Marine Biology 10, 113—133 (1971)

Ecology and distribution of the benthic fauna in the shallow waters of the Red Sea*

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Abstract

Approximately 500 animal species and plants are listed as being the most typical for the infratidal and shallow subtidal benthic fauna of the Red Sea. Most of them are divided into communities typical for various soft and hard substrata, and at different water depths. The oceanographic conditions and the development of several of the communities are discussed in general terms.

Introduction

The first basic studies of the littoral benthic fauna of the Red Sea were performed by Rüppell (1828/1830), Ehrenberg (1834), Klunzinger (1877/1879) and Heller (1861 a, b). The investigations, which were conducted under very difficult and dangerous conditions, are until the present day the primary sources for scientists working on different animal groups in this basin. Not less important is Paulson's work, published in 1875, which deals with decapod crustaceans. Later, serial publications appeared, which summarized material collected during expeditions which crossed the Red Sea.

A very intensive effort to investigate the littoral benthos of the Red Sea, especially in the northern part, started in 1950, when scientists from Israel and other countries formed teams to investigate different problems connected with the fauna of this area. As a result of this cooperation there appeared the works of Lěvi (1965) on sponges; Fauvel (1955, 1957, 1958), Day (1965) and Fishelson and Rullier (1969) on Polychaeta; Verseveldt (1965), Vervoort (1967) and Fishelson (1970) on Hexacorallia; Holthuis (1958a, b; 1967, 1968), Ruffo (1959, 1969), Ingle (1963), Por (1967) and Lewinsohn (1969) on Crustacea; papers on Mollusca were published by Adam (1958), Engel and van Eeken (1960), Leloup (1960) and Kohn (1965). Various groups of Echinodermata were identified and summarized by Tortonese (1960), Clark (1966) and Cherbonnier (1967). In addition to these investigations, which dealt with large taxonomical units numerically dominant in the investigated area, smaller ones were described by other specialists (Wesenberg-Lund, 1957; Peres, 1960; Stephen, 1965; Boschma, 1968). These, mostly taxonomic studies, form a firm and accurate basis which enables the commencement of studies of species distribution and community structures along the shallow littoral (Safriel and Lipkin, 1964; Por and Lerner-Seggev, 1966; Fishelson, 1968).

This paper summarizes information about the distribution of the shallow benthic fauna, gathered by the author during 20 years of investigation in the Red Sea.

Ecological and oceanographical characteristics

The Red Sea, one of the northernmost seas of the Indian Ocean and a part of the Syrian-African Rift System, runs in the middle of the Arabo-Nubian Massif and extends for some 1,200 miles in a N.NW to S.SE direction, from the Bab-al-Mandaba Straits in the south, to the Gulf of Aqaba and Gulf of Suez in the north (Fig. 1). This sea is surrounded by precambrain rocks, mainly magmatic and metamorphic, and is bordered by dry, hot land with huge desert areas. Closed between the narrow passage of Bab-al-Mandab in the south and ending within the Gulfs of the north, the water masses of the Red Sea are more or less sheltered. This enables the high salinity and temperature to remain stable. The Red Sea has a very high evaporation ratio of approximately 200 cm/year in the Gulf of Aqaba to 235 cm/year in the south. This and other climatologic conditions result in average salinities ranging from 40.00 to approximately 41.00‰ in the upper water layers of the open sea.

The water temperatures exhibit a more pronounced variation in the northern parts of the region as compared with the south. The minimum surface temperature of the water measured at Eilat (Gulf of Aqaba) during the nighttime in February was 18 °C, whereas, in the vicinity of Massawa (Eritrea), it is not lower than 24 °C; the maximum temperature of the surface water over the shallow bays in the south may rise to 31 °C or even 33 °C, while in the north it is not more than 26° to 27 °C. The water temperature at 100 m depth reaches a maximum at Eilat of 24.2 °C,

* Supported partly by grants 62558-4556 and F 671052 67C 0043 of the US Office of Naval Research and Grant SFC-7-0074 of the Smithsonian Institution.

while at several points close to Massawa it was found to be approximately 27 °C (Oren, 1964).

