
Taxonomic, Ecological and Historical Considerations on the Deep-Water Benthic Mollusc Fauna of the Red Sea

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Abstract

The semi-enclosed and narrow Red Sea basin is characterized by bathyal zones in its axial sectors. It is determined by extreme hydrological parameters regarding its deep-water salinity and temperature which are a serious challenge to be coped with by deep-water benthos. Besides, it is separated from the adjacent Indian Ocean (Gulf of Aden) by a remarkably shallow sill that not only opposes easy transit for deep-water benthos but also exerts a strong control on the basin's hydrology budget during sea-level fluctuations, likely causing pulsing basin-wide extinctions at times of low stands. Among the relevant macrobenthic groups inhabiting the deep Red Sea, Mollusca stand out as the more diverse phylum. Although the full taxonomic appreciation of the Red Sea deep-water molluscs is still unresolved, as many as 262 species are recorded to date from depths below 400 m (163 Gastropoda, 94 Bivalvia, 4 Scaphopoda and 1 Polyplacophora). Part of this fauna is represented by eurybathic species with a wide bathymetric range. A substantial aliquot is equipped with a larval strategy (planktotrophy) in principle enabling the crossing of the shallow sill from the Gulf of Aden. Various taxa occur also in the Indo-West Pacific, and only a few are putatively considered as Red Sea endemics.

Introduction

The astonishing advancement of deep-sea exploration in the last 40 years has refined and sometimes revolutionized (one being the discovery of chemosynthetic ecosystems) our appreciation of the ecology, diversity and evolution of benthos living at great depth (Rowe 1983; Wilson and Hessler 1987; Gage and Tyler 1991; Tunnicliffe 1991; Young and Eckelbarger 1994; Van Dover 2000; Rex et al.

2005a; Judd and Hovland 2007; Koslow 2007; Foucher et al. 2009; McClain et al. 2009; Glover et al. 2010; Taviani 2011). It is quite clear that the deep-sea realm is far from being a slowly evolving low-diversity biome mainly, if not solely, relying upon surface-produced organic fall as hypothesized by earlier scholars (see reviews by Koslow 2007 and Glover et al. 2010). On the contrary, the current view is that the deep-sea benthos is highly complex, diverse and governed by the interaction of multiple factors (Hessler and Sanders 1967; Dayton and Hessler 1972; Rex 1983; Tyler 1988; Gage and Tyler 1991; Grassle 1991; Ruhl and Smith 2004; Rex et al. 2005b; Levin and Dayton 2009; Glover et al. 2010; Rex and Etter 2010). On a global scale, a major ecological physiognomy of the deep-sea benthos is to inhabit a rather homogeneous environment, nutrient poor, and with a remarkable stability of salinity and temperature ranges (e.g. Brunn 1957; Sanders and Hessler 1969; Thiel 1975, 1989; Gage 1978). Only a few large deep-water basins of the present Earth divert from these basically stable hydrologic conditions, regarding either temperature or salinity or both, that is, the peri-Antarctic seas, the Mediterranean Sea and the Red Sea (Ekman 1953).

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The semi-enclosed Red Sea basin attains maximum depths well in excess of 2,500 m in its axial trough, and vast parts of its main trough are below 200 m, thus being suitable for the settlement of deep-water benthic life (Taviani et al. 2007). In comparison with the average situation in the ocean, the salinity of the Red Sea from the surface down to its deepest stretches is anomalous. By reaching values as high as 41 ‰ below a pycnocline at about 100–150 m (Morcos 1970; Rützen-Kositzkau 1999; Quadfasel 2001), the Red Sea deep water is, in fact, the saltiest marine water on Earth, besides the extreme values observed in some undersea brine pools or lakes, some of which are also present in the Red Sea axial trough (Antunes et al. 2011). Moreover, a temperature of 21.5 °C is observed basin-wide throughout the water column below the thermocline which is homothermic even at depths exceeding 2,000 m (Morcos 1970). Such values are aberrant when compared to temperatures met in the adjacent Gulf of Aden where temperature decreases with depth from about 13 °C at 500 m to about 3 °C below 2,000 m (Türkyay 1996; Thiel et al. 1987; Al Saafani and Shenoï 2007).

To this, we should also add the fact that the Red Sea is separated from the Gulf of Aden, the north-western extension of the Indian Ocean, by a remarkably narrow and shallow sill (Hanish Sill, 137 m; Werner and Lange 1975) which is an efficient hydrological barrier, and very sensitive to sea-level fluctuations (Siddall et al. 2003; Lambeck et al. 2011).

Not to be neglected is also the potential role played by cold upwelling waters around the Indian Ocean side of the Arabian Peninsula (Abdel-Rahman 2006; Morcos and Abdallah 2012). They could in fact represent a further barrier to the spreading from the Gulf of Aden of benthic molluscs and/or their meroplanktic larval stages into the Red Sea.

Combined all together, it is intuitive that these factors offer per se a serious constraint for the quality of the deep-sea stenoecious benthos and render this basin a unique and formidable laboratory in which to test, for instance, the relevance of abiotic stressors in shaping the deep-sea benthos diversity and evolution (Türkyay 1996; Taviani et al. 2007). Lamentably, not enough is known about the Red Sea deep benthos due to various unfavourable geo-politic circumstances which over the decades in one way or another hampered the systemic research on this region. Most information available at present still stems mainly from old expeditions in the late nineteenth and twentieth centuries, beginning with the pioneer expedition of the Austrian ship *Pola* in 1895–1898, followed much later by German surveys devoted to assessing potential environmental impacts related to metalliferous mud mining (Thiel 1979, 1980; Türkyay 1996), and to a minor extent by Italian, plus other expeditions in more recent times. Yet, published data on deep-sea benthic life is still scarce and often patchy. We have some

incomplete information about taxonomic groups such as ostracods (Bonaduce et al. 1983), foraminifera (Edelman-Furstenberg et al. 2001), cumaceans (Mühlenhardt-Siegel 2008) and a few others. Regarding megafauna and macrofauna, two taxa have attracted more attention, namely deep-water corals (Marenzeller 1907; Fricke and Hottinger 1983; Fricke and Schuhmacher 1983; Fricke and Knauer 1986; Taviani et al. 2007; Roder et al. 2013; Qurban et al. 2014) and molluscs (Sturany 1900a, b, 1901, 1904; Janssen 1989; Rützen-Kositzkau 1999). Holoplanktic and meroplanktic larval mollusc shells are common components of Red Sea bottom sediments contributing substantially to thanatocoenoses at bathyal depths. The holoplanktic mollusc fauna has been recently revised by Janssen (2007).

