Description. (Figs. 2–6) Very small (maximum length 4.9 mm), punctate, subtrigonal in outline, greatest width anterior to midvalve, gently biconvex, anterior commissure rectimarginate, ornament of broad costae, triangular in cross-section, 7–9 costae on each valve, ridges of costae smooth without tubercles (Figs. 2A, 2B; 3B; 6A, 6B). Interior rim of shell anterior slightly scalloped from interlocking costae and slightly tuberculate margin (fig. 2C, 2D). Hinge line narrow, foramen moderately large, hypothyrid, beak very attrite, pedicle collar present, teeth small, triangular; deltidial plates very small, narrow, triangular, disjunct (figs. 2D, 3C–3E). Cardinal process very small; short, low median septum extending ca. 0.25 dorsal valve length; triangular socket ridges narrow, high; crural processes short. Brachidial loop complete or incomplete, descending branches connected by transverse band in holotype and paratype from "Academik Kurchatov" station 261, but not in other specimens; where the transverse band is incomplete, descending branches may have distally serrated edges; unjoined descending branches may represent younger growth stages (figs. 2E; 3A; 4A, 4B). Lophophore tightly coiled, early plectolophous, with large lateral lobes, and a small, possibly underdeveloped central lobe; filaments very long (figs. 2C; 3F, 3G; 5A); highly spiculate, spicules in connective tissue of both lophophore arms; spicules tightly interwoven, forming a dense 3-dimensional structure (figs. 4C, 5B); pedicle
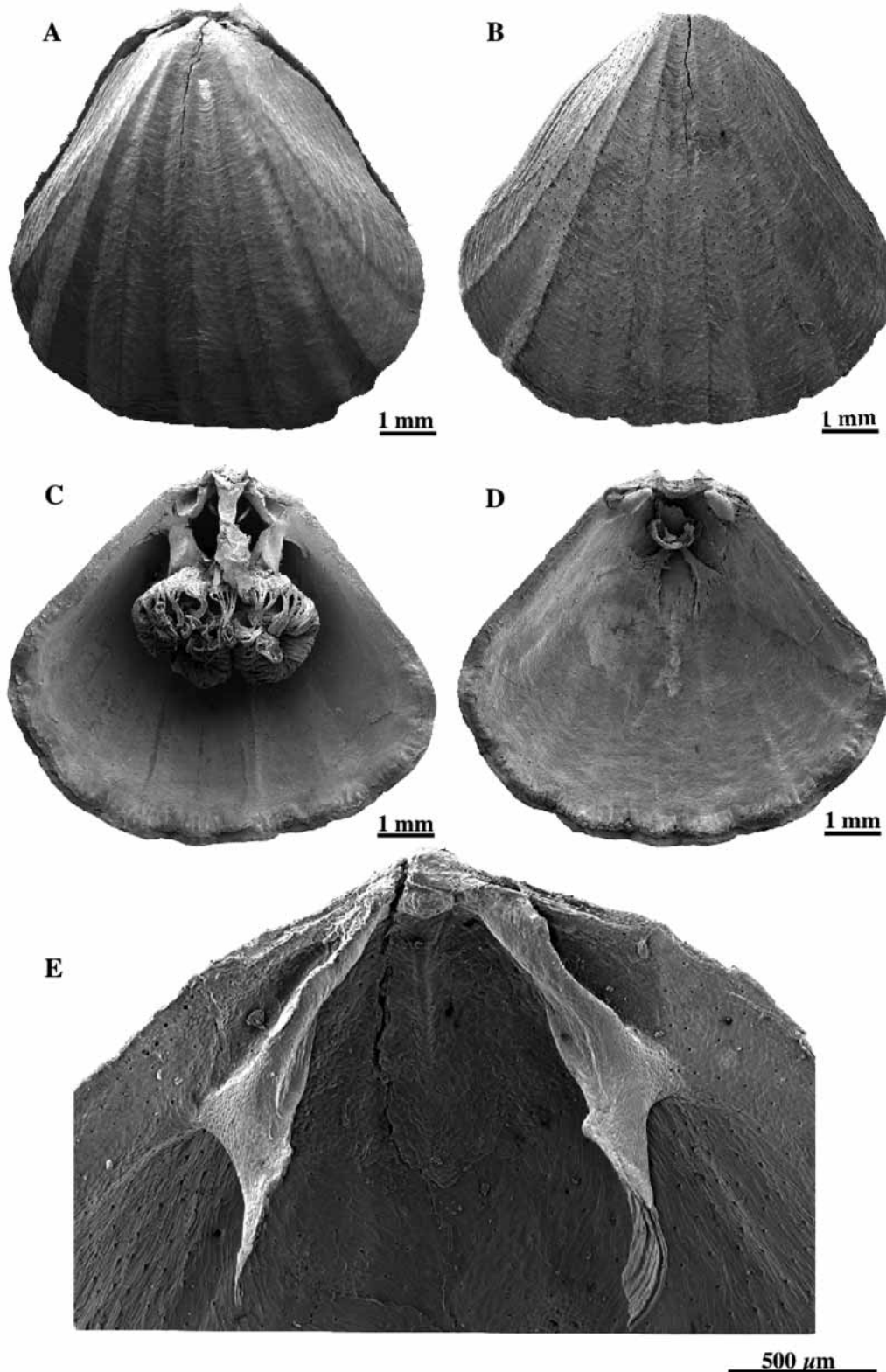
FIGURE 2. *Melvicalathis macroctena* (Zezina, 1981) from the Southeast Indian Ridge. A–B. Dorsal and ventral views of exterior of AU B320. Note that the detached valves were rejoined for photography and are slightly offset. C. Interior of dorsal valve, AU B321 showing dried pedicle and lophophore, sockets, and scalloped marginal rim. D. Interior of ventral valve, AU B321 showing small teeth, pedicle collar and foramen. E. Close-up of B320 to show small cardinal process, sockets, socket ridges, small crural processes, short median septum and broken, incomplete loop.

