

Brachiopods from cryptic coral reef habitats in the northern Red Sea

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Abstract In contrast to the Palaeozoic to Jurassic fossil record, modern tropical and subtropical shallow-water brachiopods are typically small-sized and mostly restricted to cryptic habitats in coral reefs, but information on microhabitat-composition is scant. At Dahab, northern Red Sea, living brachiopods of the genus *Argyrotheca* were only detected on massively encrusted coral colonies attached to encrusting foraminifers and coralline red algae. Three samples from autochthonous sediments underneath coral colonies are comparatively rich in the brachiopod genera *Megerlia* and *Argyrotheca*, and additionally show low numbers of *Novocrania* and *Thecidellina*. Based on a coarse-grain analysis including more than 16,000 components >1 mm, these brachiopod shells co-occur with skeletal components of 11 higher taxa. Decapods, fixosessile foraminifers, molluscs, scleractinians, and coralline red algae clearly dominate the assemblages. Brachiopods in this study always contribute less than 2% to the sediment composition. This confirms previous results that even in brachiopod habitats the contribution of brachiopod shells to the total sediment composition is almost negligible. Our study indicates that brachiopods co-occur with pteriomorph bivalves and other epifauna in the cryptic habitats with limited space for encrusters or epibionts on the undersides of scleractinians and it tentatively supports the hypothesis of brachiopods preferring habitats with low grazing pressure, because shelly components of grazers (polyplacophorans and regular echinoids) are rare in our samples.

Keywords Coarse-grain analysis · Cryptic habitats · Coral reef · Palaeoecology

Introduction

Brachiopods were abundant or dominant members of tropical, shallow-water communities during the Palaeozoic (e.g., Ziegler et al. 1968; Leighton 1999; Olszewski and Erwin 2004) and also during the Triassic and Jurassic (Ager 1965; Fürsich et al. 2001; Tomasovych 2006), although the end-Permian mass extinction severely reduced their global diversity (Gould and Calloway 1980). In the Cretaceous and Cenozoic, however, their importance decreased (Sandy 2001). Today, medium- and large-sized brachiopods can be locally or regionally abundant on the open shelf in polar (e.g., Peck et al. 2005) and cool-temperate regions (e.g., Noble et al. 1976; Tunnicliffe and Wilson 1988; Tomasovych 2008). Species from tropical and subtropical shelves, in contrast, are typically small-sized (<1 cm) and—apart from an upwelling-influenced outer shelf occurrence in the south Atlantic (Kowalewski et al. 2002)—usually occur in cryptic habitats, i.e. the undersides of corals and the interiors of crevices and caves (e.g., Jackson et al. 1971; Logan 1975, 1977; Asgaard and Stenftoft 1984; Bitner 2002; Logan et al. 2008), where their distribution is space-limited by competitive superior colonial organisms (Jackson 1977). Only very little information is available regarding the contribution of brachiopod shells to sediment composition underneath such coral habitats. Brachiopods contribute less than 1% to sediment samples from Grand Cayman (Logan 1977) and 0.5–2% to sediment samples from Barbados (Asgard and Stenftoft 1984), but nothing is known about the quantitative composition of the co-occurring biogenic particles. The purpose of this paper is to

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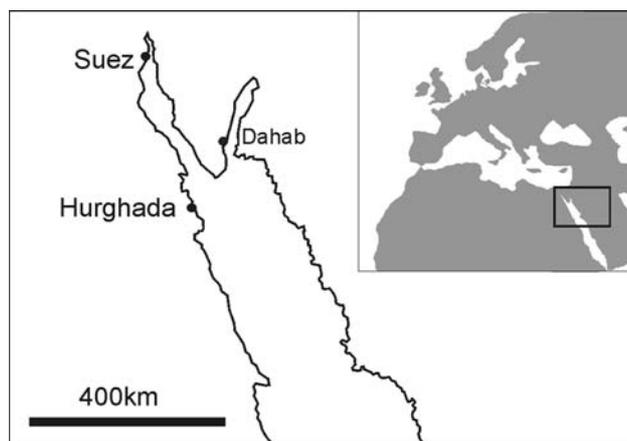


Fig. 1 Study area (modified after Logan et al. 2008)

provide information on the life habit of shallow-water brachiopods and the sediment composition of brachiopod-rich samples taken from cryptic coral reef-associated sediments in the northern Red Sea and to estimate the contribution of brachiopods to the total sediment composition.

