Recent brachiopods from the Red Sea and Gulf of Aden

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Recent brachiopods are rare in the Red Sea and Gulf of Aden, with four species: *Argyrotheca cuneata* (Risso), *Argyrotheca jacksoni* Cooper, *Megerlia echinata* (Fischer & Oehlert) and *Leptothyrella ignota* (Muir-Wood) previously identified from a total of only nine specimens. Here we report on the discovery of about 2500 specimens extracted from neritic and bathyal zone sediments obtained mainly by *Meteor* cruises in 1987 and 1995 and from shallow-water samples by various expeditions, as well as from specimens in museum collections. Preliminary identifications are: *Discinisca* sp. indet., *Novocrania* cf. *anomala* (Müller), *Cryptopora curiosa* Cooper, *Thecidellina* sp. indet., *Frenulina* sp. indet., *Argyrotheca jacksoni*, *Argyrotheca cordata* (Risso), *Argyrotheca ?cuneata*, *Argyrotheca* sp. indet., *Platidia anomioides* (Scacchi & Philippi) and *Megerlia echinata* from the Red Sea and *Cryptopora curiosa* and *Leptothyrella ignota* from the Gulf of Aden. Although the brachiopods are from death assemblages, their taphonomic preservation and between-depth differences in their composition strongly suggest they are autochthonous or parautochthonous. Multivariate analysis reveals four associations, which occupy different depth habitats and substrate types, with non-reefal shallow-water sediments virtually devoid of brachiopods. Low abundance, moderate diversity and small-shell sizes appear to characterize modern Red Sea brachiopods, although this may change with more sampling. The affinities of Red Sea brachiopods are with those of the Indian Ocean and Mediterranean, the Gulf of Aden species with the Indian Ocean. Paratethyan elements in this fauna suggest open connections between the Mediterranean, Indo-Pacific and Paratethys in the Middle Miocene. ☐ *Biogeography, Gulf of Aden, palaeoecology, Recent brachiopods, Red Sea.*

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The Red Sea and its southeastern extension into the Gulf of Aden has traditionally been a poor hunting ground for modern brachiopods. Muir-Wood (1959) described a new species *Leptothyris* (now *Leptothyrella*) *ignota* from three specimens, two of which came from the Gulf of Aden. Cooper (1973) described a new species *Argyrotheca jacksoni* from a single specimen collected from a reef cave at Ras Mohammed, southernmost Sinai Peninsula, and two specimens as *Megerlia echinata* (Fischer & Oehlert, 1890) from the same cave, while Brunton (1988) identified one specimen of *Argyrotheca cuneata* (Risso, 1826) from Mersat Abu Samra, Gulf of Aqaba, and another three from ‘south of Elat’ (Gulf of Aqaba). Thus, prior to this study, a total of four species based on only nine specimens were known from the region. Here we report on the discovery of about 2500 specimens from neritic and bathyal zone sediments obtained mainly from box-core and dredge samples by Meteor cruises to the Red Sea and Gulf of Aden in 1987 and 1995, from diver-taken samples during an intensive survey of shallow-water sediments (< 50 m) in the northern Red Sea, from isolated specimens obtained from other cruises, and from various museum collections. These discoveries suggest that brachiopods are more common in some specific habitats of the Red Sea and Gulf of Aden than previously assumed.

In this preliminary report we identify the main species, discriminate groups of samples that share a similar species composition, evaluate sample-level differences in composition of brachiopod assemblages and test whether they differ with respect to depth. This base-level analysis should be important for ecological comparisons of the Red Sea brachiopod distribution patterns with those of other regions.

Study area and samples

The Red Sea extends over a wide latitudinal range (Fig. 1) and the isolation of the area results in correspondingly large surface gradients of temperature (the latter increasing to the south) and salinity (which increases to the north) along its length. The annual

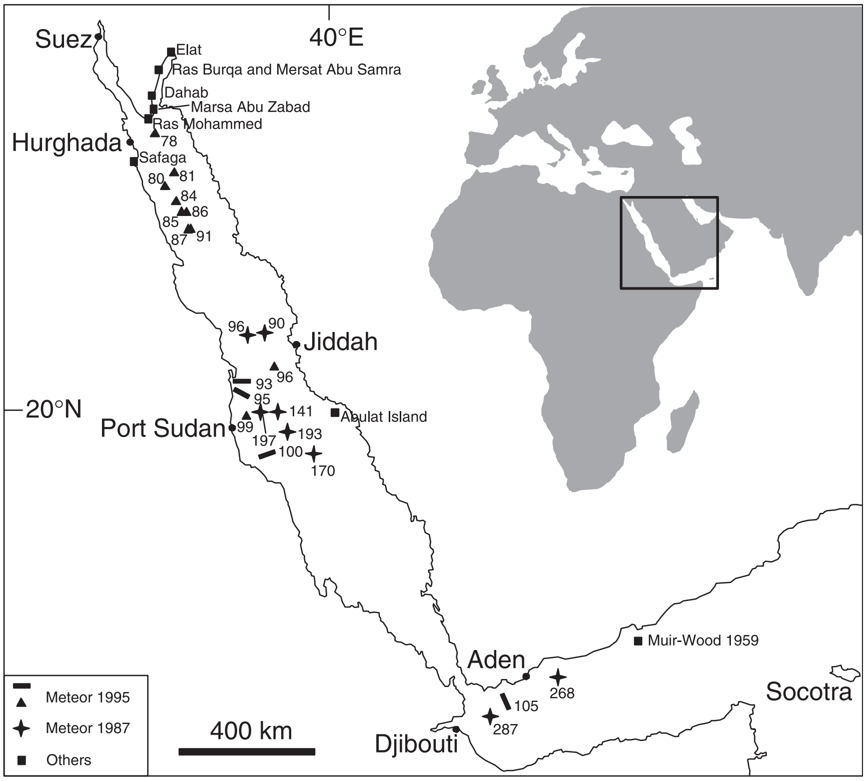

Fig. 1. Map of Red Sea and Gulf of Aden, showing collecting localities from which brachiopods were obtained. For multivariate analysis only the samples from Meteor cruises in 1987 and 1995, and two samples from Safaga (94/5 and 95/31) were used (compare Table 2).