short, branched or brush-like, posteriorly directed, attaching specimens closely and perpendicularly to rock substrates (figs. 2C; 5C, 5D). The holotype, an adult female, held 8–10 eggs in each of 4 gonads (2 in the dorsal, and 2 in the ventral valve); the eggs were at different stages (from underdeveloped to ripe); about 30 eggs were ready for spawning on 7 October 1968. The shell microstructure consists of very flattened lamellar fibres (fig. 6C).
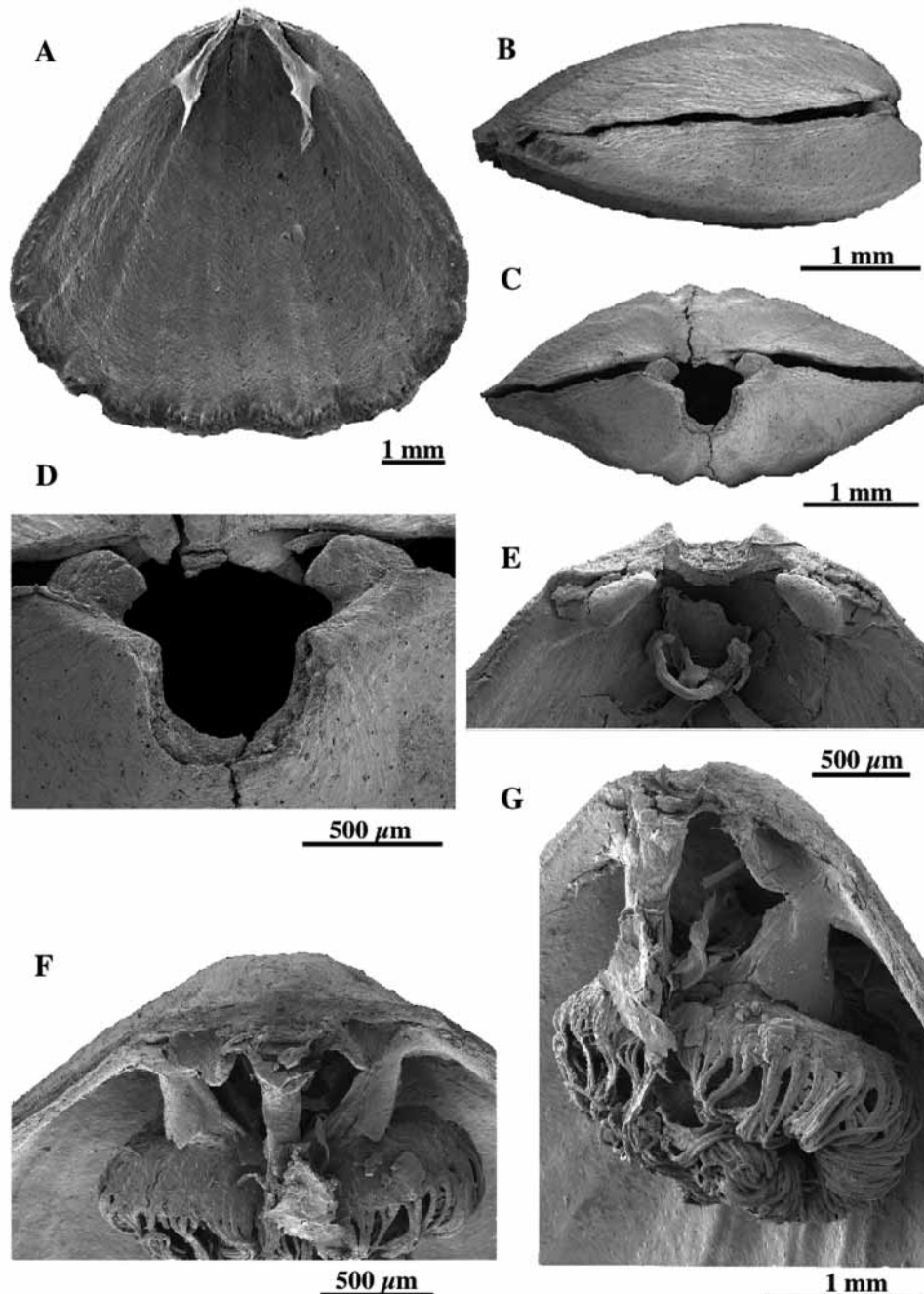