In the Red Sea and Gulf of Aden, recent investigations on quantitative samples from shallow-water to bathyal settings revealed four brachiopod associations, which occupy different depth habitats and substrate types. Low abundance, moderate diversity and small shell sizes appear to characterize modern Red Sea brachiopods, and shallow-water brachiopods occurred only in reef-associated sediments (Logan et al. 2008). In the course of a new project on comparative ecology and taphonomy, numerous samples were taken from cryptic habitats in the northern Red Sea and quantitatively evaluated for brachiopods and molluscs (unpublished data of Adam Tomasovych and Martin Zuchin). Three of these samples were chosen to characterize the microhabitat of brachiopods in some more detail. Brachiopods in the three samples belong to four genera from three orders and two classes. All three samples are dominated by the terebratulids *Megerlia* and *Argyrotheca* and show low numbers of the craniid *Novocrania*. The thecideid *Thecidellina* is only present with a few shells and occurs only in sample D05-15. Bivalves in all three samples are clearly dominated by pteriomorphs, most notably

Table 2 Percentage of brachiopods and bivalves in total assemblage and individual samples

	Dahab05-25	Dahab05-15	Dahab05-8	Total
Brachiopods	1.7	1.4	0.1	1.1
Bivalves	6.2	4.2	3.0	4.3

Whole shells of brachiopods and molluscs (see Table 1) were picked from the total sediment of each sample, all other components (Table 3) from small subfractions. The percentage of brachiopods and bivalves is therefore grossly overestimated and can only be considered as a rough approximation

the bysally attached genera *Acar*, *Barbatia* and *Septifer* and juvenile oysters.

Materials and methods

Samples were taken at Dahab, Gulf of Aqaba, located in the northern Red Sea, by SCUBA diving (Fig. 1). Living corals of the genera *Acropora*, *Montipora*, *Favia*, and *Goniastrea* and dead, unidentifiable and strongly encrusted foliate and branching coral colonies were collected in water depth between 5 and 17 m in October 2008 and investigated for the presence of living brachiopods. Small sediment samples were taken from cryptic, quiet-water habitats under or between coral colonies in October 2005. Sample D05-08 was taken from muddy sand under a large *Turbinaria mesenterina* colony in 13 m water depth, sample D05-15 from coarse sand under an *Acropora* colony in 10 m water depth, and sample D05-25 from muddy sand between faviid coral colonies in 9 m water depth. The sediment was sieved with 1-mm mesh size and air-dried. For the purpose of a comparative evaluation, brachiopods and molluscs were picked from the whole sample (Tables 1, 2), and subsequently smaller subsets of these samples were used to study the composition of the remaining sediments under a binocular microscope (Table 3). The biogenic components were distinguished into 12 higher taxonomic categories (algae, foraminifers, sponges, hydrozoans, octocorals, scleractinians, polychaetes, molluscs, brachiopods, crustaceans, bryozoans, and echinoderms), one quantitatively unimportant

Table 1 Results of coarse-grain analysis for brachiopods and molluscs

	Dahab05-25		Dahab05-15		Dahab05-8		Total	
	Number	%	Number	%	Number	%	Number	%
Brachiopods	62	10.2	110	8.0	6	1.4	178	7.38
Bivalves	226	37.1	332	24.0	151	36.0	709	29.41
Gastropods	311	51.1	919	66.4	246	58.7	1,476	61.22
Polyplacophorans	10	1.6	22	1.6	16	3.8	48	1.99
Total	609	100	1,383	100	419	100	2,411	100

Table 3 Results of coarse-grain analysis for all components except whole shells of brachiopods and molluscs

	Dahab05-25		Dahab05-15		Dahab05-8		Total	
	Number	%	Number	%	Number	%	Number	%
Algae								
Coralline red algae	87	2.8	432	6.6	471	10.2	990	7.0
Green algae	0	0.0	5	0.1	1	0.0	6	0.0
Tubular algae	3	0.1	31	0.5	30	0.6	64	0.4
Foraminifera								
Fixosessile forams	420	13.7	774	11.8	299	6.5	1,493	10.5
Semisessile and vagile forams	22	0.7	148	2.3	219	4.7	389	2.7
Porifera								
Sponge spicules	0	0.0	10	0.2	4	0.1	14	0.1
Hydrozoa								
Hydrozoans	33	1.1	64	1.0	59	1.3	156	1.1
Anthozoa								
<i>Tubipora</i>	6	0.2	24	0.4	19	0.4	49	0.3
Octocoral sclerites	1	0.0	18	0.3	77	1.7	96	0.7
Scleractinians	591	19.3	259	4.0	275	5.9	1,125	7.9
Polychaeta								
Serpulids	59	1.9	137	2.1	45	1.0	241	1.7
Mollusca								
Unidentifiable molluscan fragments	151	4.9	565	8.6	519	11.2	1,235	8.7
Crustacea								
Balanids	0	0.0	4	0.1	0	0.0	4	0.0
Decapods	573	18.7	954	14.6	454	9.8	1,981	13.9
Ostracods	0	0.0	9	0.1	2	0.0	11	0.1
Bryozoa								
Branching bryozoans	55	1.8	201	3.1	19	0.4	275	1.9
Encrusting bryozoans	112	3.7	205	3.1	59	1.3	376	2.6
Echinodermata								
Ophiuroids	22	0.7	177	2.7	15	0.3	214	1.5
Asteroids	6	0.2	5	0.1	6	0.1	17	0.1
Regular echinoids	41	1.3	147	2.2	67	1.4	255	1.8
Irregular echinoids	3	0.1	14	0.2	10	0.2	27	0.2
Crinoids	0	0.0	44	0.7	9	0.2	53	0.4
Unidentifiable echinoderm fragments	99	3.2	21	0.3	3	0.1	123	0.9
Indeterminata	0	0.0	14	0.2	6	0.1	20	0.1
Degraded biogenic particles	775	25.3	2,289	34.9	1,961	42.4	5,025	35.3
Total	3,059	100.0	6,551	100.0	4,629	100.0	14,239	100.0