pumping of water from the Gulf of Aden into the Red Sea from southwest monsoon-induced upwelling causes a gradient of nutrients, where the south is eutrophic and the north is oligotrophic. The Red Sea is unusual in having no marked thermoclines, resulting in constantly high temperatures in deep-water settings (for reviews see Medio *et al.* 2000 and Sheppard *et al.* 2000).

Brachiopods were obtained from neritic and bathyal zone sediments collected during several different sampling projects: Meteor cruise M5 (1987) to the central Red Sea (nine stations between 648–1463 m depth range) and western Gulf of Aden (two stations at 472 and 1654 m), and Meteor cruise 31/2 (1995) to the northern (eight stations between 648–1537 m) and central (11 stations between 12–580 m) Red Sea and the western Gulf of Aden (two stations between 321–506 m). Brachiopods were also obtained from shallow water (< 50 m) sediments of the Bay of Safaga, northern Red Sea by Zuschin. Collecting localities are shown in Table 1 and Figure 1.

There is strong evidence to indicate that while brachiopods are clearly part of death assemblages, relatively low proportions of fragmented specimens and distinctive between-depth differences in assemblage composition indicate that they have undergone very little transportation and have not been affected by any substantial between-community mixing (see later discussion). We thus suppose that they represent autochthonous or parautochthonous assemblages (Zuschin & Hohenegger 1998; von Rützen-Kositzkau 1999; Grill & Zuschin 2001).

Additional specimens were obtained from the Calypso cruise to the Red Sea in 1951–1952 and from the Hebrew and Tel Aviv University collections in Israel.

Systematics

The suprafamilial classification below follows that of Williams *et al.* (1996). Some identifications are provisional, pending the study of recently discovered specimens that will necessitate a more detailed taxonomic treatment later.

Unless otherwise stated all figured specimens are housed in the Natural History Museum in Vienna, Austria (NHMW). Other abbreviations used here are NHM (Natural History Museum, London) and TAU (Tel Aviv University, Israel).

Phylum Brachiopoda Duméril, 1806

Subphylum Linguliformea Williams *et al.*, 1996

Class Lingulata Gorjansky & Popov, 1985

Table 1. Species, size range of ventral valve length (mm), localities and depth range (m) for each species.

Species	LV size range (mm)	Stations (for locations see Fig. 1 and Grill & Zuschin 2001)	Depth range (m)
Novocrania cf. *anomala* (Müller)	No ventral valves	93/7, 93/10, 94/1c, 94/5, 95/31, 100/2–3, 100/5–6, 100/8	10–669
Discinisca sp. indet.	No ventral valves	93/6, 100/7	567–646
Cryptopora curiosa Cooper	1.8–4.8	81/2b, 81/3, 84/1, 85, 85/2, 86, 87/1, 93/4, 93/6–7, 93/9–10, 95/5, 95/7–13, 100/5–7, 105/1–4	56–1537
Thecidellina sp. *indet.*		87/12, 93/8, 93/10, 100/3, 100/5–6, 100/8	56–1463
Argyrotheca jacksoni Cooper	1.4–1.9	94/5, 95/31, 100/8 + Calypso (Abulat Is.), + Ras Burqa, Gulf of Aqaba	12–90
Argyrotheca cordata (Risso)	2.0	Marsa Abu Zabad, Gulf of Aqaba	?
Argyrotheca sp. A	1.3–3.2	93/6, 95/5, 100/2, 100/6, 100/8	47–669
Argyrotheca ?cuneata (Risso)	?	Marsat Abu Samra, Gulf of Aqaba (Brunton 1988)	46–49
Frenulina sp. indet.	19.7	Elat, Gulf of Aqaba	?
Platidia anomioides (Scacchi & Philippi)	1.6–4.0	78/4, 80/6, 81, 81/2b, 81/3, 81/5, 84/1, 85, 85/2, 86, 87/1–3, 87/12, 92/1, 93/6, 93/9, 95/5, 96GTV, 99/3 + Meteor 1987: M5-90, 96, 141, 170, 193, 197 Ku	567–1537
Leptothyrella ignota (Muir-Wood)	?	Meteor 1987: M5-268, 287 Ku and Muir-Wood (1959) Gulf of Aden locality	472–1987
Megerlia echinata (Fischer & Oehlert)	1.8–4.3	87/1, 87/3, 87/12, 91, 93/6, 93/8, 93/10, 94/5, 95/5, 95/31, 100/2–3, 100/5, 100/7–8 and Dahab (12 m), Ras Mohammed (Cooper 1973) and G. of Aqaba (Brunton 1988) localities	< 10–1537

Order Lingulida Waagen, 1885

Superfamily Discinoidea Gray, 1840

Family Discinidae Gray, 1840

Genus *Discinisca* Dall, 1871

Type species. – Orbicula lamellosa Broderip, 1833

Discinisca sp. indet.

Fig. 2A–B

Remarks. – All nine examples in the collection are dorsal valves. The Red Sea form is unusual for the genus in having a centrally placed umbonal region and a radially pustulose rather than radially costate shell, thus separating it from *D. indica* from the Indian Ocean (Cooper 1973). *Discinisca* is not known from the Mediterranean.