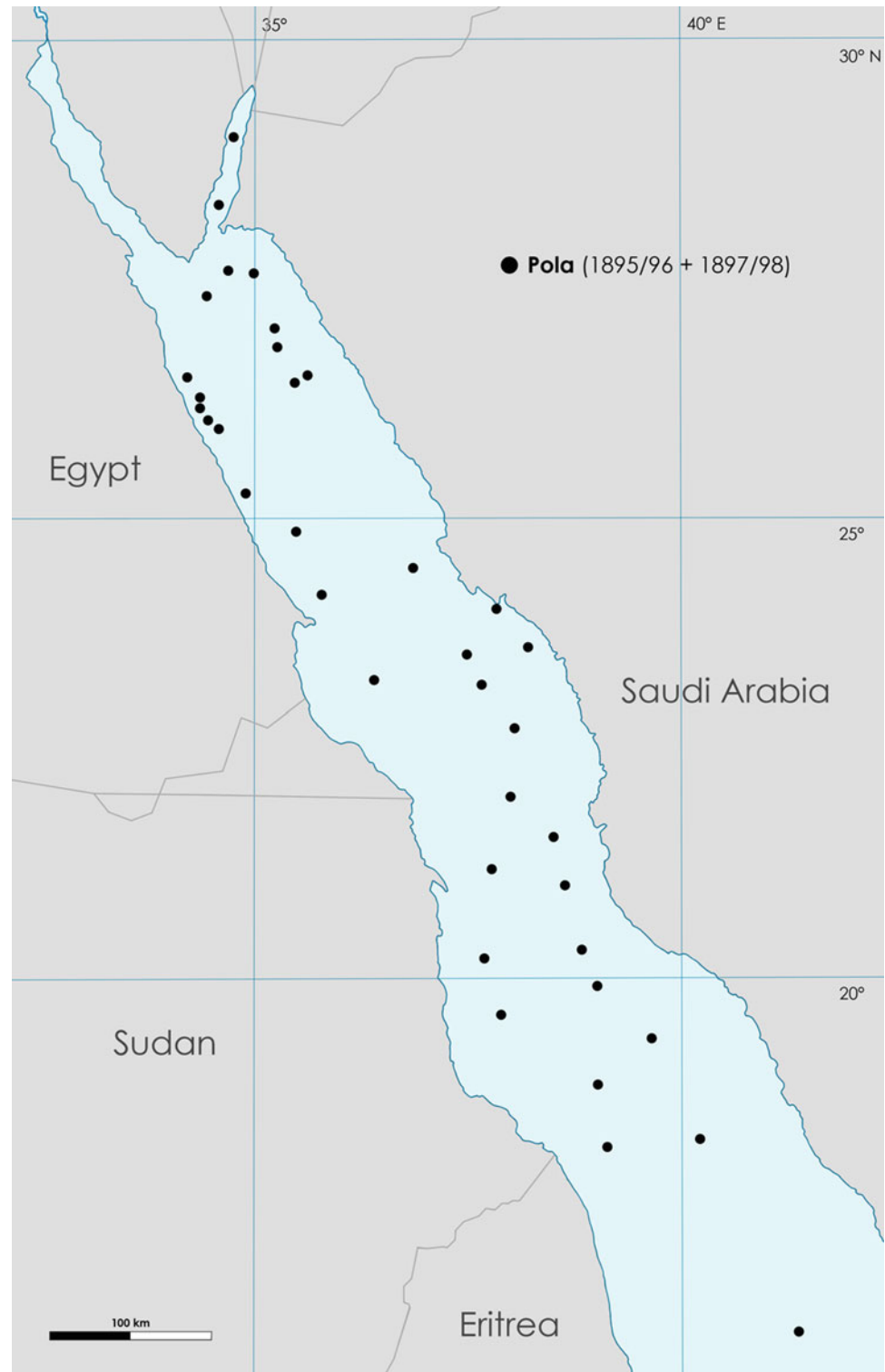
The Red Sea deep-sea benthos is clearly facing at the same time challenges and opportunities coping with a highly peculiar if not extreme environment. It has been hypothesized that the stenoecious marine biota of the Red Sea has been annihilated in this basin at the time of the last glaciation, in response to intolerable high-salinity conditions at the times of sea level lows (Taviani 1994, 1998a, b, with references therein). The present shallow and deep benthic fauna might, therefore, represent the post-glacial re-colonization (Gvirtzman et al. 1977; Taviani 1998a, c; Taviani et al. 2007). Firstly, the Red Sea is separated from the Indian Ocean by a very shallow sill (about 137 m) that imposes a strong geometric filter to potential propagules of the deep-sea Indian Ocean species trying to enter the basin (Janssen and Taviani 1985). Thus, deep-sea benthic organisms should rely upon special reproductive and dispersal mechanisms to cross the sill. Secondly, present oceanographic conditions in the Red Sea itself are very challenging for the survival of larvae and later establishment of viable populations in the bathyal zone, because of the unusual higher salinity and temperature of the deep-water than in any other marine basin on the planet.

The scope of this paper was to present a first critical account of the mollusc fauna inhabiting at present the Red Sea at depths exceeding 400 m, discussing taxonomic, ecological and biogeographical traits. The choice of such a bathymetric threshold is merely dictated by the fact that no information is virtually available regarding deep-sea molluscs distributed in the 200–400 m range.

The Mollusc Fauna of the Deep Red Sea: Composition, Distribution and Relationships

Much could be learned about the colonization of this unique environment by using molluscs as tracers. In fact, the phylum Mollusca is the most diversified group of macrobenthic organisms inhabiting the deep Red Sea, overwhelming

Fig. 1 Location of deep-water stations (>400 m) of the Austrian *Pola*-expeditions (modified after Türkay 1986)



corals, bryozoans, crustaceans, brachiopods and other groups in terms of diversity. Furthermore, their shells often retain memory records of their early developmental stages, thus informing us about larval strategies functional to understanding dispersal mechanisms (Sabelli and Taviani 2014).

First information on deep-water molluscs was gained by the pioneer expedition of the Austrian ship *Pola* in 1895–1898, whose molluscs were studied by Sturany (1900a, b, 1901, 1904: Figs. 1 and 2). Later, several German oceanographic expeditions surveyed and sampled Red Sea deep-water habitats, that is, the missions of research vessels *Sonne*

Fig. 2 Frontispiece of the publication of Sturany devoted to the Gastropoda of the *Pola* expedition. NB: There is controversy about the correct publication dates of the works of Sturany. Separate prints bear the publication dates 1899 for the bivalve part and 1903 for the gastropod part. However, actually, there is no unquestionable evidence that such dates are correct and reprints had really been published earlier than the respective volumes of the “Denkschriften”. At present, we prefer therefore to refer to the dates of publication in the “Denkschriften” in agreement with the prevailing custom in the literature



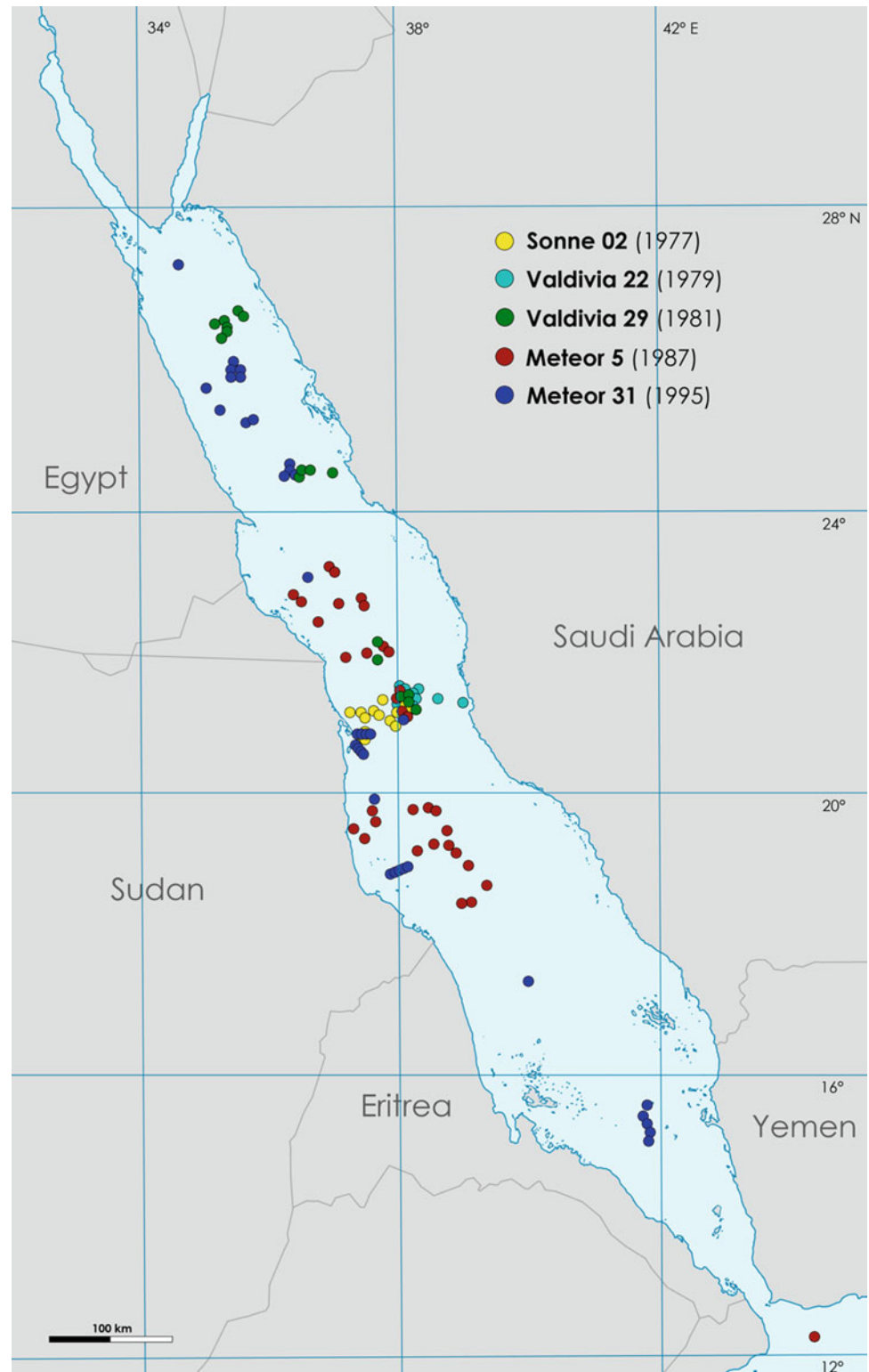
(1977), *Valdivia* (1979, 1981) and *Meteor* (1987, 1995) (see Thiel 1980; Türkay 1996). The material from German collections forms the basis of the present article (Fig. 3). Molluscs were also obtained by the Italian expeditions MR79 (Cablesip *Salernum*, 1979) and MR83 (RV *Urania*, 1983). Although this latter material is still unpublished, it was the source of the putative deep-sea endemic architectonicid gastropod *Pseudotorinia yaroni* described by Bieler (1993).