group of Indeterminata (i.e., components showed distinct morphological features, but we were unable to identify them) and one quantitatively dominant category of biogenic components, which no longer showed diagnostic features due to taphonomic degradation. The higher taxonomic groups were distinguished into subcategories, based on taxonomic and/or ecological features. Accordingly, algae were divided into coralline red algae, green algae and tubular

algae, foraminiferans into fixosessile versus semisessile and vagile forms, molluscs into bivalves, gastropods and polyplacophorans, crustaceans into balanids, decapods and ostracods, bryozoans into branching and encrusting forms, echinoderms into ophiuroids, asteroids, regular and irregular echinoids and crinoids. Finally, unidentifiable molluscan and echinoderm fragments were summarized into categories of their own (Tables 1, 3; Figs. 2, 3, 4, 5).

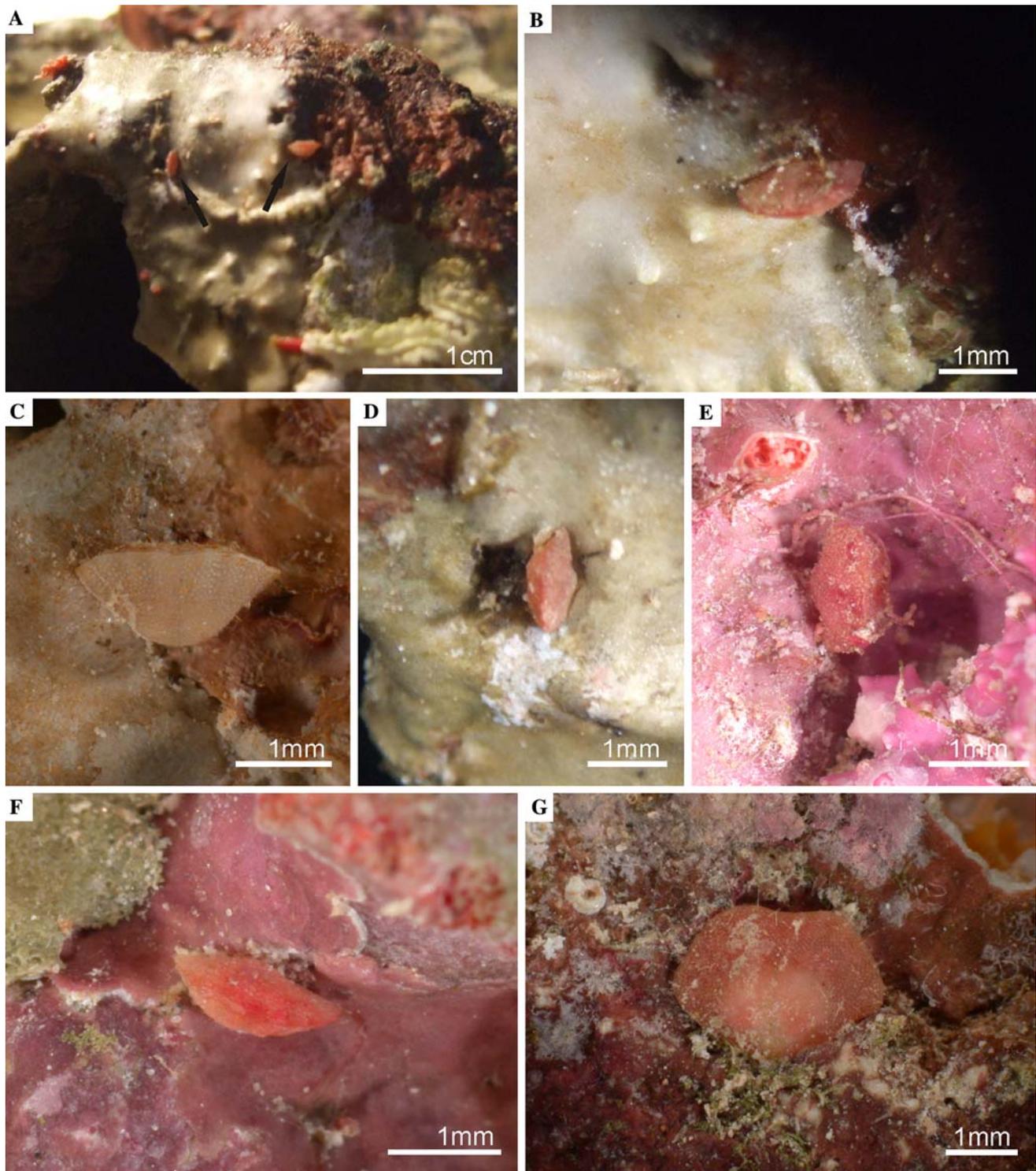


Fig. 2 Living *Argyrotheca* cf. *jacksoni* on massively encrusted dead coral colonies. **a** Image taken immediately after collection showing encrusted, unidentified coral colony with two living animals (*arrows*) attached to *A. inhaerens* and at the contact between *A. inhaerens* and coralline red algae. Note the presence of unidentified serpulid and *Homotrema*. **b** Image taken immediately after collection showing *Argyrotheca* at the contact between *A. inhaerens* and coralline red