Subphylum Craniiformea Popov *et al.*, 1993

Class Craniata Williams *et al.*, 1996

Order Craniida Waagen, 1885

Superfamily Cranioidea Menke, 1828

Family Craniidae Menke, 1828

Genus *Novocrania* Lee & Brunton, 2001

Type species. – Patella anomala Müller, 1776

Novocrania cf. *anomala* (Müller, 1776)

Fig. 2C

Remarks. – Novocrania anomala is well known from the eastern Atlantic and Mediterranean. The Red Sea specimens are all small and mostly dorsal valves but have the subdued muscle scar pattern typical of *N. anomala* rather than *N. turbinata*, the more common species in the eastern Mediterranean (Logan & Long 2001).

Subphylum Rhynchonelliformea Williams *et al.*, 1996

Class Rhynchonellata Williams *et al.*, 1996

Order Rhynchonellida Kuhn, 1949

Superfamily Dimerelloidea Buckman, 1918

Family Cryptoporidae Muir-Wood, 1955

Genus *Cryptopora* Jeffreys, 1869

Type species. – Atretia gnomon Jeffreys, 1876

Cryptopora curiosa Cooper, 1973

Fig. 2D–G

Remarks. – This small rhynchonellid is very common in Red Sea sediments and may be locally abundant, with almost 600 specimens in one box core sample from locality 93/9. The shell is typically thin and transparent, with a distinctive secondary layer microstructure forming a coarsely fibrous mosaic.