It should be noted that there is a considerable lack of comprehensive studies on the composition of the deep Red Sea mollusc fauna proper in comparison with that of the

adjacent Gulf of Aden. An exception in this respect is the study of Rützen-Kositzkau (1999), mostly focused on taphonomic and ecological aspects.

Therefore, most observations discussed herein are based on our own observations and the evaluation of the rich material collected by the expeditions mentioned before, above all the German ones between 1977 and 1995. Many data, although sometimes of preliminary character, are presented here for the first time. Taxonomic work is in progress but, for many species identifications, further comparative work is necessary. Because of taxonomic problems, there is

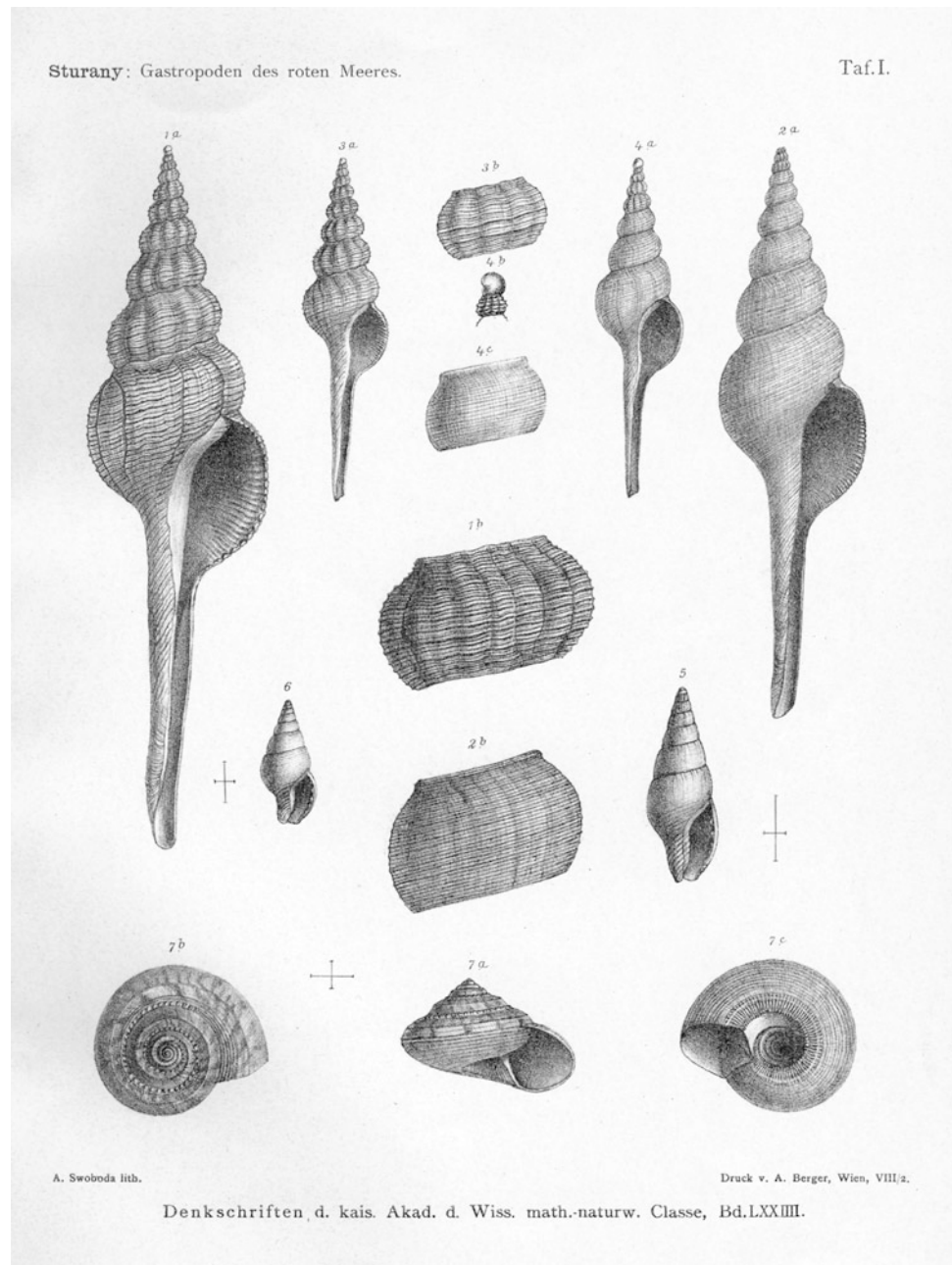
Fig. 3 Location of deep-water stations from the German *Sonne*, *Valdivia* and *Meteor* expeditions



still much uncertainty about the distribution and relationships of certain species, in particular those so far considered endemic to the Red Sea. Altogether, the samples collected

by these expeditions provide basic observations on taxonomy, diversity and bathymetric range useful to categorize the Red Sea deep-water mollusc fauna.

Fig. 4 Reproduction of a plate with gastropods from Sturany's work on the *Pola* expedition



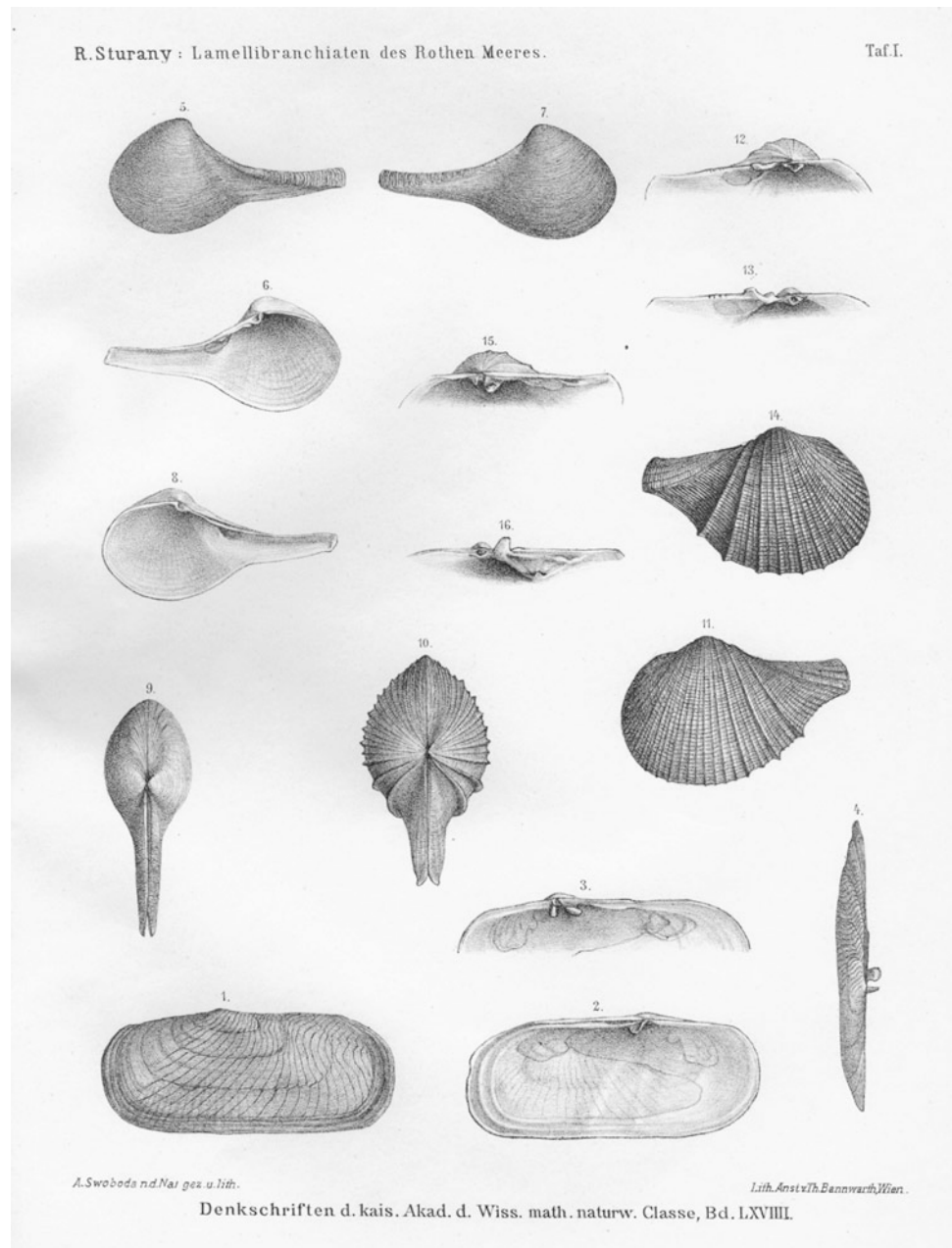
Whereas the first exploration of the deep Red Sea by the *Pola* expedition revealed 35 species recorded from depths below 400 m (Figs. 4 and 5), the various German expeditions especially helped in increasing considerably this number. To date, as many as 262 species are recorded from deep-water (163 Gastropoda, 94 Bivalvia, 4 Scaphopoda and 1 Polyplacophora: see Appendix).