algae. Note *red color* of the brachiopod. **c** Close up of same animal as shown in **b**, after discoloration due to preservation in ethanol **d** Image taken immediately after collection showing *Argyrotheca* attached to *A. inhaerens*. **e** *Argyrotheca* attached to crevice in crust of coralline red alga. **f** *Argyrotheca* attached to coralline red algae. **g** *Argyrotheca* attached to crevice in crust of coralline red alga. Field photograph showing being oriented almost perpendicular to the substrate

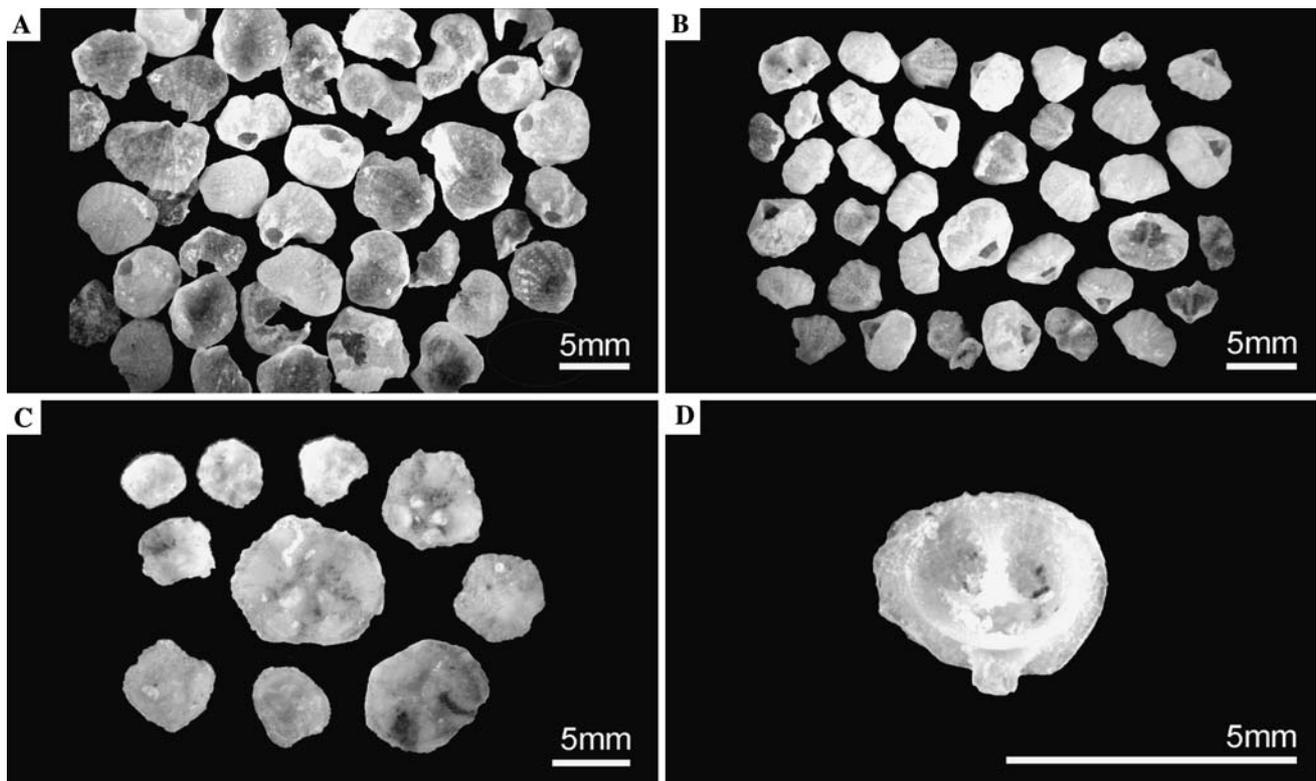


Fig. 3 Brachiopods from coarse-grain analysis. **a** *Megerlia* sp., **b** *Argyrotheca* sp., **c** *Novocrania* sp., **d** *Thecidellina* sp.