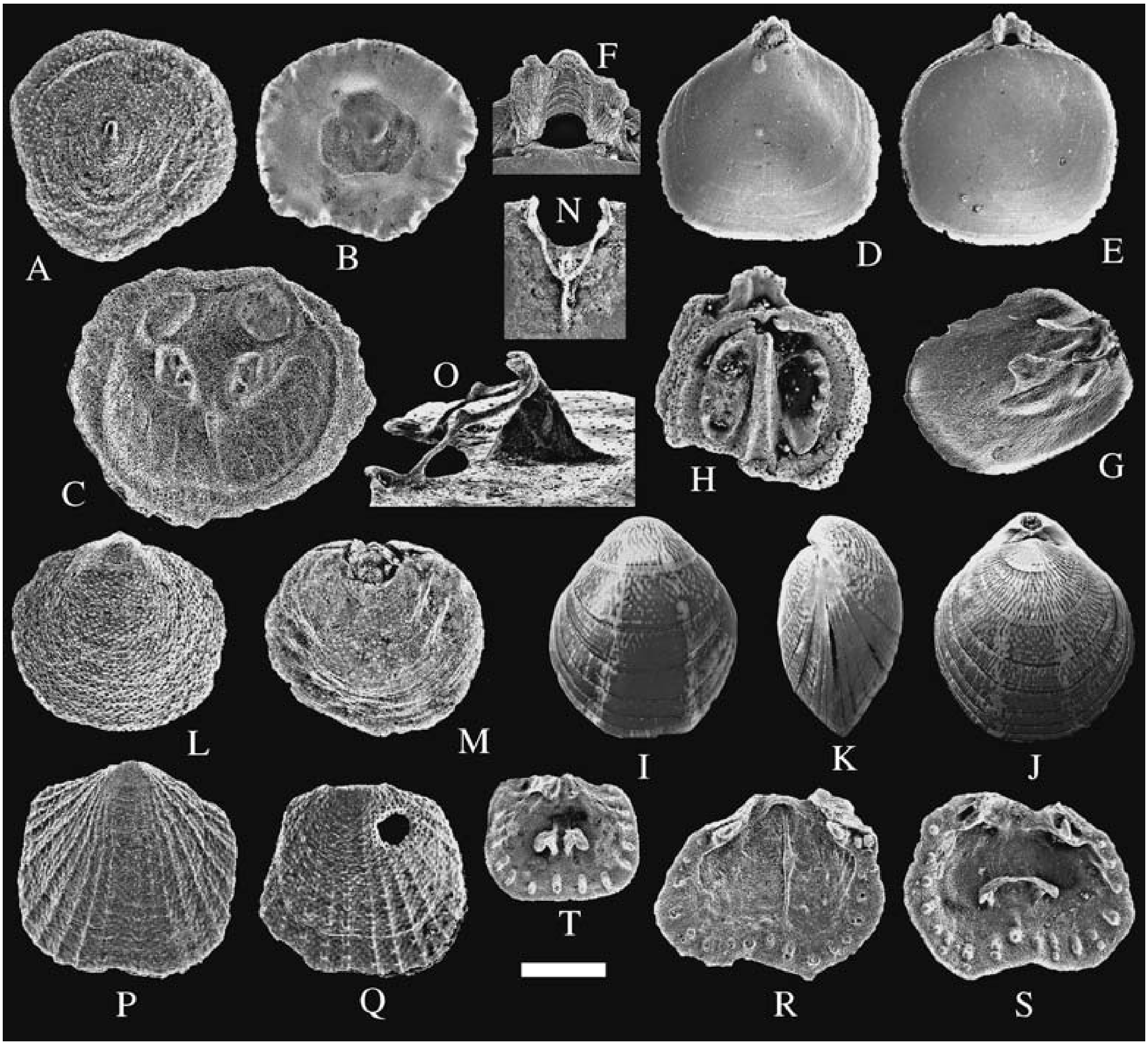

Fig. 2. □A, B. *Discinisca* sp. indet. exterior and interior of dorsal valve, loc. 93/6, 567 m, NHMW 103321-2. □C. *Novocrania* cf. *anomala*, interior of dorsal valve, loc. 95/31, 12 m, NHMW 103323. □D–G. *Cryptopora curiosa*, ventral, dorsal exteriors, enlarged umbonal region of previous specimen and interior of dorsal valve, loc.93/9, 313 m, NHMW 103324-6. □H. *Thecidellina* sp. indet., dorsal valve interior, loc. 100/8, 90 m, NHMW 103327. □I–K. *Frenulina* sp. indet., ventral, dorsal and side views, Elat, Gulf of Aqaba, depth unknown, Hadar Collection, Tel Aviv University. □L–O. *Platidia anomioides*, ventral, dorsal and interior of dorsal valve with brachial skeleton, Meteor 1987 MS 197 Ku, 747 m, NHMW 103328-30. □P–T. *Megerlia echinata*, ventral and dorsal exteriors, ventral and dorsal interiors with immature loops, loc. 100/8, 90 m, NHMW 103331-5. (Scale bar represents 0.3 mm for F and O, 0.6 mm for N, 8.0 mm for figs I–K and 1.0 mm for all others.)

C. curiosa was first described by Cooper (1973) from shallow water (< 80 m) off Cape Guardafui, Somalia, and is characterized by elaborately developed wing-shaped (auriculate) disjunct deltidial plates (Fig. 2F). The Red Sea specimens range deeper, where their deltidial 'wings' may function to prevent sinkage of the posterior end into the bathyal muds (Curry 1983). Although none of our specimens have soft parts preserved, it is likely that the pedicle is long and anchored to shell fragments in the sediments (Curry 1983).

Order Thecideida Pajaud, 1970

Superfamily Thecideoidea Gray, 1840

Family Thecidellinidae Elliott, 1958

Genus *Thecidellina* Thomson, 1915

Type species. – *Thecidea barretti* Davidson, 1864

Thecidellina sp. indet.

Fig. 2H

Remarks. – *Thecidellina* is represented in the collections mainly by dorsal valves but there is no doubt of the generic identification. The Red Sea form may be comparable with *T. blochmanni* Dall from the Indian Ocean (Cooper 1973) but the holotype and only specimen is missing (Florence, *in litt.*). *Thecidellina* is not recorded from the Mediterranean (Logan 1979), although it occurs in the Cape Verde Islands and the Caribbean (Logan 1988).

Order Terebratulida Waagen, 1883

Superfamily Laqueoidea Thomson, 1927

Family Frenulinidae Hatai, 1938

Genus *Frenulina* Dall, 1895

Type species. – *Anomia sanguinolenta* Gmelin, 1792

Frenulina sp. indet.

Fig. 2I–K

The single complete specimen is from Elat, Gulf of Aqaba, depth unknown. It shows conjunct deltidial plates and two cream-white diverging bands on an orange-white variegated shell. It is closest to *F. cruenta* Cooper, 1973, from shallow depths off Cape Guardafui, Somalia, but its colour patterns differ in degree of development. In addition it is larger, although *F. cruenta* also has conjunct deltidial plates. The Pacific species *F. sanguinolenta* (Gmelin) is also present in the reefs of Madagascar, but this species is smaller than the Red Sea form and has disjunct deltidial plates. The loop in the Gulf of Aqaba specimen is missing but the unisulcate mottled shell, cardinal process with myophore, strong teeth and dental plates, and shape of the median septum in the dorsal valve are all typical of the genus.

Superfamily Megathyridoidea Dall, 1870

Family Megathyrididae Dall, 1870

Genus *Argyrotheca* Dall, 1900

Type species. – *Terebratula cuneata* Risso, 1826

Argyrotheca cordata (Risso, 1826)

Fig. 3A–F

The single specimen of this species is from Marsa Abu Zabad, Gulf of Aqaba, depth unknown. *A. cordata* is a typical Mediterranean species (Logan 1979) with a distinctive dorsal valve interior showing a discontinuous serrated median septum and a row of submarginal ridges noded at their anterior extremities, all of which are seen in the Red Sea example (Fig. 3A–C). A typical Mediterranean example from Cassis, southern France is figured for comparison (Fig. 3D–F).

Argyrotheca jacksoni Cooper, 1973

Fig. 3G–O

This form is common in the Red Sea and has a narrower hinge line than morphotype A and more numerous, gently rounded costae. Comparison with the holotype and only specimen of *A. jacksoni* Cooper, 1973 suggests its identity with that species.

Argyrotheca sp. A

Fig. 3P–T

Remarks. – This form is characterized by a wide hinge line, two to three heavy rounded ribs and a deep sinus in the dorsal valve bounded by the two innermost ribs. In ornamentation it resembles *A. grandicostata* described by Logan (1983) from the Canary Islands but has a much wider hinge line.

Argyrotheca? *cuneata* (Risso, 1826)

(not figured)

Remarks. – Brunton (1988) identified *A. cuneata* in a collection sent to him from Israel. Seventeen complete shells and two ventral valves were from the eastern Mediterranean, where *A. cuneata* is common (Logan *et al.* 2002), and showed the typical pink-red intercostal coloration and forked prongs arising from the anterior end of the median septum in mature specimens (Logan 1979). However, four complete specimens in the collection were from the Gulf of Aqaba and lacked the pink stripes and forked prongs. These comprise a single complete example (NHM ZB 3971, TAU 17) from Mersat Abu Samra, Gulf of Aqaba, from 46–49 m depth, and three complete specimens (unregistered at NHM, TAU 12) from unknown depths 'south of Elat', all of which are here questionably assigned to *A. cuneata* pending further investigation.