A substantial share of the known Red Sea deep-water mollusc fauna inhabits fine-grained bottoms, living either infaunally (the majority of bivalves and scaphopods) or as vagrants (the majority of gastropods). An exception is provided by three species [*Bentharca asperula* (Dall 1881), *Dimya* sp. and *Xylophaga* sp. 1], whose life habit requires

hard substrate for their settlement instead of soft sediment. *Bentharca* and *Dimya* species are byssally fixed or cemented on hard substrates such as small stones or carbonate concretions or hard grounds which are widespread in the axial trough and on seamounts (Taviani 1998a). *Xylophaga* instead is related to sunken wood. Accordingly, specimens of these species have been found only at a smaller number of stations: *Bentharca asperula* at 48, *Dimya* sp. at 22 and *Xylophaga* sp. 1 at only 8 stations compared to about 50–70 stations for the other species.

So far, only 35 species have been collected alive, a mere 13.36 % of the entire deep-sea mollusc fauna. Table 1 shows the abundance and ranking of species, arranged as the total

Fig. 5 Reproduction of a plate with bivalves from Sturany's work on the *Pola* expedition



number of specimens and identifying shells versus live-recorded individuals. The very low fraction of living individuals among the total amount of specimens of each species is striking. Eight species contribute more than 51 % of all recorded specimens, while 76 % of the total material is represented by only 20 species, that is, 7.6 % of the species hitherto known from depths exceeding 400 m. The remaining 242 species (accounting for 92 % of the fauna) are found in much smaller numbers and in a limited number of stations. Nearly 60 % of the species, namely 158 species, are found at very few, often only one or two stations, and the

possibility of downbasin transport of empty shells for some of them cannot be a priori excluded. A similar pattern is shown by the steadiness of distribution (Table 2); the most abundant species do also occur at most stations, not showing any distinct patchiness. These recurrent taxa seem to represent, therefore, the core of the deep-water mollusc fauna of the Red Sea. Overall, our data indicate a remarkably low population density. Such low biomass in the Red Sea benthic standing stocks, in spite of a primary production being far from negligible, is an established fact (Thiel et al. 1987; Pfannkuche 1993).

Table 1 Most common deep-sea molluscs in the Red Sea benthos

Rank (dead)	Rank (living)	Species	No. of specimens (total)	Living specimens	% of total specimens	Cumulative (%)
1	10	<i>Limopsis elachista</i>	2,025	7	11.40	11.40
2	8	<i>Nassarius lathraius</i>	1,614	11	9.10	20.50
3	10	<i>Cardiomya alcocki</i>	1,243	7	7.00	27.50
4	6	<i>Cuspidaria steindachneri</i>	1,202	19	6.77	34.27
5		<i>Jupiteria</i> sp.	983	4	5.54	39.81
6		<i>Clathurella pertabulata</i>	722	0	4.07	43.88
7	5	<i>Cuspidaria brachyrhynchus</i>	705	25	3.97	47.85
8	4	<i>Cetoconcha intracta</i>	629	59	3.54	51.39
9	8	<i>Parvamussium siebenrocki</i>	611	11	3.44	54.83
10	2	<i>Bentharca asperula</i>	568	256	3.20	58.03
11	9	<i>Pseudoneaera thaumasia</i>	499	8	2.81	60.84
12		<i>Bathyarca</i> sp.	443	6	2.49	63.33
13	1	<i>Dimya</i> sp.	409	312	2.30	65.63
14		<i>Costellaria casta</i>	400	0	2.25	67.88
15		<i>Gemmula</i> aff. <i>monilifera</i>	320	4	1.80	69.68
16	3	<i>Xylophaga</i> sp. 1	270	200	1.52	71.20
17		<i>Corbula</i> sp.	228	0	1.28	72.48
18		<i>Leiocithara</i> sp.	217	0	1.22	73.70
19		<i>Cuspidaria dissociata</i>	201	3	1.13	74.83
20		<i>Rhinoclama</i> sp.	197	2	1.11	75.94
21		<i>Haliris</i> sp.	175	0	0.98	76.92
22		<i>Gadila</i> sp.	168	0	0.94	77.86
23	7	<i>Fusinus bifrons</i>	164	15	0.92	78.78
24		<i>Lucidestea</i> ? sp.	156	0	0.88	79.66
25		<i>Cardiomya</i> sp.	155	0	0.87	80.53

Bathymetric Trends

The bathymetric distribution of the most common species shows that nearly all present a wide depth range, extending from waters shallower than 400 m even to depths exceeding 1,900–2,000 m (Table 3). However, due to the fact that the great majority of stations are located in the deep-water, the living records are mostly confined to a depth between about 400 and 1,400 m, only very few species having been observed living in depths exceeding 1,900 m. Although the more common species belong to bivalve groups which usually have their main depth range in deep-water (Fig. 6), such as Limopsidae, *Bathyarca*, Propeamussiidae and septibranchs (Cuspidariidae, Poromyidae, Verticordiidae), the depth ranges show that none of them is confined to true bathyal or abyssal depths. Some of them are even recorded from much shallower depths outside the Red Sea. Most of them also occur in depths above 400 m. The same pattern is

shown by the commoner gastropods (Fig. 7) belonging to the families Nassariidae, Costellariidae, Fascioliidae and “Turridae” s.l., which do not even belong to families with an exclusive bathyal distribution.

This pattern suggests that we are not really dealing with “deep-sea species” sensu stricto but rather with eurybathic taxa. In conclusion, judging from the mollusc component, it appears that the Red Sea seems deprived of a “true” deep-sea fauna, that is, species exclusively known from depths well in excess of 500 m. In this respect, it is noteworthy that there are practically no species shared between the deep Red Sea and the cold deep-water of the Gulf of Aden (see below).

The Red Sea deep-water mollusc fauna can be suitably clustered into three distinct groups of bathymetric significance (Janssen 1989). A first group of species appears more characteristic of a depth interval between about 400 and 600 m. Typical species are *Propeamussium steindachneri* (Sturany 1901), *Ilanga illustris* (Sturany 1900), *Nassarius steindachneri* (Sturany 1900) and *Conus grangeri* (Sowerby

Table 2 The most evenly distributed species

Rank	Rank (living)	Rank (abundance)	Species	No. of stations	% of stations	No. of stations with living specimens
1		1	<i>Limopsis elachista</i>	74	77	4
2	3	7	<i>Cuspidaria brachyrhynchus</i>	72	75	9
3		2	<i>Nassarius lathraius</i>	70	73	3
	5	3	<i>Cardiomya alcocki</i>			5
4	5	9	<i>Parvamussium siebenrocki</i>	67	70	5
5	4	4	<i>Cuspidaria steindachneri</i>	64	67	7
6		6	<i>Clathrella pertabulata</i>	62	64	0
7	1	8	<i>Cetoconcha intracta</i>	60	62	16
8	5	11	<i>Pseudoneaera thaumasia</i>	59	61	5
	4	12	<i>Bathyarca</i> sp.			7
9		19	<i>Cuspidaria dissociata</i>	56	58	2
10		5	<i>Jupiteria</i> sp.	55	57	2
11		21	<i>Haliris</i> sp.	54	56	0
12		14	<i>Costellaria casta</i>	53	55	0
13	2	10	<i>Bentharca asperula</i>	48	50	15
		20	<i>Rhinoclama</i> sp.			2
14		25	<i>Cardiomya</i> sp.	46	48	1

1900) (synonym: *Conus batheon* Sturany 1904). A second group occurs mainly between about 600 and 1,500 m, characterized by *Cuspidaria dissociata* Sturany 1901, *Vissayaseguenzia compsa* (Melvill 1904), *Costellaria casta* (H. Adams 1872) and *Gadila* sp. A third group of species displays a wide bathymetric range, with taxa distributed between 400 and 2,000 m and deeper. The majority of species, including also the most abundant, belongs to this category. To this stock pertain *Jupiteria* sp., *Bathyarca anaclima* (Melvill and Standen 1907), *Limopsis elachista* Sturany 1901, *Parvamussium siebenrocki* (Sturany 1901), *Cetoconcha intracta* (Sturany 1901), *Pseudoneaera thaumasia* (Sturany 1901), *Cardiomya alcocki* (E.A. Smith 1894), *Cuspidaria brachyrhynchus* Sturany 1901, *Cuspidaria steindachneri* Sturany 1901, *Murex forskoehlili* (Röding 1798), *Nassarius lathraius* (Sturany 1900), *Fusinus bifrons* (Sturany 1900) and *Gemmula* aff. *monilifera* (Pease 1860). Only 10 species (e.g. *Parvamussium siebenrocki*, *Cardiomya alcocki*, *Cuspidaria steindachneri*, *Cuspidaria brachyrhynchus* and *Fusinus bifrons*) are recorded from a depth below 2,000 m, the deepest record being 2,120 m. However, it must be emphasized that these species groups do not represent well-defined associations, but only show a certain consistency in their abundance and distribution.