FIGURE 3. *Melvicalathis macroctena* (Zezina, 1981) from the Southeast Indian Ridge. A. Interior of AU B320 showing small cardinal process, internal view of costae, and correspondence between costae and scalloped margin. B. Lateral view of AU B320 showing slightly biconvex valves and strongly attrite beak. C. Posterior view of AU B320 to show hypothyrid foramen and costae. D. Close-up of C, showing pedicle collar, teeth and punctae. E. Close-up of ventral valve of AU B321 showing pedicle collar, teeth, and very narrow deltidial plates. F. Close-up of dorsal valve of AU B321 showing retracted dried pedicle, sockets and socket ridges, proximal end of crura, and part of dried lophophore. G. Lateral view of AU B321 to show rounded, ventrally-directed crural processes and dried lophophore.
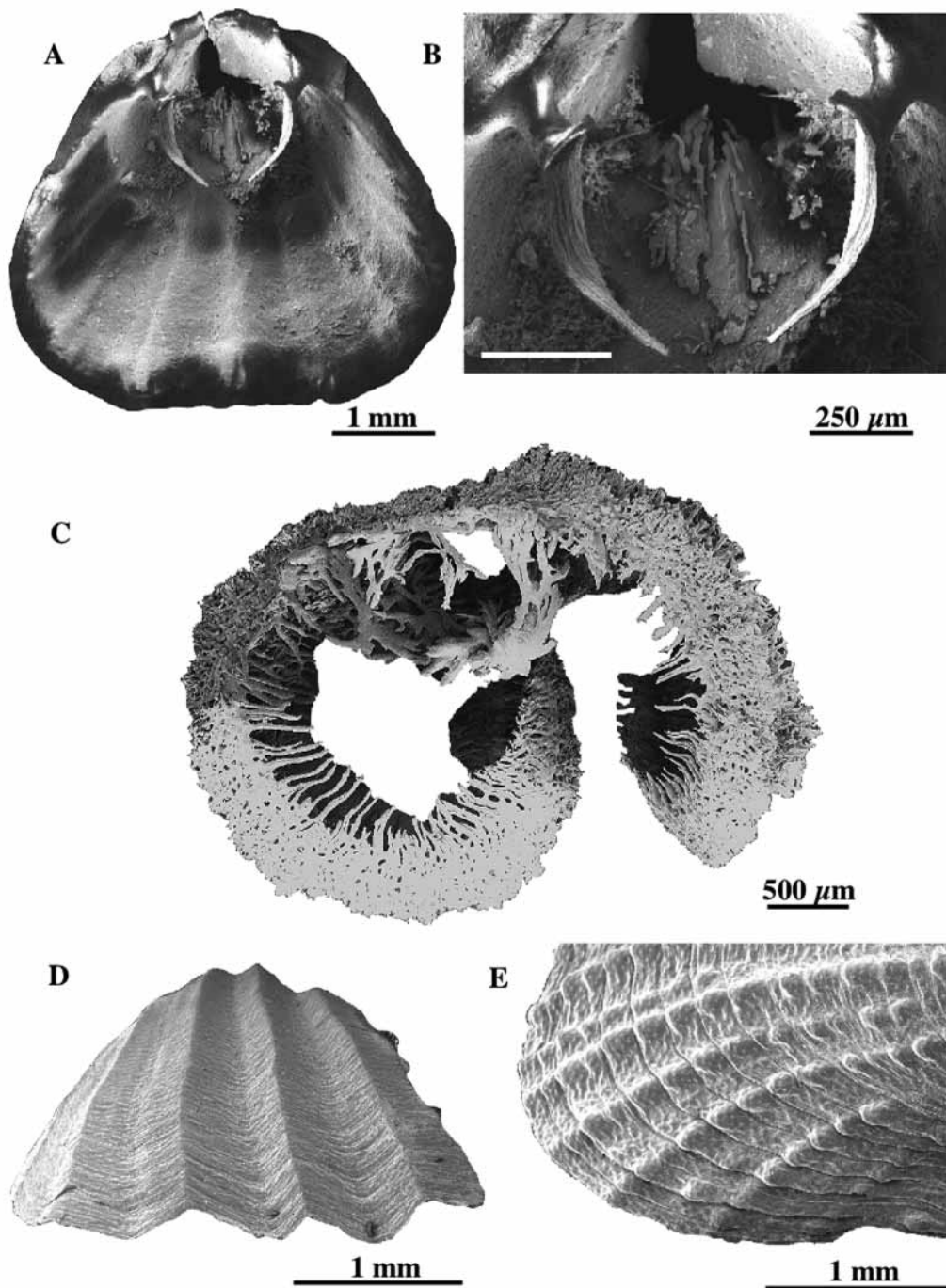
FIGURE 4. *Melvicalathis macroctena* (Zezina, 1981) from the Galapagos Spreading Centre. A. Interior of dorsal valve of ZMB Bra 2014 showing descending branches of crura with incomplete transverse band, and internal ridges corresponding to external costal troughs. B. Close-up of previous photograph to show details of descending branches and incomplete loop. C. Spicular skeleton after dissolution of soft tissue. D. Close-up of triangular costae showing numerous closely spaced growth lines. E. Close-up of a valve of *Eucalathis* to show typical beaded tuberculate costae for comparison with D.