Components within each category were counted and compared in tables and diagrams. For a statistical evaluation, only the distinct subcategories were used; this excluded the categories Indeterminata, degraded biogenic components, molluscan- and echinoderm fragments. Additionally, all categories with less than 50 components were not included (green algae, sponge spicules, *Tubipora*, balanids, ostracods, asteroids, irregular echinoids). Due to different quantitative treatment of brachiopods and molluscs versus the remaining component categories, only very limited statistical evaluations were possible. Brachiopods were compared with all other categories in a correlation analysis using Pearson's product-moment correlation coefficient; low number of samples, however, largely prohibited significant results despite high correlation coefficients. Since brachiopods, bivalves, and gastropods are from the same amount of sediment, the raw abundances were used for the correlation analysis. For the correlation analysis of all other categories with raw abundances of brachiopods, their proportions were used, which were arcsine-root transformed to gain linear data (Linder and Berchtold 1976). To visually summarize relationships among taxa, an R-mode non-metric multidimensional scaling (MDS, Kruskal 1964) was performed after standardizing the abundance data by the total of each sample and each variable. Statistical analysis was performed with the programs PAST

version 1.82 (Hammer et al. 2001) and PRIMER version 6.1.6 (Clarke and Warwick 1994).

Results

Ten specimens of living brachiopods of the genus *Argyrotheca* were detected on strongly encrusted (but unidentifiable) dead coral branches, where they occurred on encrusting foraminifers (*Acervulina inhaerens* and *Homotrema* sp.) and coralline red algae (Figs. 2, 3b). None of the other brachiopod genera (*Megerlia*, *Novocrania*, *Thecidellina*), which were present in the sediment samples (Fig. 3a, c, d), was found alive. Generally, brachiopods were not found on dead parts of the living coral colonies studied. Living *Argyrotheca* was attached with the pedicle and some animals occurred at the plane substrate surface, with shells being oriented almost perpendicular to the substrate (Fig. 2a–d). Some animals, however, settled in crevices (Fig. 2e–g) and their shells were inclined or even parallel to the surface of the substrate (Fig. 2g). Shells of the living animals typically measure less than 5 mm, are pink, and free of encrusters (Fig. 2).

Brachiopods, which contribute between 1.4 and 10.2% to the shells of the brachiopod–mollusc assemblage, are always less abundant than bivalves, which contribute