Based upon species abundance, Rützen-Kositzkau (1999) differentiated five species associations in the deeper water of the Red Sea:

1. *Jupiteria* sp. 1—*Limopsis elachista* association between 1,351 and 1,898 m
2. *Limopsis elachista*—*Nassarius lathraius* association between 343 and 646 m
3. *Ilanga illustris*—*Limopsis elachista* association between 237 and 567 m
4. *Nassarius lathraius*—*Cardiomya potti* association between 557 and 685 m
5. *Nassarius lathraius*—*Limopsis elachista* association between 308 and 1,410 m

However, these show a broad overlap of their depth ranges, plus a considerable number of species in common. Therefore, it has been already argued by Rützen-Kositzkau (1999: 88) that these presumed associations are better interpreted as reflecting faunal responses to some local sedimentary parameters (such as differing mineral contents and granulometry) rather than a bathymetric control. Our own observations on the occurrence of species show that nearly all the more common species occur together at the same stations over their whole depth range. At present, it can only be speculated whether a structured pattern perhaps might be detected by some sophisticated statistical analyses.

Any kind of bathymetric zonation or species associations necessarily would be based on differences in ecological parameters, such as bottom type, temperature and food supply. The rather uniform structure and conditions of the deep Red Sea environment, however, seem to speak against

Table 3 Distribution in depth

Species	Depth range in the Red Sea
<i>Limopsis elachista</i>	428– 490–1975 –2120
<i>Nassarius lathraius</i>	332– 507–1032 –1977
<i>Cardiomya alcocki</i>	428– 490–1975 –2120
<i>Cuspidaria steindachneri</i>	363–778 –2120
<i>Jupiteria</i> sp.	428– 740–517 –1977
<i>Clathurella pertabulata</i>	428–2120
<i>Cuspidaria brachyrhynchus</i>	363–1032 –2160
<i>Cetoconcha intracta</i>	363–2120
<i>Parvamussium siebenrocki</i>	56– 490–847 –2120
<i>Bentharca asperula</i>	537–1135 –1528
<i>Pseudoneaera thaumasia</i>	363–1175 –1972
<i>Bathyarca</i> sp.	428–1424 –1977
<i>Dimya</i> sp.	740– 753–1135 –1377
<i>Costellaria casta</i>	58– 490–507 –1672
<i>Gemmula</i> aff. <i>monilifera</i>	212– 363–383 –1977
<i>Xylophaga</i> sp. 1	363– 519–600 –1975
<i>Corbula</i> sp.	487–1480
<i>Leiocithara</i> sp.	487–1977
<i>Cuspidaria dissociata</i>	428– 772–779 –1558
<i>Rhinoclama</i> sp.	578– 1972–1975 –1977
<i>Haliris</i> sp.	487–1977
<i>Gadila</i> sp.	487–1135
<i>Fusinus bifrons</i>	487– 696–1972 –2120
<i>Lucidestes</i> ? sp.	428–1128
<i>Cardiomya</i> sp.	363– 428–459 –2120

Records of living specimens in bold, based only on material collected by the above-mentioned German cruises

the possibility of forming a structured pattern of the mollusc fauna. In summary, there are no strong arguments thus far to substantiate a convincing bathymetric zonation of the deep Red Sea benthic mollusc fauna.

Chemosynthetic Habitats

The Red Sea is characterized by multiple situations which are suitable to sustain deep-sea chemosynthetic habitats and, therefore, associated chemosymbiotic fauna. For instance, this basin contains active submarine volcanoes, hydrocarbons, brine lakes and pools (e.g. Bonatti et al. 1984; Hovland and Judd 1988; Michaelis et al. 1990; Antunes et al. 2011; Ligi et al. 2011; Ligi et al., this volume; Schmidt et al., this volume). All such environments are potential sites for chemosynthesis and therefore specialized metazoan life. For example, the similarly semi-enclosed Mediterranean hosts a variety of parallel situations well exploited by chemosymbiotic molluscs (Taviani 2014). Admittedly, the shallower

sill and stressing hydrologic conditions may interfere with the development of well-structured seep/vent communities in the Red Sea. Recently, Batang et al. (2012) reported on the very first discovery of active cold seeps (Tuwal Seeps) with associated macrofauna between 840 and 850 m off the central Red Sea continental margin. An unusual density of *Corbula* clams was noticed as well as another still undetermined bivalve. What is most remarkable is that salinity in the brine of the Tuwal Seeps attains 74 ‰. Furthermore, the occurrence of certain species such as the vent gastropod *Provanna* sp. and a rather large *Myrtea* sp. identified at very few stations (e.g. VA29, stations 740b, 741 at 1,480 and 1,465 m respectively) provides indications for the existence of widespread communities in the Red Sea. In fact, provannids are typical elements of hydrothermal habitats elsewhere in the oceans and lucinids, such as *Myrtea*, are known for their chemosymbiosis with sulphide oxidizing bacteria. These species are apparently associated with the “usual” non-vent common Red Sea deep-water species at stn VA 29-741, but this fact may only reflect contrasting mosaic-like adjacent microhabitats or pulsing times of fluid seepage.

Biogeographic Aspects

Due to the persisting situation of yet unresolved taxonomic questions, it is difficult to be conclusive on geographical relationships of the Red Sea deep-water species. However, among the most common species inhabiting this basin, there are several taxa which occur outside the Red Sea. Both *Limopsis elachista* and *Bathyarca anaclima* are recorded from 73 to 285 m in the Gulf of Oman (Melvill and Standen 1907), *Cardiomya potti* as originally described from the Red Sea by Sturany (1901) is synonymized with *C. alcocki* E.A. Smith (Poutiers and Bernard 1995) which is recorded as being widespread in the Indo-West Pacific in depths of 60–1,150 m. *Cuspidaria steindachneri*, too, is recorded with an Indo-West Pacific distribution and a depth range of 106–1,308 m. *P. thaumasia* is known also from the Indian Ocean (Poutiers and Bernard 1995). Not less than 10 of 16 pectinoidean species of the deep Red Sea occur even outside of that region (Dijkstra and Janssen 2013). The gastropod species *Gemmula* aff. *monilifera* and *Costellaria casta* are equally widely distributed in the Indo-West Pacific.

Propeamussium steindachneri, *Parvamussium siebenrocki*, *Cetoconcha intracta*, *Cuspidaria brachyrhynchus*, *Fusinus bifrons* and *Nassarius steindachneri* have for long been considered endemic to the Red Sea. They have been found in the Gulf of Aden (Rützen-Kositzkau 1999, own obs.), but never deeper than 500 m. Most of these species have been found at stn. 287 (in 472–479 m) in the inner Gulf of Aden under the hydrological influx of the Red Sea outflow (see below). This observation is important since,