Shell structure. Zezina (2003: 267) noted that in the shell microstructure of deep-sea brachiopods the fibres are composed of very flattened (lamellar) fibres, whereas the fibres in related shallow-water species "have rounded or rhomboidal sections". She attributed this to "a saving in building material in deepwater forms subject to high calcium carbonate solubility at depths below 2000 m". The fibres in *Melvicalathis* exhibit the lamellar structure described by Zezina. We speculate that there may be some advantage to the brachiopods from living on plagioclase-rich glassy basalts. Dissolution of the unstable glass may leach small

quantities of Ca and O which may partly compensate for the difficulties involved in producing a calcite shell at great depths. Note that the *Melville* brachiopods live at depths between 3820–4900 m at 48–50ºS in the Indian Ocean where the carbonate compensation critical depth is at about 3900 m between 50–60ºS (Demopoulos *et al*. 2003).

Remarks. The new genus can readily be distinguished from the other four genera in the subfamily Eucalathinae (Lee *et al*. 2006). *Melvicalathis* possesses broad smooth costae that are triangular in cross-section (figs. 4D; 6A, 6B). These differ markedly from the costae of species of *Eucalathis* which possess beaded, tuberculate radial ribs (fig. 4E; 5E). The cardinal margin of the shell in *Eucalathis* is often extended into "ears", thereby forming a straight line (fig. 5F). In *Melvicalathis* the hinge line is narrow, and slightly curved due to the lack of "ears" (fig. 2D). From *Bathynanus*, *Melvicalathis* differs in outline, larger size, shape of crura, and well-defined ribs that are triangular in cross section. *Nanacalathis* differs in its subpentagonal outline, conjunct deltidial plates, and beaded costae, while *Notozyga* has the typical beaded costae of the subfamily, and thick wide crural bases and crura.

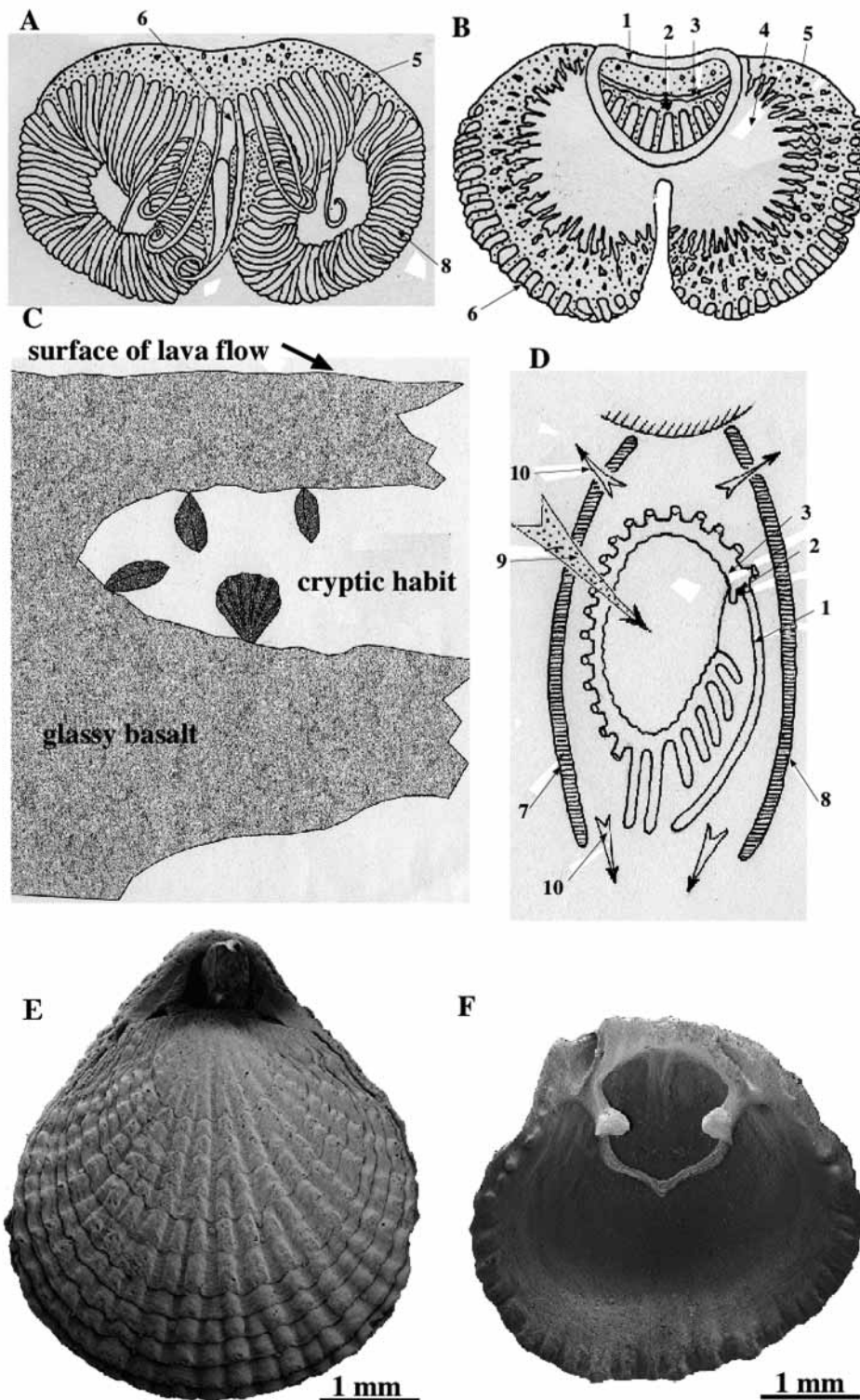## Distribution and ecology of deep-sea brachiopods