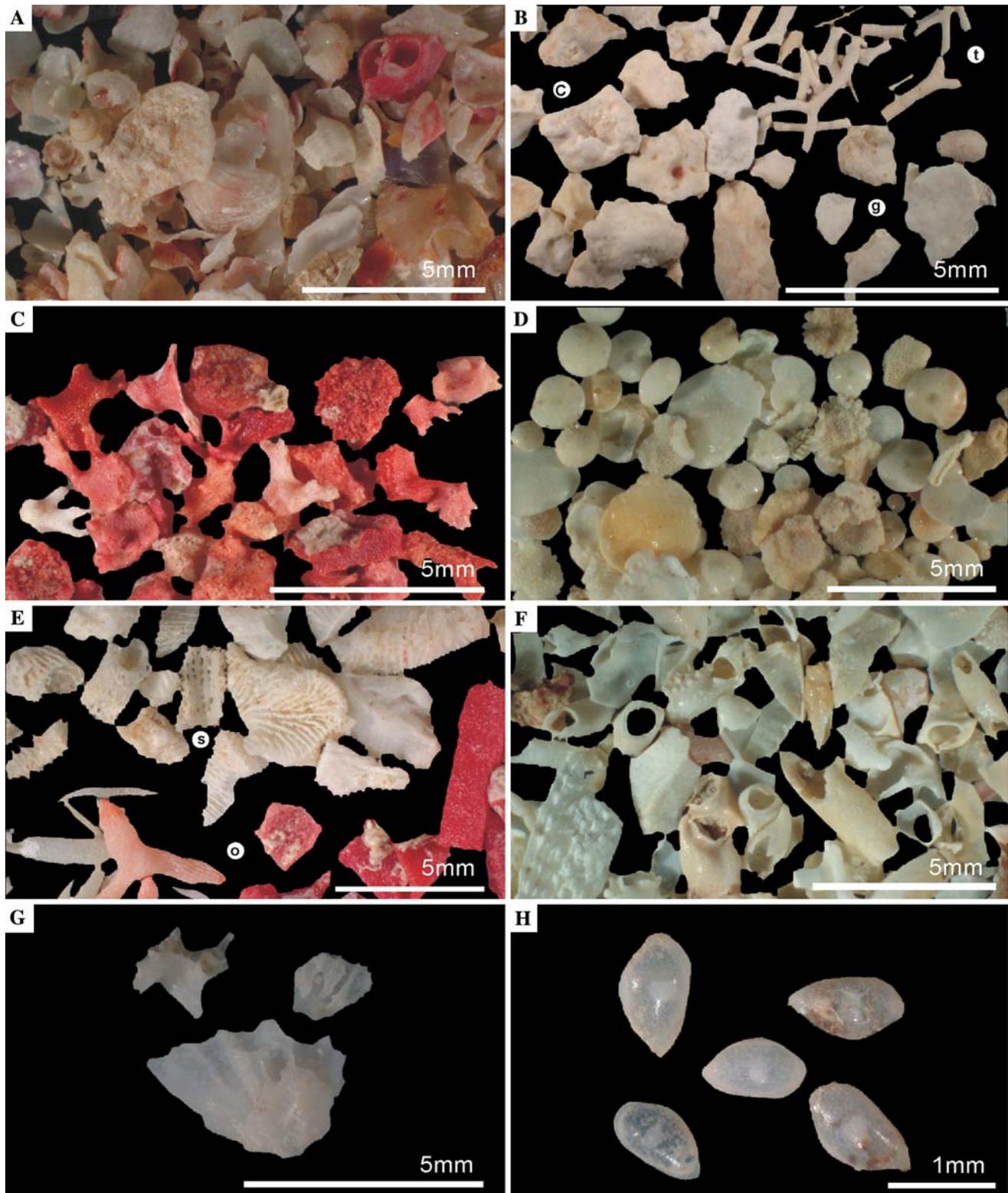


Fig. 4 Biogenic components of coarse-grain analysis. **a** Molluscan fragments, **b** algae (*t* tubuli, *g* green algae, *c* corallinaceans), **c** *Homotrema* (benthic fixosessile foraminifer), **d** benthic semisessile and

vagile foraminifers, **e** corals (*s* scleractinians, *o* octocorals), **f** decapods, **g** balanids, **h** ostracods

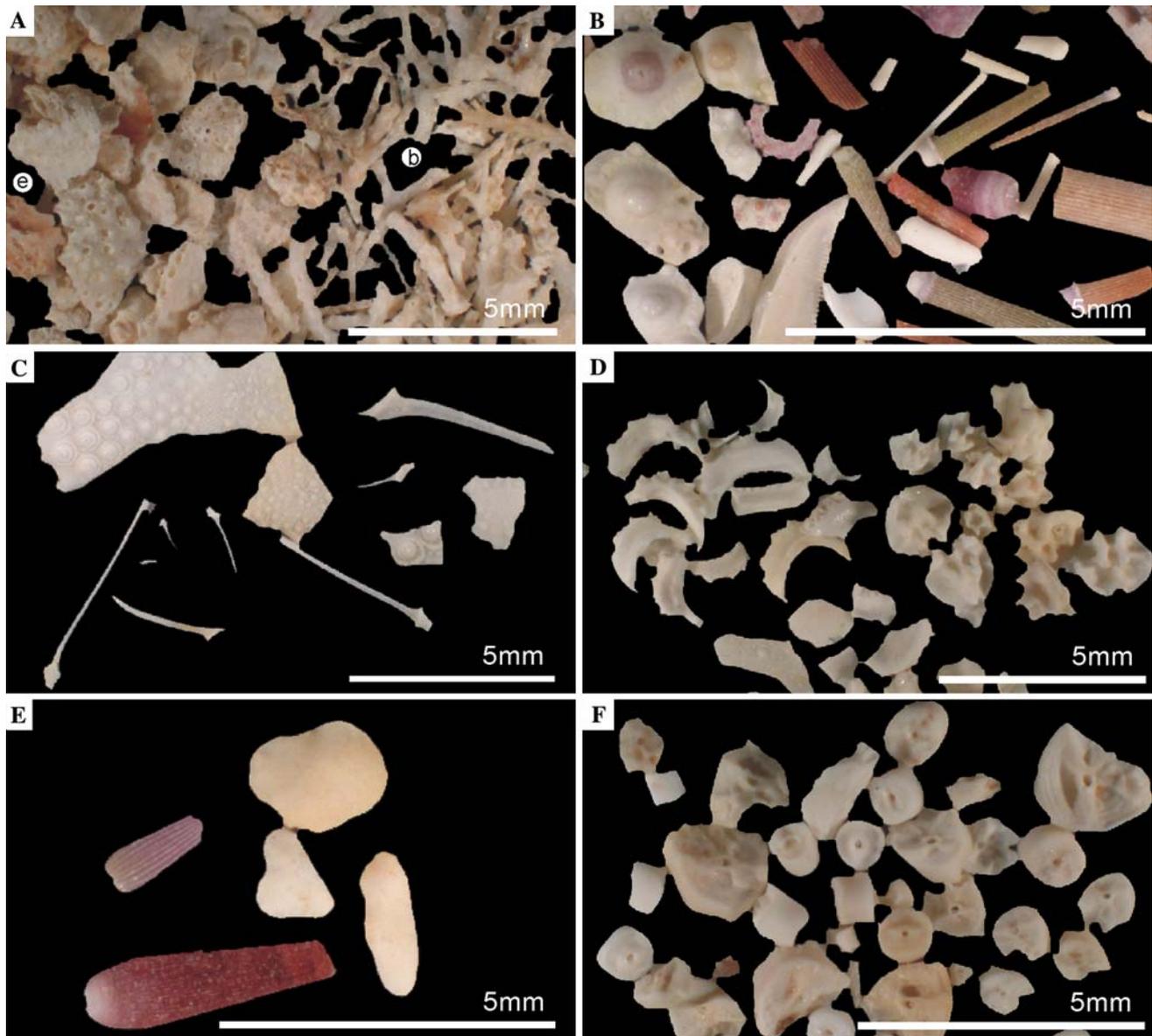


Fig. 5 Biogenic components of coarse-grain analysis. **a** Bryozoans (*e* encrusting, *b* branching), **b** regular echinoids, **c** irregular echinoids, **d** ophiuroids, **e** asteroids, **f** crinoids

between 24 and 37.1% (Table 1). In a comparison of brachiopods with the total coarse-grain composition, which is strongly biased towards brachiopods because they were picked together with molluscs from a much higher amount of sediment than the rest of components, brachiopods make up only 1.1% of the total assemblage, with a range from 0.1 to 1.7% in individual samples (Table 2). Bivalves in contrast contribute 4.3% to the total assemblage and show a range from 3 to 6.2% in individual samples.