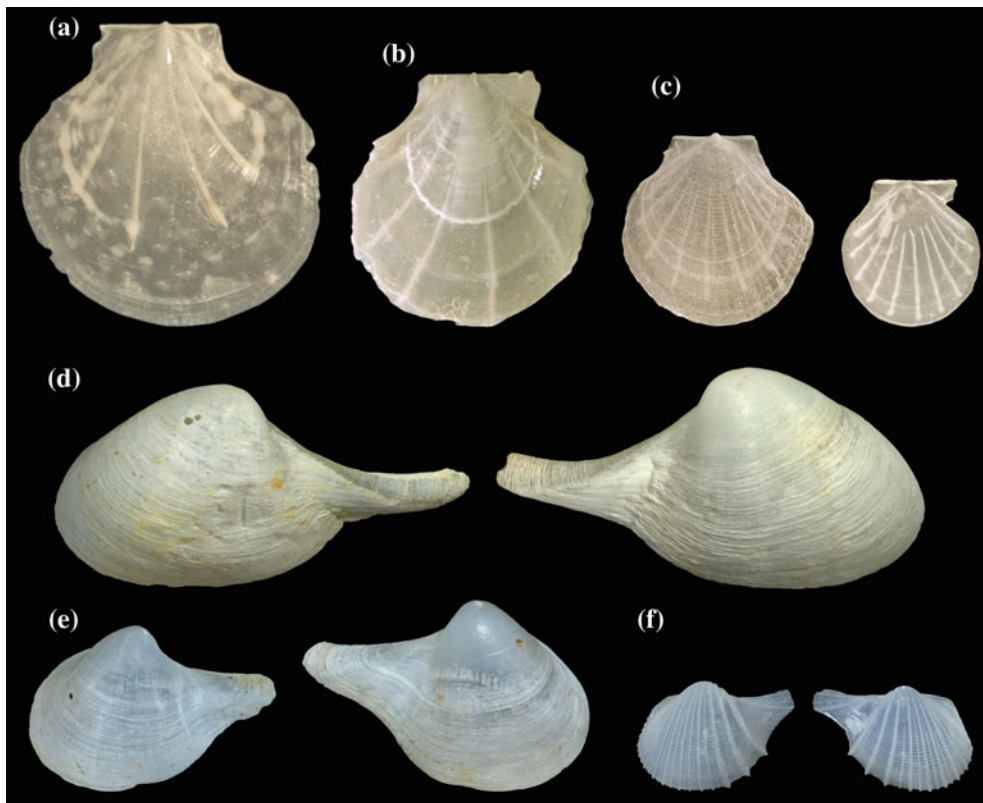


Fig. 6 Characteristic deep-sea bivalves from the Red Sea. **a** *Propeamussium steindachneri* (383 m; left valve, h = 12.6 mm), **b** *Propeamussium steindachneri* (479 m, Gulf of Aden, from outflow of Red Sea water; right valve, h = 10.6 mm), **c** *Parvamussium siebenrocki* (1,377 m; left valve, h = 6.4 mm, right valve, h = 4.9 mm),

d *Cuspidaria steindachneri* (1,228 m; left valve, l = 22.8 mm, right valve, l = 23.5 mm), **e** *Cuspidaria brachyrhynchus* (1,995 m; left valve, l = 12.2 mm, right valve, l = 13.5 mm), **f** *Cardiomya alcocki* (487 m; left valve, l = 6.5 mm, right valve, l = 6.6 mm). (Photographs by S. Hof, Senckenberg Research Institute, Frankfurt a. M.)

differently from the Red Sea, the Gulf of Aden cold deep-sea realm hosts a deep-water mollusc fauna sensu stricto (e.g. *Limopsis pelagica* E.A. Smith 1885, *Propeamussium alcocki* (E.A. Smith 1894), *P. caducum* (E.A. Smith 1885), *P. meridionale* (E.A. Smith 1885), *Amygdalum politum* (Verrill and Smith 1880), *Myonera caduca* (E.A. Smith 1894), *Stellaria testigera digitata* (Martens 1878)) and many deep-water turrid gastropods (Knudsen 1967; Sysoev 1996). Regarding diversity versus depth, there is a decrease in species numbers with increasing depth (Table 4). While numbers of species are comparable for both regions, the Gulf of Aden shows a slightly higher diversity. This is even more important if the very different numbers of stations is accounted for. Compared to the neighbouring Gulf of Aden as a part of the Indian Ocean, it is obvious that the semi-enclosed deep Red Sea only has a rather impoverished and not very diverse mollusc fauna. Although only 13 stations in the Gulf of Aden have been sampled (*Meteor 5* expedition) in contrast to 97 stations in the Red Sea, these stations yielded a total of 148 species compared to 194 species in the Red Sea. On average, every station in the Gulf yielded 11.3

species in contrast to only 2.0 in the Red Sea (own obs., based on *Somme*, *Valdivia* and *Meteor-5* expeditions).

As said, there are, therefore, several species formerly deemed to be endemic to the deep Red Sea, e.g. *Fusinus bifrons*, *Nassarius steindachneri*, *Cuspidaria brachyrhynchus* and *Propeamussium steindachneri*. However, as has been shown above, all these species are now known to have a wider geographic distribution (such as *P. steindachneri*) at least in the Indian Ocean or have been found just outside the Red Sea proper in the neighbouring Gulf of Aden. This occurrence could be uniquely linked to the outflow of warm and salty Red Sea water into the Gulf of Aden rather than being regarded as geographically endemic (see also Türkay 1996). However, *Fusinus bifrons* in the meantime has been recorded from localities in the Indian Ocean (Snyder 2002) and is no longer Red Sea endemic. Another presumed endemic is the gastropod *Pseudotorinia yaroni* (Bieler 1993), but its true geographic range could be much wider than supposed since shells tentatively attributed to this elusive taxon are occasionally reported from the Philippines (unpublished data).

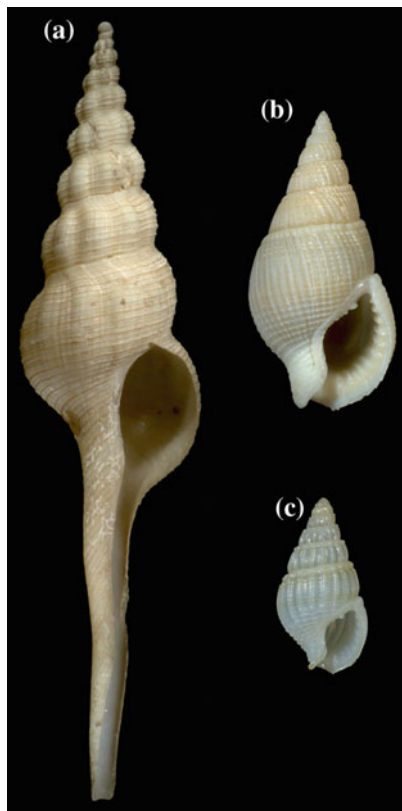


Fig. 7 Emblematic deep-sea gastropods from the Red Sea. **a** *Fusinus bifrons* (863 m; h = 79.3 mm), **b** *Nassarius steindachneri* (459 m; h = 22.9 mm), **c** *Nassarius lathraius* (487 m; h = 9.0 mm). (Photographs by S. Hof, Senckenberg Research Institute, Frankfurt a. M)

Results regarding deep-water crustacean decapods (Türkay 1986) agree fairly well with the pattern shown by Mollusca. Two main groups of species can be distinguished, that is, species common to both the Red Sea and the Indian Ocean (accounting for about one-third of the total), most of them being eurybathic and reaching greater depths in the Red Sea than in the Indian Ocean, and species only known at present from the Red Sea. Of these, however, for about half of the species it is not certain that they were true endemics. For the remaining approximately 30 %, very probable true endemism can be assumed. Concerning the ichthyofauna, Klauswitz (1986) assumed that a different degree of specific

differentiation could be related to a different age of immigration to the Red Sea during the Pleistocene.

Türkay (1996) indicated a degree of endemism attaining at least 30 % of the total fauna. As for the mollusc fauna, due to the still unresolved taxonomy and systematic relationships of the greater part of the observed species at present, this conclusion cannot be confirmed. Of 142 taxa hitherto identified to species level, only 20 species, that is 14 % of the entire fauna, are considered endemics as far as is known. It is equally important to consider that no genomic studies have been made on Red Sea endemics to control their links (and co-specificity in some cases) with extra-basinal potential counterparts.

In general, the data presented here demonstrate the obvious distinctiveness of the mollusc fauna of the deep Red Sea which is in sharp contrast to the neighbouring Gulf of Aden regarding species diversity and composition. The character of this fauna must be explained as resulting from the peculiar physical factors constraining the benthic fauna of the Red Sea.