Superfamily Platidioidea Thomson, 1927

Family Platidiidae Thomson, 1927

Genus *Platidia* Costa, 1852

Type species. – *Orthis anomioides* Scacchi & Philippi, 1844

Platidia anomioides (Scacchi & Philippi, 1844)

Fig. 2L–O

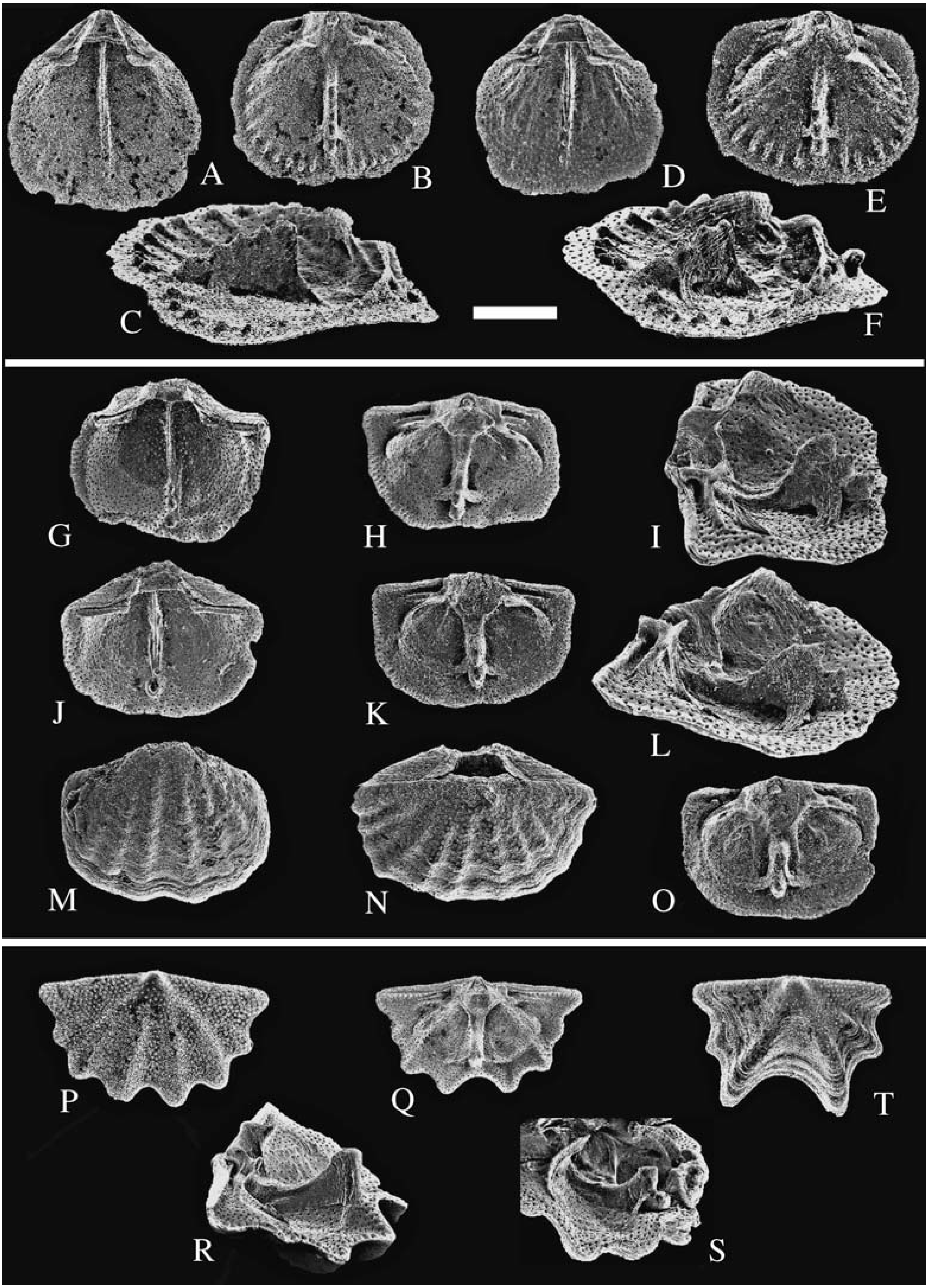
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Table 2. Summary table of 31 samples used in the multivariate analyses. The depth and substrate assignments are simplified according to von Rützen-Kositzkau (1999).

Sample no.	Substrate	Depth (m)	Sample group	Sample no.	Substrate	Depth (m)	Sample group
81/2b	Concretions/crusts	1302–860	*Platidia*	95/12	Bioclastic sand	308	*Cryptopora*
81/3	Concretions/crusts	1295–1329	*Platidia*	95/13	Bioclastic sand	311	*Cryptopora*
81/5	Concretions/crusts	1410–841	*Platidia*	95/11	Mud	497	*Cryptopora*
84/1	Mud	736	*Platidia*	95/9	Mud	569	*Cryptopora*
85-85/2	Mud	648–702	*Platidia*	95/7	Mud	575	*Cryptopora*
86	No data	941	*Platidia*	95/8	Mud	580	*Cryptopora*
87/1	Concretions/crusts	1359–1537	*Platidia*	100/8	Mud	90	*Megerlia*
87/3	Concretions/crusts	1380–1463	*Platidia*	100/5	Mud	343	*Argyrotheca*
93/10	Mud	56	*Megerlia*	100/2	Mud	404	*Megerlia*
93/8	Bioclastic sand	80	*Argyrotheca*	100/3	Mud	557	*Argyrotheca*
93/9	Mud	313	*Cryptopora*	100/6	Mud	669	*Argyrotheca*
93/7	Mud	374	*Cryptopora*	105/1	Bioclastic sand	71	*Cryptopora*
93/6	Mud	567	*Platidia*	105/2	Mud	179	*Cryptopora*
94/5	Reef slope sand	19	*Argyrotheca*	105/3	Mud	321	*Cryptopora*
95/31	Reef slope sand	12	*Argyrotheca*	105/4	Mud	506	*Cryptopora*
95/5	No data	237	*Megerlia*	–	–	–	–

This cosmopolitan species is common in the Red Sea and Gulf of Aden where it forms a distinctive assemblage in bathyal sediments. All shells are small but no smaller than a collection of 53 specimens from Canyon de la Cassidaigne, southern France, which were measured for comparison. The brachial skeleton is diagnostic for the species (Logan 1979), although there is some variation in this feature (compare Fig. 2N and O).