In the total assemblage, degraded, unidentifiable biogenic particles make up the majority of components, followed by decapods, fixosessile foraminifers, molluscan fragments, scleractinians and coralline red algae; all other

categories contribute less (mostly much less) than 400 components each (Table 3; Fig. 6). However, distinct differences in the composition between samples are evident. The quantitatively important degraded biogenic particles and unidentifiable molluscan fragments have the highest proportions in sample D05-8 and lowest proportion in sample D05-25. Coralline red algae make up the majority of algal components in individual samples and are most abundant in sample D05-8. Algal tubes and green algae are very rare in all samples. Fixosessile foraminifers are much more abundant than semisessile and vagile forams and their proportion ranges from 6.5 to 13.7%. Scleractinians are much more abundant than octocorals and their proportion ranges

Fig. 6 Proportional abundances of grain categories in the total assemblage and in individual samples. Only categories that contribute more than 1% to the total assemblage are shown

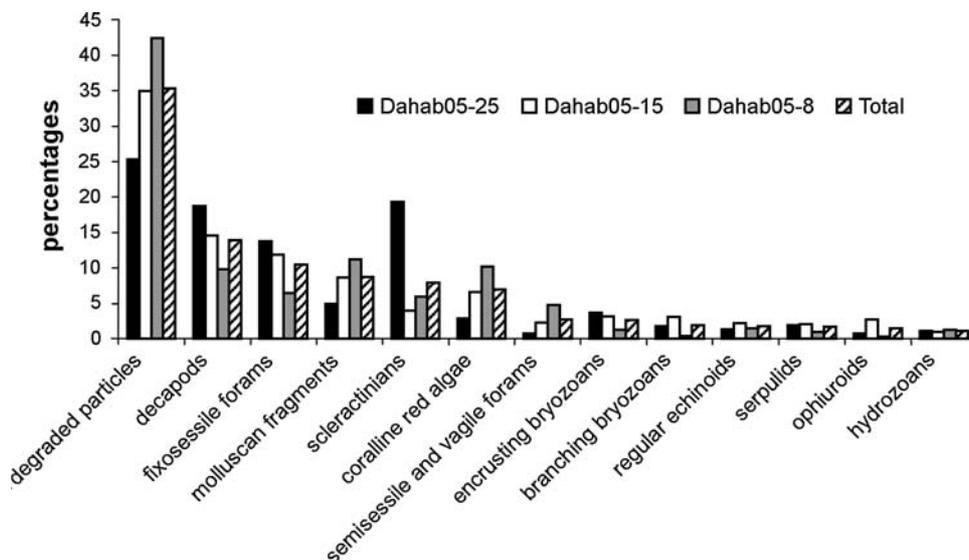


Table 4 Results of correlation analysis between brachiopods and other component categories (excluding Indeterminata, degraded biogenic components, molluscan- and echinoderm fragments and all categories with less than 50 components)

	Pearson's <i>r</i>	<i>P</i> -value
Coralline red algae	−0.530	0.644
Tubular algae	−0.366	0.761
Fixosessile forams	0.912	0.269
Semisessile and vagile forams	−0.592	0.597
Hydrozoans	−0.829	0.378
Octocoral sclerites	−0.726	0.483
Scleractinians	−0.276	0.822
Serpulids	1.000	0.012
Decapods	0.718	0.490
Branching bryozoans	0.999	0.029
Encrusting bryozoans	0.898	0.290
Ophiuroids	0.909	0.274
Regular echinoids	0.359	0.766
Crinoids	0.366	0.761
Bivalves	0.990	0.091
Gastropods	0.887	0.306
Polyplacophorans	0.461	0.695

Bold values indicate significant correlations

from 4 to 19.3%. Among crustaceans, the decapods clearly dominate and make up between 9.8 and 18.7%. In contrast, the abundance of balanids and ostracods is negligible. The overall importance of bryozoans is low, and encrusting forms are somewhat more important than branching forms. Similarly, echinoderms are quantitatively unimportant; only regular echinoids and ophiuroids contribute more than 1% to some samples (Table 3; Fig. 6).