Melvicalathis macroctena (Zezina) is recorded from 6 localities at depths ranging from 3820 m and 4900 m from the Southeast Indian Ridge, and from depths between 2009 m and 4851 m in the south and southeast Pacific. These sites are more than 5,000 km apart, and span 180° of longitude. Four of the other six extant genera of small, ribbed brachiopods included in family Chlidonophoridae have similarly wide geographic and bathymetric distributions (Zezina 1985). *Chlidonophora* has a depth range of 534m to 4798 m in the Caribbean, Atlantic and Indian Oceans. Species of *Bathynanus* are reported from depths between 610 and 5160 m in the Indian Ocean, the south and east Pacific, and the mid-Atlantic Ridge near the Azores (Zezina 1985). *Nanacalathis* (depth range 289 - 3731m) is reported from the Indian Ocean and the Caribbean. *Eucalathis* is known from depths between 185 and 3374 m in the Indian, Atlantic, and north and south Pacific Oceans. Another related small, ribbed, species-rich genus, *Terebratulina*, has representatives in all oceans at depths from c. 10-4640 m.

Other articulated brachiopods that occur at depths >2000m include the rhynchonelloids *Abyssorhynchia*, *Cryptopora*, *Hispanirhynchia* and *Neorhynchia*; the terebratuloids *Abyssothyris* and *Liothyrella*, the zeillerioid *Macandrevia*, the platidioid *Annuloplatidia*, and possibly the terebratelloid *Dallina* (Zezina, 1985; Logan, 2007).

Deep-sea environments, substrates and associated fauna

The deep sea floor has traditionally been regarded as a stable, oligotrophic region of the ocean. Temperatures in the deep sea are nearly constant (<4ºC), except adjacent to hydrothermal vents (Gage & Tyler 1991). However, other parameters may vary considerably. In particular, substrate, of major importance to sessile filter-feeding animals such as brachiopods, may vary from soft ooze on the abyssal plains to vast expanses of hard volcanic rock exposed on mid ocean ridges and on the myriad seamounts. The majority of brachiopods in the deep-sea, as elsewhere, attach permanently to hard substrata such as rock or shell, although unfortunately many published records omit details of either the macro- or microsubstrates (Lee 1978) to which the brachiopods are attached.

A few brachiopods including *Chlidonophora* are known to attach to foraminiferal ooze by means of a branched pedicle (Rudwick 1970), although Zezina (personal observation, 2000) noted that this brachiopod has a short, unbranched pedicle when attached to rock. *Abyssothyris wyvillei*, one of the most widespread deep-sea terebratulides, attaches to foraminifera, shell fragments, and manganese nodules (Richardson 1997, Fig. 394). At least some of the *Melvicalathis* specimens described in this paper were attached perpendicularly

FIGURE 5. A–B. Line drawings of *Melvicalathis macroctena* (Zezina, 1981) from the type locality, south east Pacific. A. View of lophophore from the ventral side. B. View of lophophore from the dorsal side. C. Schematic illustration of the cryptic habit of *Melvicalathis macroctena* around the walls of small tabular voids immediately beneath basalt flow surfaces. The tubes with the brachiopods were found in larger boulders of fresh, glassy basalt at *RV Melville* Stn #116, Southeast Indian Ridge. D. Sketch of attachment of *Melvicalathis* on hard substrate and probable current system around lophophore. Key. 1, place where the lophophore was removed from the mantle and the dorsal body wall—internal details are seen through the transparent ventral wall of the lophophore; 2, mouth; 3, lip; 4, transparent (soft) dorsal wall of the

around under surfaces of glassy basaltic lava tubes (fig. 5C) (M. R. Gregory personal observation). Other specimens from the southeast Pacific were attached to manganese crusts on rock, probably basalt. Outcrops of basalt appear to be the most common attachment sites for brachiopods in the deep-sea.