Genus *Leptothyrella* Muir-Wood, 1965

Type species. – Leptothyris ignota Muir-Wood, 1959

***Leptothyrella ignota* (Muir-Wood, 1959)**

(Not figured)

Remarks. – Muir-Wood (1959) described two specimens of *Leptothyris* (now *Leptothyrella*) *ignota* from the Gulf of Aden at about 2000 m depth. Single specimens from each of Meteor 1987 stations 268 and 287 at depths of 1654 m and 472 m respectively, are identified with Muir-Wood's species from the same area.

Superfamily Kraussinoidea Dall, 1870

Family Kraussinidae Dall, 1870

Genus *Megerlia* King, 1850

Type species. – Anomia truncata Linnæus, 1767

***Megerlia echinata* (Fischer & Oehlert, 1890)**

Fig. 2P–T

Remarks. – Cooper (1973) identified this species from southern Sinai and we have found this species to be wide-ranging in depth but most common in bathyal sediments where it forms a distinctive association. Most dorsal valve specimens show immature loops, which account for the small size range of the specimens. The species is known from the Indian Ocean and the closely related *M. truncata* from the eastern Atlantic and Mediterranean (Logan 1979).

Multivariate Analysis

Methodology

Although the number of specimens per sample can be low, we have decided to include all samples with $n > 10$, as our dataset reflects an exhaustive sampling effort of brachiopods by several cruises and shallow-water surveys (Grill & Zuschin 2001). All specimens were counted, using the maximum number of individuals approach of Gilinsky & Bennington (1994), and absolute abundances were converted into relative abundances, because of different sample sizes. Non-transformed relative

Fig. 3. □A–F. *Argyrotheca cordata* □A–C. Ventral, dorsal and side views of interiors of a complete specimen, Marsa Abu Zabad, Gulf of Aqaba, depth unknown, Hebrew University of Jerusalem. □D–F. Ventral dorsal and side views of specimen from Cassis, southern France, 85 m. NHMW 103336-8. □G–O. *Argyrotheca jacksoni.* □G–I. Ventral, dorsal and side views of interiors of a complete specimen, *Calypso*, 1951-2, Abulat Island, 20–28 m, NHMW 103339-40. □J–L. Ventral, dorsal and side views of interiors, loc. 95/3, 12 m, NHMW 103341-2. □M–O. Exteriors of ventral and dorsal valves and interior of dorsal valve, loc. 94/5, 19 m, 103343-5. □P–T. *Argyrotheca* sp. A. □P–S. Dorsal valve exterior, interior, and dorsal interior side views, loc. 100/8, 90 m, NHMW 1033346-9. □T. Exterior of dorsal valve of possible aberrant individual with only two costae, loc. 100/8, depth 90 m, NHMW 103350. (Scale bar represents 0.5 mm for C and F, 0.7 mm for I and L and 1.0 mm for all others.)

abundances were used for multivariate analyses. With the exception of *Argyrotheca*, they are run on species level. In order to discriminate groups of samples with similar taxonomic composition, a Q-mode cluster analysis of 31 samples (Table 2) based on Bray–Curtis similarity coefficient and group-average linking was performed. To display relationship of samples in a low-dimensional space, a non-metric multidimensional scaling (NMDS) based on rank Bray–Curtis dissimilarity matrix was used. One-way analysis of similarities (ANOSIM) was used to test if there is some relationship between habitat properties and taxonomic composition (Clarke & Green 1988).

The samples were assigned to three depth habitats: above 100 m, between 100 and 600 m, and deeper than 600 m. These habitats were chosen based on the known bathymetric zones in the Red Sea and previous studies of benthic faunas. The coastal shelves descend from the shore to the main trough at 300–600 m (Medio *et al.* 2000) but an area where the water is less than 100 m is considered a distinct depth habitat of its own, because it is characterized by broadly overlapping molluscan assemblages (Grill & Zuschin 2001). Environments deeper that 600 m are generally characterized by rather uniform environments (Medio *et al.* 2000).

Four substrate types were also chosen: reef substrates, bioclastic sands, muds, and concretions/carbonate crusts. These substrate types are subdivided according to their dominant components (i.e. macrosubstrate). Note that we do not assume that they are completely equivalent to attachment sites of brachiopods. For example, brachiopods might be attached to shell debris or non-preservable organisms in muddy substrates.

At the spatial scale of a shallow water bay in Safaga, molluscan death assemblages are interpreted as products of the local fauna, because they correlate so strongly with the sedimentary facies and because there is no sedimentological or taphonomic evidence for considerable transport that would produce allochthonous assemblages (Zuschin & Hohenegger 1998). The restriction of shallow-water brachiopods to samples from coral-associated sediments in our study supports this view. In the case of significant transport, brachiopods should also be found in other nearby bottom facies, but no brachiopod shells occurred in samples from mud, muddy sand, seagrass or mangrove facies. Also at the basin scale no faunal mixing was observed for bivalve death assemblages, which are strongly separated by water depth and bottom types, especially the bathyal assemblages that differ strongly from those of the shallow and deeper shelf (Grill & Zuschin 2001). Also in our study, brachiopod assemblages are very well separated by water depth and substrate types, which supports the interpretation of negligible habitat mixing due to transport.