The Colonization of the Red Sea Deep-Sea

A major question regarding the Red Sea deep-water mollusc fauna (but it could be extrapolated to other groups as well) is the following. Is this fauna as a whole represented by viable (reproductive) Red Sea populations, or is it at least partly dependent upon its “mother” Indian Ocean? It is, in fact, possible that part at least of the present deep-water Red Sea mollusc fauna is not represented by stable and self-reproducing populations, but results from meroplanktic larval influx from the adjacent Gulf of Aden via shallow water inflow (Janssen and Taviani 1985; Taviani 1985). Therefore, it cannot be excluded that we are at times facing the existence of pseudopopulations, rather than viable permanent populations, a case similar to what has been postulated for the Mediterranean Sea by Bouchet and Taviani (1992). The type of larval development exhibited by the deep-water molluscs of the Red Sea has not yet been examined systematically and is unknown, at least for most of the bivalves. However, some data have been provided by Rützen-

Table 4 Diversity arranged by bathymetric ranges

Depth (m)	Red Sea: no. of species (living)	No. of stations	Gulf of Aden: no. of species (living)	No. of stations
400–800	27 (6)	34	30 (14)	2
800–1,200	18 (3)	28	20 (7)	3
1,200–1,600	8 (3)	21	16 (9)	3
1,600–2,000	12 (4)	12	6 (1)	2
>2,000	8 (1)	2	12 (8)	3

Comparison Red Sea–Gulf of Aden (for species numbers, only stations sampled with comparable gear are considered; number of species recorded living in brackets)

Kositzkau (1999) that documents that there is a rather high percentage of species with planktotrophic development among gastropods. This is in accordance with observations on deep-water faunas in other regions (Bouchet and Warén 1979; Bouchet 1976; Jablonski and Lutz 1980, 1983). Among the 25 commonest species of the gastropods found (Table 1), only *Fusinus bifrons* has a non-planktotrophic development. Obviously, this accounts for a limited distribution of that species in the Red Sea and the neighbouring parts of the Gulf of Aden and Indian Ocean. Among bivalves, Rützen-Kositzkau (1999) stated dominance of non-planktotrophic ontogeny which is in agreement with observations made by Knudsen (1967, 1970) and others. Since a consistent part of the non-planktotrophic species seems apparently distributed also in rather shallow environments (therefore in principle capable of crossing a shallow sill at the metamorphosed stage), we cannot exclude a later migration from shallow settings to the warm deeper habitats in the Red Sea.

However, among the 25 commonest species, at least *Limopsis elachista* and *Bathyarca anaclima* follow a planktotrophic development strategy, whereas species such as *Jupiteria* sp., *Bentharca asperula*, *Cardiomya alcocki* and *Pseudoneaera thaumasia* are non-planktotrophic. Nevertheless, at least *Bentharca asperula* and *Cardiomya alcocki* are widespread in the Indo-West Pacific region. A larval supply from the Indian Ocean can be admitted as a likely hypothesis for planktotrophic species. This could be an easy mechanism to facilitate re-colonization of the Red Sea basin by deep-water elements after glacial crises thought responsible for basin-wide faunal annihilation (Taviani 1998c, with references). This mechanism admittedly would not fully explain the occurrence of the putative endemics in the Red Sea fauna. Various, not mutually exclusive, scenarios can be envisaged. The first would basically question the existence of Red Sea endemics as a whole. Endemism would only be apparent, simply reflecting our incomplete knowledge of the deep Indian Ocean fauna due to a bias in sampling. Another option is that the peculiar stress conditions of the Red Sea are forcing adaptive speciation on aliquots of the Indian Ocean faunal stocks at a short temporal rate computable over the few thousand years of the Holocene (cf. the analogy with the Gulf of Gabès in the Mediterranean Sea: Sabelli and Taviani 2014). Thirdly, the level of hyperhaline conditions imprinting basin wide on the Red Sea water masses during glacial times has been overestimated by paleo-oceanographers and did not reach up to lethal conditions for the stenoeicous benthos.

None of these hypotheses is supported by any conclusive evidence, requiring further comparative biological exploration of the deep fauna inside and outside the Red Sea as a fundamental prerequisite to unravel the dispersal patterns and evolutionary trends.

Final Remarks

As reported in this overview on deep-water molluscs, it is documented that the Red Sea hosts a relatively diverse, somewhat peculiar, deep-water fauna that shares some traits with its counterparts in the Indo-West Pacific.

Many questions still remain regarding the Red Sea deep-water benthos, as interpreted through its mollusc component:

Firstly, the taxonomic appreciation of many species is still unresolved since many taxa are known so far by their shells only and no biomolecular studies have been undertaken to check the Red Sea taxa versus their putative extra-basin occurrences to assess their specific validity.

Secondly, no experimental work has been done or is yet planned to test the planktotrophic hypothesis by intercepting meroplankton on both sides of Bab-al-Mandab and along the length of the Red Sea and checking the postulated presence of such trans-basinal deep-sea elements.

Thirdly, the fact that the Red Sea hosts some chemosymbiotic elements in its deep-water mollusc fauna warrants a dedicated exploration of its hydrothermal and potential cold seepage situations.

Moreover, in general, there is basic lack of information, and therefore of understanding, on the faunal metabolic requirements to cope with demands set by the extreme hydrologic conditions of the basin deep waters (cf. Seibel and Drazen 2007; Naumann et al. 2013). In such a perspective, the deep Red Sea is really a formidable laboratory where many important biological issues could be analysed and tested under natural conditions.

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Appendix

Preliminary list of benthic mollusc species from the deep Red Sea (> 400 m) (compiled by the senior author)

Enumeration of species is based exclusively on reliable autochthonous records. Species recorded by fragments only or by single, often badly preserved specimens which obviously have been transported from shallow water environments are not taken into account.

Polyplacophora

Ischnochitonidae

Ischnochiton sp.

Bivalvia

Nuculidae

Nucula consentanea Melvill and Standen 1907

Manzanellidae

Nucinella sp.

Nuculanidae

Jupiteria sp.

Nuculana (Lembulus) sculpta (Issel 1869)

Crenellidae

Dacrydium sp.

Solamen vaillanti (Issel 1869)

Mytilidae

Amygdalum aff. *watsoni* (Smith 1885)

Brachidontes pharaonis (Fischer 1870)

Idas sp.

Modiolus sp.

Septiferidae

Septifer forskali (Dunker 1855)

Arcidae

Acar plicata (Dillwyn 1817)

Arca sp.

Barbatia sulcata (Lamarck 1819)

Bathyarca anaclima (Melvill and Standen 1907)

Bathyarca sp.

Bentharca asperula (Dall 1881)

Bentharca sp.

Ribriarca polycymoides (Thiele & Jaeckel 1931)

Limopsidae

Limopsis elachista Sturany 1901

Gryphaeidae

Parahyotissa numisma (Lamarck 1819)

Ostreidae

Ostrea deformis Lamarck 1819

Pteriidae

Pteria sp.

Malleidae

Malvufundus regulus (Forsskal 1775)

Pectinidae

Cryptopecten nux (Reeve 1853)

Delectopecten alcocki (E.A. Smith 1904)

Delectopecten musorstomi Poutiers 1981

Spondylidae

Spondylus proneri Lamprell & Healy 2001

Anomiidae

Pododesmus caelata (Reeve 1859)

Anomia achaeus Gray 1850

Dimyidae

Dimya sp.

Limidae

Ctenoides annulata (Lamarck 1819)

Limea pectinata H. Adams 1870

Entoliidae

Pectinella aequoris Dijkstra 1991

Propeamussiidae

Cyclopecten erythraeensis Dijkstra and Janssen 2013

Cyclopecten meteorae Dijkstra and Janssen 2013

Parvamussium formosum (Melvill and Standen 1907)

Parvamussium scitulum (E.A. Smith 1885)

Parvamussium siebenrocki (Sturany 1901)

Parvamussium thyrideum (Melvill and Standen 1907)

Propeamussium steindachneri (Sturany 1901)

Similipecten eous (Melvill and Standen 1907)

Carditidae

Cardites variegata Bruguière 1792

Lucinidae

Anodontia aff. *edentula* (Linnaeus 1758)

Codakia sp.

Ctena divergens (Philippi 1850)

Lamellolucina dentifera (Jonas 1846)

Lucinidae sp. 1

Lucinidae sp. 2

Myrtea ? sp.

Myrtea sp. 1

Myrtea sp. 2

Parvilucina sp.

Thyasiridae

Thyasira sp.

Cardiidae

Fulvia australis (Sowerby 1834)

Fragum nivale (Reeve 1845)

Papillocardium papillosum (Poli 1795)

Tellinidae

Angulus flaccus (Römer 1871)

Arcopella isseli (H. Adams 1871)

Moerella lactea (H. Adams 1871)

Psammotreta praerupta (Salisbury 1934)

Semelidae

Ervilia scaliola (Issel 1869)

Leptomyaria etesiaca (Hedley 1909)

Semele fragillima (Issel 1869)

Syndosmya cistula Melvill and Standen 1907

Solecurtidae

Azorinus coarctatus (Gmelin 1791)