lophophore; 5, spiculated (hard) part of the lophophore; 6, long filaments (tentacles); 7, ventral valve; 8, dorsal valve; 9, inhalent flow of water; 10, exhalent flow of water. (Figures A, B, D drawn by O. Zezina; Figure C provided by M. R. Gregory). E. Dorsal view of specimen of *Eucalathis* to show typical beaded costae. F. Interior of valve showing loop of *Eucalathis*, and strong elevated socket ridges that form "ears" protruding above posterior margin of valve.
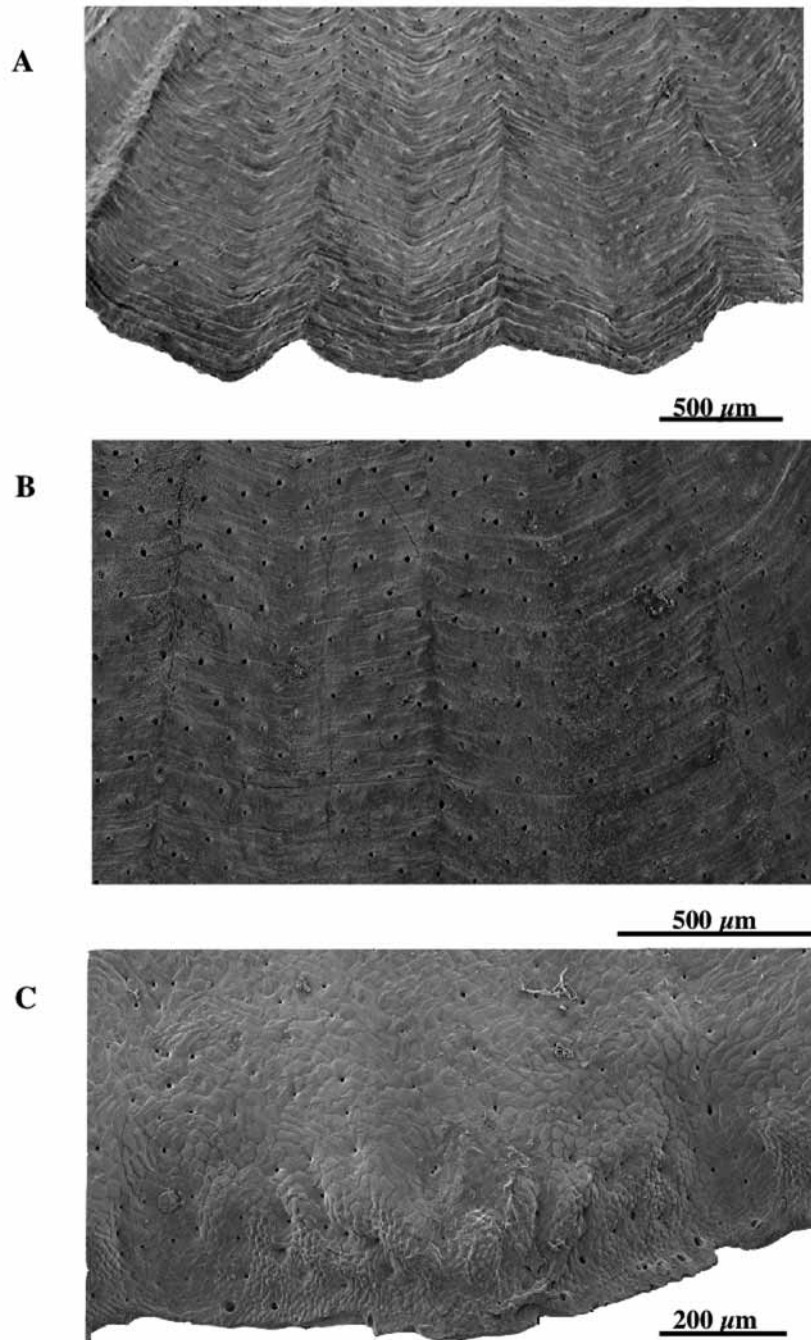

FIGURE 6. *Melvicalathis macroctena* (Zezina, 1981) from the Southeast Indian Ridge A. Close-up of AU B320 to show detail of angular costae, triangular in cross section, numerous closely spaced growth lines, and small, evenly spaced punctae. B. Close-up of costae showing quincunx arrangement of punctae. C. Interior of valve margin to show shell fibres, punctae and slightly tuberculate margin.

Although hard substrates in the deep sea are sometimes assumed to be of limited extent, the often sediment-free "rocky mountains of the mid-ocean ridges" (Marshall 1979: 158) which rise 2 to 4 km off the ocean floor extend for an aggregated distance of about 60,000 km and, in conjunction with the escarpments of offset-

ting (transform) fracture zones occupy a vast, more or less continuous area of the sea floor. These substrates are extremely problematic to sample (Lewis 1999), and their faunas, in marked contrast to those associated with hydrothermal vents (Tunnicliffe 1992), are poorly known. Marshall (1979: 158) commented "that the fauna fastened to the rocky mountains of the deep sea is not only remote but very difficult to investigate. ...To learn something of this fauna, the marine biologist should go to sea with a geologist and look in his rock dredge. He should also study all relevant photographs which might suggest, inter alia, ways of sampling the fauna." The advice is pertinent: the small, inconspicuous brachiopods collected from the SEIR on a geophysical cruise were recognised and collected by MRG just before the basalt samples were returned to the sea floor. Some small animals might be visible on a photographic survey (Genin *et al.* 1992), but not specimens such as *Melvicalathis* that occupy cryptic habitats within lava cavities (fig. 5C).