The null hypothesis of ANOSIM is that the average of pairwise rank dissimilarities within habitats is equal to the average of pairwise rank dissimilarities between habitats, that is, there are no differences in taxonomic composition between habitats. The test statistic R is unity if there is a complete between-habitat separation in taxonomic composition and zero if the null hypothesis is true. The probability distribution of R when the null hypothesis is true is generated by Monte Carlo randomization approach. Although the number of samples from some habitats can be too low for estimation of reliable significance level, the R statistic is calculated as it still has an interpretative value and NMDS with sufficiently low stress can also give a reliable picture of habitat differentiation (Clarke & Warwick 2001). The analyses were performed using the PRIMER software (Clarke & Warwick 2001).

Cluster analysis and non-metric multidimensional scaling

Four sample groups were discriminated by cluster analysis (Fig. 4A). In NMDS (Fig. 4B), the *Platidia* and *Cryptopora* sample groups are well segregated. The *Argyrotheca* and *Megerlia* sample groups show rather continuous transition in terms of their composition but are still separated.

In addition to the most common *Argyrotheca* (32% relative abundance) the *Argyrotheca* sample group ($n = 344$) contains *Novocrania* cf. *anomala* (24%), *Thecidellina* sp. (23%) and *Megerlia echinata* (21%). It is represented by six samples. Two samples are derived from shallow (above 20 m), reef slope habitats (coralgal deposits) in the northern Bay of Safaga (Zuschin & Hohenegger 1998). Four samples from deeper habitats with foraminiferal sand or muddy substrates (80–669 m in depth) are derived from two transects near Port Sudan.

The *Megerlia* sample group ($n = 560$) is dominated by *Megerlia echinata* (64%), with *Argyrotheca* sp., *Platidia anomioides, Novocrania* cf. *anomala* and *Thecidellina* sp. less common. This sample group, represented by four samples, is derived from moderate depths (56 – 404 m) near Port Sudan (Grill & Zuschin 2001). The substrate is of bioturbated muds with a sandy–bioclastic admixture.

The *Cryptopora* sample group ($n = 937$) occurs in 12 samples and contains *Cryptopora curiosa* as the strongly dominant brachiopod taxon. Eight samples were derived from slope transects near Port Sudan