- Kelliellidae
Kelliella sp.
 Ungulinidae
Diplodonta subrotundata Issel 1869
 Veneridae
Paphia undulata (Born 1778)
Tapes cf. *deshayesi* (Hanley 1844)
 Basterotiidae
Basterotia borbonica (Deshayes 1863)
 Galeommatidae
Amphilepida ? sp.
Kellia ? sp.
 Pholadidae
Xylophaga sp. 1
Xylophaga sp. 2
 Teredinidae
 Teredinidae sp. 1
 Teredinidae sp. 2
 Corbulidae
Corbula sp.
Varicorbula sp.
 Cetoconchidae
Cetoconcha intracta (Sturany 1901)
 Cuspidariidae
Cardiomya alcocki (Smith 1894)
Cardiomya sp.
Cuspidaria brachyrhynchus Sturany 1901
Cuspidaria corrugata Prashad 1932
Cuspidaria dissociata Sturany 1901
Cuspidaria hindsiana (A. Adams 1864)
Cuspidaria steindachneri Sturany 1901
Pseudoneaera minor Thiele & Jaekel 1931
Pseudoneaera thaumasia Sturany 1901
Rhinoclama sp.
 Parilimyidae
Panacca sp.
 Verticordiidae
Haliris sp.
Euciroa sp.
 Lyonsiidae
Lyonsia sp.
- Scaphopoda**
 Dentaliidae
Graptacme sp.
 Fustiariidae
Pseudantalis sp.
 Gadilidae
Gadila sp.
Polyschides sp.
- Gastropoda**
 Fissurellidae
Emarginula sp. 1
Emarginula sp. 2
Rimula cumingii A. Adams 1853
Zeidora (Nesta) nesta (Pilsbry 1891)
Zeidora calceolina A. Adams 1860
 Lepetellidae
Lepetella simplicior (Melvill 1912)
Lepetella ? sp.
 Anatomidae
Anatoma agulhasensis (Thiele 1925)
Anatoma japonica (A. Adams 1862)
 Scissurellidae
Scissurella reticulata Philippi 1853
Scissurella rota Yaron 1983
Scissurella sp.
Sinezona singeri Geiger 2006
Sukashitrochus dorbignii (Audouin 1826)
 Seguenziidae
Visayaseguenzia compsa (Melvill 1904)
 Chilodontidae
Danilia sp.
Herpetopoma xeniolum (Melvill 1918)
Perrinia stellata (A. Adams 1864)
 Solariellidae
Ilanga illustris (Sturany 1900)
Zetela mutabilis (Schepman 1908)
 Trochidae
Fossarina mariei (Fischer 1890)
Pagodatrochus variabilis (H. Adams 1873)
Pseudostomatella papyracea (Gmelin 1791)
 Areneidae
Arene echinacantha (Melvill & Standen 1903)
 Turbinidae
Bolma sp.
 Skeneidae
Cirsonella sp. 1
Cirsonella sp. 2
Leucorhynchia crossei Tryon 1888
 Skeneidae sp. 1
 Skeneidae sp. 2
 Cocculinidae
 Cocculinidae ? sp. 1
 Cocculinidae ? sp. 2
 Provannidae
Provanna ? sp.
 Cerithiidae
Cerithium gloriosum Houbriek 1992
 Turritellidae
Turritella sp.
 Naticidae
Natica sp.
 Iravadiidae
Ceratia sp.
 Rissoidae

- Lucidestea* ? sp.
Rissoina sp.
 Tornidae
Circulus octoliratus (Carpenter 1856)
Cochliolepis sp.
Teinostoma sp.
 Bursidae
Bufonaria gnorima (Melvill 1918)
Bufonaria albivariosa (Reeve 1844) ? (fide Sturany)
 = *gnorima* ?
 Cassidae
Semicassis saburon (Bruguière 1792) (fide Sturany)
 = *faurotis* (Jousseau 1888) ?
 Tonnidae
Tonna galea (Linnaeus 1758)
 Hipponicidae
Cheilea cicatricosa (Reeve 1858)
 Xenophoridae
Stellaria solaris (Linnaeus 1764)
 Epitoniidae
Epitonium cf. *scalare* (Linnaeus 1758)
Epitonium cultellicostatum (Boury 1913)
Epitonium deflersi (Jousseau 1912) ?
Epitonium umbilicatum (Pease 1869)
Opalia bicarinata (Sowerby 1844)
 Epitoniidae ? sp.
 Eulimidae
Eulima (s.l.) sp. 1
Eulima (s.l.) sp. 2
Melanella sp. 1
Melanella sp. 2
Niso sp.
 Triphoridae
Euthymella concors (Hinds 1843)
Inella sp.
Metaxia sp.
Triphora adamsi (Deshayes 1863)
Viriola tricineta (Dunker 1860)
 Cerithiopsiidae
Cerithiopsis sp.
 Newtoniellidae
Cerithiella ? sp.
 Buccinidae
Pollia rubiginosa (Reeve 1846) (fide Sturany)
 Colubrariidae
Colubraria cf. *tenera* (Gray 1839)
 Columbelloidea
Euplica festiva (Deshayes in Laborde 1834)
Mitrella erythraeensis Sturany 1900
Mitrella nomanensis (Sturany 1900)
 Fascioliidae
Fusinus bifrons (Sturany 1900)
 Nassariidae
Nassarius lathraeus (Sturany 1900)
Nassarius steindachneri (Sturany 1900)
Note There is controversy about the taxonomy and nomenclature of the *Nassarius* species described by Sturany. The view adopted here is that of the senior author, based on examination of type material. Further study is necessary to solve the problems.
 Muricidae
Murex forskoehlii Röding 1798
 Costellariidae
Costellaria casta (H. Adams 1872)
 Cystiscidae
Granulina sp.
 Mitridae
Mitra gonatophora Sturany 1903
 Olividae
Ancilla eburnea (Deshayes 1830)
Ancilla lineolata (A. Adams 1853)
Ancilla cinnamomea Lamarck 1801 ? (fide Sturany)
 Borsoniidae
Microdrillia circumvertens (Melvill and Standen 1901)
Tomopleura reevei (C.B. Adams 1850)
 Clathurellidae
Clathurella pertabulata (Sturany 1903)
 Cochlespiridae
Thatcheriasyrinx orientis (Melvill 1904)
 Conidae
Conus grangeri G.B. Sowerby III 1900
 Drilliidae
Clavus inchoatus (Sturany 1903)
Clavus siebenrocki (Sturany 1903)
Clavus sp. 1
Clavus sp. 2
Splendrillia sp. 1
Splendrillia sp. 2
 Horaiclavidae
Paradrillia nannodes (Sturany 1903)
 Mangeliidae
Antiguraleus sp.
Leiocithara sp.
Pseudoraphitoma ? sp.
Pseudoraphitoma kilburni Morassi & Bonfitto 2001
Pseudoraphitoma sp. 1
Pseudoraphitoma sp. 2
 Pseudomelatomidae
Compsodrillia ? sp. 1
Compsodrillia ? sp. 2
Inquisitor ? sp.
Ptychobela cf. *flavidula* (Lamarck 1822)
Ptychobela sp.
 Raphitomidae

Aliceia sp.
Daphnella sp.
Favriella sp.
Mioawateria sp.
Pseudodaphnella ? sp.
Rimosodaphnella ? sp.
Taranidaphne amphitrites (Melvill & Standen 1903)
Taranidaphne dufresnei Morassi & Bonfitto 2001
Teretia sp.
Vepracula vepratrica (Hedley 1903)
 Turridae
Gemmula aff. *monilifera* (Pease 1860)
Gemmula sp. 1
Gemmula sp. 2
Unedogemmula indica (Röding 1798)
 Xylodisculidae
Xylodiscula sp.
 Acteonidae
 „*Acteon*“ sp. 1
 „*Acteon*“ sp. 2
 „*Acteon*“ sp. 3
 Architectonicidae
Pseudotorinia yaroni Bieler 1993
Solatisonax acutecarinata (Thiele 1925)
 Pyramidellidae
Chrysallida comacum (Melvill 1910)
Chrysallida pupula A. Adams 1861
Chrysallida sp.
Miralda gemma (A. Adams 1861)
Odostomella chorea (Hedley 1909)
Odostomia anabathmis Melvill 1910
Odostomia eutropia Melvill 1899
Odostomia sp.
Ondina? sp.
Oscilla appeliusi (Hornung & Mermod 1925)
Pyramidella pulchella (A. Adams 1854)
 Pyramidellidae gen. sp. indet.
Pyrgulina comacea Melvill 1910
Pyrgulina tenerrima (Melvill 1906)
Syrnola massauensis (Hornung & Mermod 1924)
Syrnola sp. 1
Syrnola sp. 2
Syrnola sp. 3
Turbonilla sp. 1
Turbonilla sp. 2
Turbonilla sp. 3
Turbonilla sp. 4
Turbonilla sp. 5
Turbonilla sp. 6
Turbonilla sp. 7
Turbonilla sp. 8
Turbonilla sp. 9
Turbonilla sp. 10

Turbonilla sp. 11
Turbonilla sp. 12
 Ringiculidae
Ringicula sp.
 Haminoeidae
Haminoea sp.
Diniatys dentifer (A. Adams 1850)
 Cylichnidae
Mnestia sp.
Roxania lithensis (Sturany 1903)
 Philinidae
Phanerophthalmus smaragdinus (Rüppell & Leuckart 1830)
Philine sp.
 Retusidae
Retusa sp.
Volvulella sp.

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