Although the number of samples is low, brachiopods show significant positive correlations with serpulids and

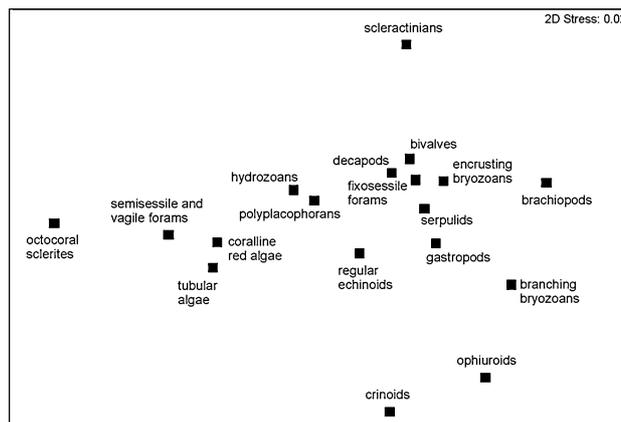


Fig. 7 R-mode multidimensional scaling (MDS). Points close to one another represent taxa that co-occur in the studied samples

branching bryozoans. Additionally, brachiopods show high positive correlations to fixosessile foraminifers, encrusting bryozoans, bivalves, ophiuroids, but these are not significant. Notable negative correlations with brachiopods include the hydrozoans, Alcyonaria sclerites, and the semisessile and vagile foraminifera; all these correlations, however, are not significant (Table 4). The R-mode non-metric multidimensional scaling also suggests a co-occurrence of brachiopods with grazing-sensitive bryozoans and with fixosessile foraminifers and serpulids (Fig. 7).

Discussion

Tropical and subtropical shallow-water brachiopods usually occur in cryptic habitats, i.e., the undersides of corals and the interiors of crevices and caves (e.g., Jackson et al. 1971; Logan 1975, 1977; Asgaard and Stenfort 1984;

Logan et al. 2008). With respect to corals, brachiopods live preferentially attached to the undersides of foliaceous or between the branches of branching scleractinians (Jackson et al. 1971; Logan 1977; Asgaard and Stentoft 1984). These findings are confirmed by our study and it is important to note that living brachiopods were only found on dead and strongly degraded, massively encrusted coral colonies. Accordingly, non-reefal shallow-water sediments in the northern Red Sea are virtually devoid of brachiopods (Logan et al. 2008). Similar to findings from Bermuda (Logan 1975), such cryptic brachiopods are typically found on encrusting foraminifers (acervulinids, *Homotrema*) and co-occur with pteriomorph bivalves (*Acar*, *Barbatia*, *Sep-tifer*, and juvenile oysters). These bivalves have about the same size and we estimate that their density on the corals was rather lower than that of brachiopods. Conversely, however, even in their preferred habitats, the contribution of brachiopod shells to sediment composition is very small, particularly compared to bivalves, which suggests that post-mortem brachiopods remain attached with the pedicle and frequently get overgrown in situ, whereas bysally attached bivalves and the upper valves of oysters contribute proportionally more to the sediment composition. However, considering that brachiopods and molluscs were picked from a much larger part of the sediment than all other components, it is safe to conclude that brachiopods contribute much less than 1% to the sediment composition. This confirms previous results, because brachiopods contribute less than 1% to sediment samples from Grand Cayman (Logan 1977) and 0.5–2% to sediments samples from Barbados (Asgard and Stentoft 1984).

Hypotheses to explain this restriction of micromorphic brachiopods include high predation pressure (Vermeij 1977), competition with bivalves or other groups that limit their resources (Thayer 1985), and high grazing pressure (Vermeij 1977; Asgaard and Stentoft 1984; Tomasovych 2006). Non-reefal shallow-water sediments in the northern Red Sea, which are virtually devoid of brachiopods are dominated by infaunal heterodont bivalves (Zuschin and Hohenegger 1998; Grill and Zuschin 2001; Zuschin and Oliver 2003). In contrast, in this study, the brachiopods under coral colonies co-occur with abundant bysally attached or cemented pteriomorph bivalves. This may indicate that predation pressure in open habitats is too high for brachiopods (and pteriomorph bivalves), but at least the high proportion of decapod fragments in our samples contradicts the hypothesis that predation pressure is low in these cryptic habitats. Alternatively, both groups may not be well adapted to the relatively mobile sediments of the open shelf, which are preferentially inhabited by heterodont bivalves (cf. Stanley 1977). Our study indicates, however, that brachiopods are able to compete for space with pteriomorph bivalves in the cryptic habitats on the undersides of

scleractinians. Our study finally supports the hypothesis of low grazing pressure in cryptic habitats, because shelly components of grazers (polyplacophorans and regular echinoids) are rare in our samples. Moreover, brachiopods show significant positive correlations with the proportion of grazing-sensitive branching bryozoans and serpulids (Table 4) and high positive correlations (although not significant due to the low number of samples) with proportions of other sessile epifauna (fixosessile foraminifera, encrusting bryozoans). In contrast, brachiopods show a negative correlation (although again not significant, due to the low number of samples) with coralline red algae, which require regular grazing for their growth (Steneck 1983). However, living brachiopods on degraded coral colonies are typically associated with ubiquitous crusts of coralline red algae. Correlations from death assemblages may therefore not faithfully reflect ecological relationships, because compared to shells, crusts of corallines probably contribute only minor to the sediment composition.

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