Surprisingly little has been written on the biotas attached to non-hydrothermal, deep-sea basaltic substrates, which have generally been considered to be impoverished (Genin *et al.* 1992; Tyler 1995). This may reflect the sampling difficulties and that few workers seem to have seriously considered the vast expanse of volcanic rock as a major marine habitat even though occasional photographs of guyots show an abundance of large sessile macroinvertebrates (Van Dover 2000, Fig. 1.2). However, Tunnicliffe (1992: 339, fig. 2) commented that "the vent fauna is becoming better known than the fauna of the surrounding deep-sea" and demonstrated that the diversity of deep-sea ridge (non-vent) faunas was considerably greater than that of vent faunas in the same region.

There have been suggestions that Fe/Mn encrustations on basalts may inhibit epifaunal organisms, but two of the specimens of *Melvicalathis* were attached to this crust. Mullineaux (1987, 1988) has demonstrated that manganese nodules and crust from three North Pacific sites support a diverse and abundant hard substrate community that is dominated by suspension feeders and is much more widespread than vent faunas" (Mullineaux 1987: 165).

Melvicalathis was the only macro organism seen on the numerous basalt samples from the 70 or so Melville stations on the SEIR: this brachiopod may be a primary coloniser on fresh glassy basalt. Zezina noted fragments of empty shells of the rhynchonellide *Hispanirhynchia craneana* (Dall) with the holotype (Stn 261), and live specimens of the terebratulide *Abyssothyris wyvillei* (Davidson) were collected with the paratype from Stn 271. No epibionts have been seen on specimens of *Melvicalathis*.

Other macro epibionts described from deep-sea basalt substrata include stalked sponges, sea-anemones, gorgonians, crinoids, barnacles and molluscs (Marshall 1979; Gage & Tyler 1991). Although deep-sea hard substrate communities appear to be characterised by large numbers of rare species, this may be partly a function of the difficulty of obtaining samples of animals which have patchy distribution on substrates which are difficult to sample. We predict that *Melvicalathis* will prove to be relatively abundant on suitable basalt substrata along the mid-ocean ridge systems of the Southern Hemisphere.

Ecological requirements. Although brachiopods are known from deep-sea fossil seeps (e.g. Campbell & Bottjer 1995a, b) they are rarely reported from the modern hydrothermal "vent oases" (Tunnicliffe 1992). Brachiopods have been recovered from carbonate-paved pockmarks (Hovland & Judd 1988), and from some modern cold seeps, but there is no evidence that the brachiopods in these situations are surviving chemosynthetically. Like the species described in this paper, they are simply opportunistic colonisers of an available hard substrate.

Brachiopods are active ciliary suspension feeders, using the lophophore as a food collecting organ, and they may consume "phytoplankton, organic detritus and organic molecules adsorbed onto inorganic particles" (James et al. 1992: 306), as well as taking up dissolved nutrients directly through the body wall (Steele-Petrovic 1976). The deep-sea rocky substrates on which the brachiopods live are oligotrophic (nutrient poor), although the ridge systems pass beneath surface zones of high and low productivity, which may have an effect on the organisms colonising the rock substrates several kilometres beneath (Marshall 1979). It is likely that these brachiopods live on dissolved organic matter and/or bacteria but there are as yet no nutrient uptake stud-

ies on deep-water brachiopods. Future studies should examine the substrate and digestive system of the animals to elucidate this problem. Gregory & Lee (1995) initially suggested that the small brachiopods from the South East Indian Ridge (SEIR) might live chemosynthetically, obtaining nutrition from association with vents or regions of diffuse warm flow. Some hydrothermal vents are known from the SEIR (Southward *et al.* 1997) but plots of the stations from which *Melvicalathis* and similar brachiopods are known show no close correspondence with submarine vents. On the other hand, although vent fields may occur at less than one kilometre intervals along axial rifts (Crane & Ballard 1980), no detailed surveys for these were made in the vicinity of the brachiopods.

Reproduction, growth rates and age. Very little is known about the reproduction and life history traits of brachiopods in the deep sea (Young 2003). Many brachiopods, including all 15 species of Chlidonophoridae, are micromorphic and appear to exhibit paedomorphosis; i.e. they reach maturity at a less advanced stage of ontogenetic development than is typical for terebratulide brachiopods. For instance, Zezina (2003: 267) noted that all deep-water cancellothyridoids "have simplified (hypomorphic) lophophores, which are different variants of the so-called 'early plectolophe' which evolves through underdevelopment of the 'full plectolophe'" that is characteristic of shallow-water cancellothyridoids. Similarly, the minute holotype of *Melvicalathis macroctena* (length 3.7 mm) was a female carrying about 30 eggs in different stages of development with some obviously ripe and ready to be released in the Southern Hemisphere spring (O. Zezina personal observation) (specimen collected 7 October 1968). The "presence of multiple egg sizes" may be suggestive of semi-continuous reproduction (Young 2003: 409). Paedomorphic features appear to have been a characteristic of chlidonophorid brachiopod species since Cretaceous times (Lee *et al.* 2006).