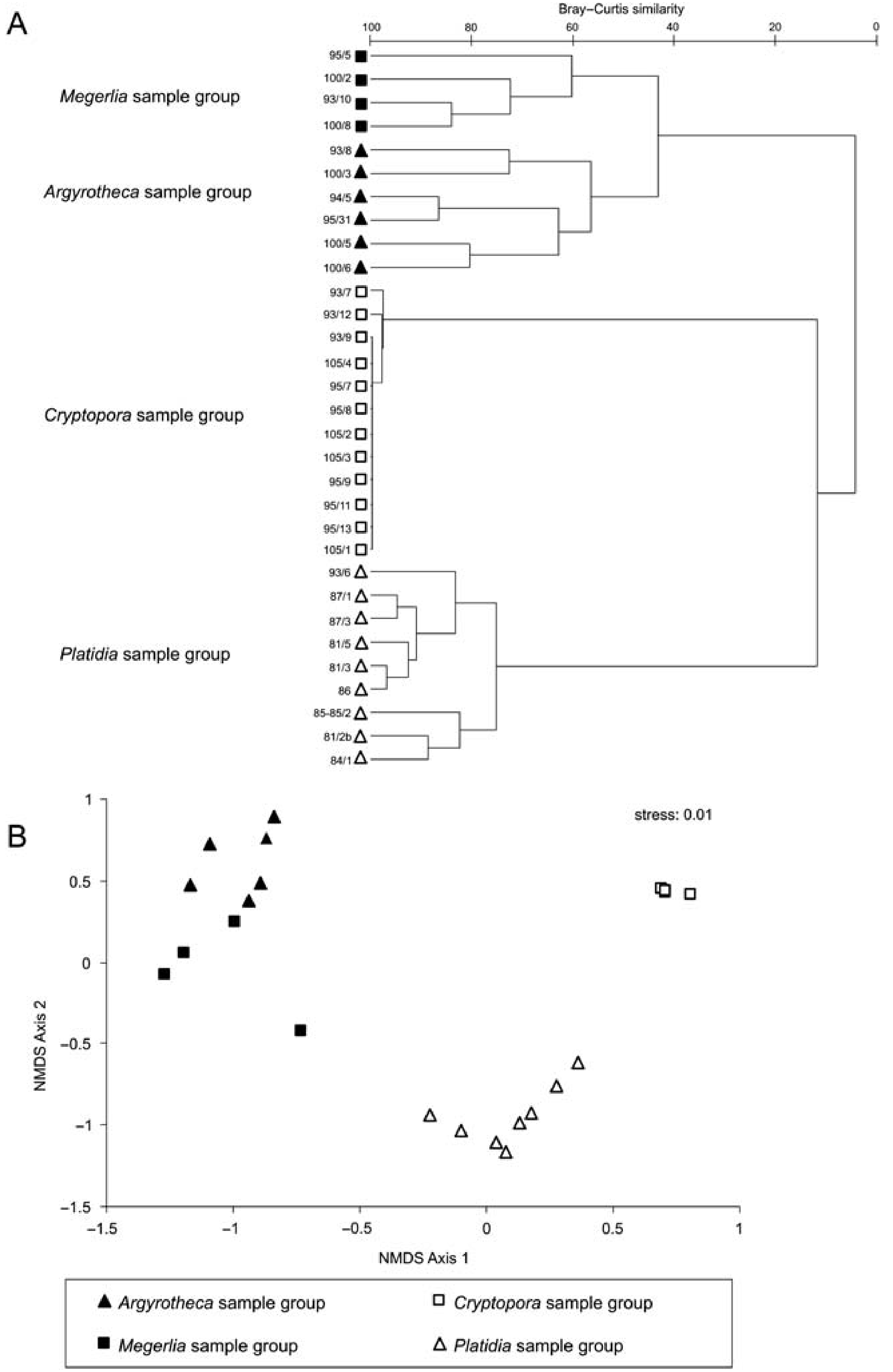

Fig. 4. □A. Q-mode cluster analysis of 31 samples with four discriminated sample groups. □B. Q-mode non-metric multidimensional scaling showing interrelationship of the sample groups. Nine monospecific samples of the *Cryptopora* sample group are represented by one point.

Table 3. Results of analysis of similarities (ANOSIM) that tests differences in taxonomic composition among three depth habitats. The adjusted level of significance for three pairwise comparisons is 0.0166.

	R-statistic	*P*-level	Number of permutations	Number of permuted statistics greater than or equal to observed R
Global test	0.203	0.017	10000	166
Pairwise tests				
Concretions/crusts vs. mud	0.255	0.02	10000	195
Concretions/crusts vs. bioclastic sand	0.71	0.016	126	2
Concretions/crusts vs. reef slope sand	1	0.048	21	1
Mud vs. bioclastic sand	−0.088	0.77	10000	7737
Mud vs. reef slope sand	0.311	0.023	171	4
Bioclastic sand vs. reef slope sand	0.564	0.048	21	1

Table 4. Results of analysis of similarities (ANOSIM) that tests differences in taxonomic composition among four substrate types. The adjusted level of significance for six pairwise comparisons is 0.0083. Note that the number of permutations is too low in some cases.

	R-statistic	*P*-level	Number of permutations	Number of permuted statistics greater than or equal to observed R
Global test	0.438	< 0.0001	10000	0
Pairwise tests				
Above 100 m vs. 100–600 m	0.39	0.002	10000	15
Above 100 m vs. below 600 m	0.847	0.0003	3003	1
100–600 m vs. below 600 m	0.343	0.007	10000	69

and four samples from the Gulf of Aden. Only three samples contain brachiopod taxa other than *Cryptopora*. Note that nine monospecific samples with *Cryptopora* fall in one point in NMDS (Fig. 4B). Near Port Sudan, the species occurs at greater depths (311–580 m) in habitats with bioclastic muds and sands. It is the only known sample group from the Gulf of Aden, where it occurs also at shallower depths (71–506 m).

The *Platidia* sample group ($n = 245$) is dominated by *Platidia anomioides* (82%), followed by less common *C. curiosa* and rare *Megerlia*, *Discinisca* and *Argyrotheca*. With the exception of one sample near Port Sudan (sample 93/6 at 567 m in depth) this sample group typically occurs in the northern part of the Red Sea in the depth range between 675 and 1448 m, although this may be due to sampling bias towards this area. The substrate is either represented by pteropod–foraminiferal muds (samples 85, 85/2), or by carbonate crusts and sulphidic concretions (locally with phosphatic and Mn coatings and encrusting oysters and polychaetes), thus indicating hard-bottom conditions.

Analysis of similarities

As follows from ANOSIM, there are significant compositional differences among three depth habitats (Table 3). The first three sample groups dominated by *Argyrotheca, Megerlia* and *Cryptopora* usually do not exceed 600 m depth; in contrast, *Platidia* dominates in the deepest habitats (i.e. below 500–600 m). In habitats shallower than 100 m, *Argyrotheca* and *Megerlia* are usually common. *Cryptopora* is most abundant at depths between 300–600 m. However, in the Gulf of Aden it is present also in the shallowest habitats, similar to depths reported for this species by Cooper (1973) off northeastern Somalia at the entrance to the Gulf. Global ANOSIM also shows that there are some compositional differences among habitats with different substrates ($R = 0.203$, $P = 0.017$, Table 4). However, muddy substrates can be inhabited by all four sample groups and some sample groups occupy several substrate types. The habitats with reef slope sands are occupied by the *Argyrotheca* sample group only. In addition, this sample group inhabits also muddy and sandy substrates. The *Cryptopora* and *Megerlia* sample groups are limited to sandy or bioclastic muds or bioclastic sands substrates. Three samples of the *Platidia* sample group are derived from muds with pteropods and foraminifers, otherwise this sample group is confined to habitats with concretions/carbonate crusts.

Affinities of the Red Sea and Gulf of Aden brachiopods

The affinities of present-day Red Sea brachiopods are with those of the Indian Ocean and Mediterranean, the Gulf of Aden species with the Indian Ocean. During the Middle Miocene, the Mediterranean, Indo-Pacific and Paratethys formed a system of well-connected basins with brachiopod species easily migrating between them (Bitner 1990, Rögl 1998). Paratethyan elements that are presently in the Red Sea and Mediterranean Sea include *Argyrotheca cuneata, A. cordata,* and *Platidia anomioides,* with *Cryptopora lovisati* (Dreger) closely related to modern *Cryptopora curiosa* from the Indian Ocean, and Miocene *Megerlia truncata* present in the modern Mediterranean and closely related to modern *Megerlia echinata* from the Red Sea and Indian Ocean (Bitner 1990; Bitner & Cahuzac 2004). *Megathiris detruncata* (Gmelin), which usually occurs with the micromorphic argyrothecids throughout the eastern Atlantic and Mediterranean (Logan 1979), was common in Paratethys (Bitner 1990) and should also be present in the Red Sea.

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