No age data is available for deep-sea brachiopods, but estimates could be made from the pronounced growth rings which imply seasonality of food supply, even at abyssal depths of more than 4000 m. The high numbers of evenly spaced (seasonal?) growth bands (between 20-30/mm) observed for *Melvicalathis* specimens (Fig. 2A, 2B; 4D; 6A, 6B) indicate that an adult 4–5 mm in length might be 80-100 years old. This is comparable with estimates for the life spans of some small deep-sea bivalves (Thistle 2003). However, according to Paine (1969) brachiopods can produce non-annual growth lines (observed in the shallow water species *Terebratalia transversa*), which may substantially reduce the above age assumption. In general, the estimated age for shallow water brachiopods is 8–15 years (Doherty 1979; Thayer 1981; James *et al.* 1992). Based on growth ring analysis, Curry (1984) suggested a possible age of 30 years for shallow water species settling in deeper waters. An increasing longevity of brachiopods with depth would fit the model of the deep sea as an environment of slow metabolism and correspondingly slow reproduction and would correspond to the observed number of growth rings and assumed age in *Melvicalathis* specimens.

Because of the wide geographical range of *Melvicalathis* and related deep-sea brachiopods, we speculate that their larval stages may be long-lived, and that the larvae may be transported long distances by strong currents running parallel to the mid-ocean ridge systems. Peck *et al.* (2001) noted that larvae of the large terebratuloid, *Liothyrella uva,* were released at a wide range of developmental stages, and that settlement time varied from minutes to up to 100 days. It is likely that *Melvicalathis*, like many articulated brachiopods, broods its larvae (James *et al.* 1992). Obviously further research is needed to resolve questions about the growth rates, longevity, brooding, and dispersal of these brachiopods.

Brachiopod dispersal along mid-ocean ridges—submarine superhighways?

The discovery of populations of *Melvicalathis* at widely spaced intervals along the mid-ocean ridge systems raises important questions about larval dispersal and biogeography of deep-sea brachiopods whose larvae require a hard substrate for settlement.

We suggest here that the extensive basalt outcrops exposed on either side of the mid-ocean ridge axes

function as laterally extensive, continuous deep-sea "superhighways" for dispersal of some brachiopod species and a variety of other hard substrate, epifaunal, benthic suspension feeders including gorgonian corals and crinoids. The occurrence of the same species of *Melvicalathis* at sites along the Southeast Indian Ridge separated by ~500 km, and some 5000 km further east along the Southeast Pacific Rise and its offsets appears to indicate that this is indeed the case. Similarly, species of the related micromorphic *Bathynanus* are reported from volcanic substrates at 3843 m in the south east Pacific (Foster 1974), 3429 m off Japan (Davidson 1878), from 4600–5160 m in the eastern and central Indian Ocean (Zezina 1981), from 2520–3490 m in the north west Indian Ocean, and 3984 m on the Mid-Atlantic Ridge, near the Azores (Zezina 1981) (Fig. 1).

The mid ocean ridges can also act as conduits between shallow-water and deep-water habitats for other hard substrate epifaunas, where the ridges impinge on continental margins (as in the north west Pacific), or rise to the surface (as in Iceland) (Copley *et al.* 1996), as well as facilitating "island hopping" along chains of submerged seamounts (e.g., Tonga-Kermadec Ridge; Norfolk Ridge) (Roux 1982; Tunnicliffe & Fowler 1996). Closely related species of the brachiopod *Eucalathis* are recorded from near the Kermadec Islands (Davidson 1880), the South Pacific Uplift, the Pacific-Antarctic Ridge (Foster 1974), the east Atlantic and the Azores (Cooper 1981).

Finally, although the chances of finding *Melvicalathis macroctena* fossils are infinitesimal, the distribution of this species along the mid-ocean ridge system has important implications for brachiopod paleobiogeography. Other deep-sea brachiopods with similar life habits are likely to have used the mid-ocean ridges as submarine superhighways in the past. These ridges may have been a very important means of dispersal of brachiopods between oceans, and from deep-water into shallow water, and vice versa, during the Paleozoic and Mesozoic (Vörös 2005).

Conclusions

We suggest that the small, inconspicuous brachiopods described in this paper are cryptic representatives of the rarely sampled and poorly known, but widely distributed deep-sea epifaunal community, which may occur, and disperse readily along the entire length (>60,000km) of the mid-ocean ridge system. This fauna comprises small animals, adapted to early colonisation of newly formed basalt or glassy substrates. These organisms may be dredged only rarely, and sampling difficulties may account for the apparent sporadic distribution of these and a variety of other small inconspicuous epibenthic animals. We would encourage scientists who work on mid-ocean ridge rocks to carefully check for the presence of small brachiopods, and to preserve samples of these animals with their substrate so that some of the puzzles associated with their distribution in the very deep ocean can be resolved.

Acknowledgements

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