As for the water movements, the southern and central parts of the Red Sea are strongly influenced by SN winds which move large water masses towards the north, predominantly to the Gulf of Suez, and only partly into the Gulf of Aqaba (Fig. 5). Over the shallow, wide open Gulf of Suez, this water movement raises and transports large amounts of mud and other sediments, thus strongly lowering the illumination in the water. This seems to be one of the factors which prevent intensive coral-reef development in this Gulf, at least along the Sinai coast. This is not observed in the Gulf of Aqaba,

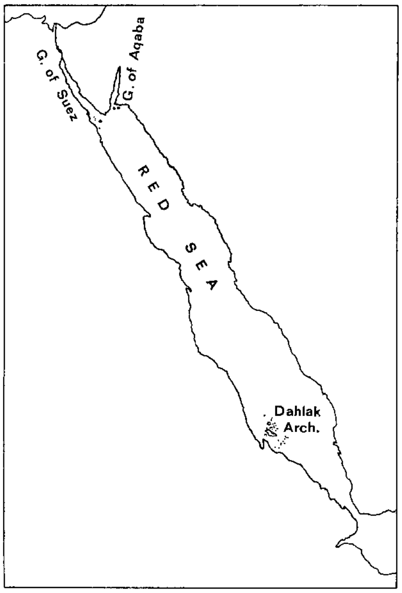

Fig. 1. The Red Sea

isolated from the main part of the Red Sea by the shallow and narrow Tiran Straits. This passage of approximately 170 m depth, is crossed by two currents; the surface current moves water from the Red Sea into the Gulf of Aqaba, while the bottom current flows in the opposite direction. The narrow and steep littoral shelf of this Gulf, and its great depth, enable the rising and sinking of sediment only over narrow, isolated areas; thus, the water of the Gulf remains clear and illuminated at great depths. Due to these features, which are common also in numerous places in the Red Sea, a rich animal world has developed, which has dispersed around corals and within various corallogenous formations and econiches.

The isolation of the Red Sea from other nearby water bodies, especially in the northern part, became less pronounced with the opening of the Suez Canal in 1869. This man-made connection between the eastern Mediterranean Sea and the Gulf of Suez reestablished the junction of Tethys and caused an interchange of faunal and floral elements between the Indian Ocean and the Atlantic Ocean. As summaries have shown (Peres, 1967; Steinitz, 1968), the most frequent animal migration occurs from the Red Sea to the Mediterranean Sea, although a notable number of species have been found to migrate in the opposite direction. Several of these emigrants to the Mediterranean Sea, the fish *Saurida undosquamis*, the crustacean *Squilla massawaensis*, the polychaetes *Eurythoë complanata* and *Dasychone lucullana*, as well as the plant *Halophila stipulacea*, dominate along various localities of the eastern Mediterranean Sea, being found as far as Cyprus.

Sampling stations

Dahlak Archipelago — Ethiopia (Fig. 2)

This Archipelago consists of approximately 140 islands; the central parts are located at a distance of 50 nautical miles from the Eritrean coast. We visited this area twice, the first time in 1962 during the first Israeli Expedition to the Southern Red Sea (Oren, 1962) and the second time in 1965, during the second Expedition (Lewinsohn and Fishelson, 1967). The results of these expeditions are partly published in the Reports of ISRSE/1962 in the Bulletin of the Sea Fisheries Research Station, Israel, and in Reports of the Second Expedition (ISRSE/1965) published in various scientific journals.

The reason for such great interest in this Archipelago is its unique character, as the only group of coral islands in this part of the Red Sea, along the Eritrean Continental Shelf. According to the results of the investigation published after the second Expedition by Horowitz (1968), and C_{14} analyses, this group of islands is of relatively recent, Holocene origin, built mainly of coralline limestone deposited during the Upper Pleistocene epoch and, according to the name of one of the islands, named by Horowitz the Entedebir Formation. The whole group was probably raised with the Dankalic uplift, which is still taking place (Nir, in press). Extending over an area of approximately 40,000 km^2, this complex was later faulted in the style of tensional faulting, which produced the recent pattern of small and large table-like islands with deep sea troughs inbetween. This formation is built mainly of calcareous skeletons of reef organisms, among which the corals are the most dominant. Wide flats, which interrupt the fossil reef blocks on most of the islands, convert close to the water line into shallow sandy or muddy bays. Farther from the sea they are covered by typical zones of halophytic vegetation, of which the most typical seems to be species of the genera *Sueda*, *Euphorbia*, *Salvadora* and others. On places where mangrove growths are found, these plant species form

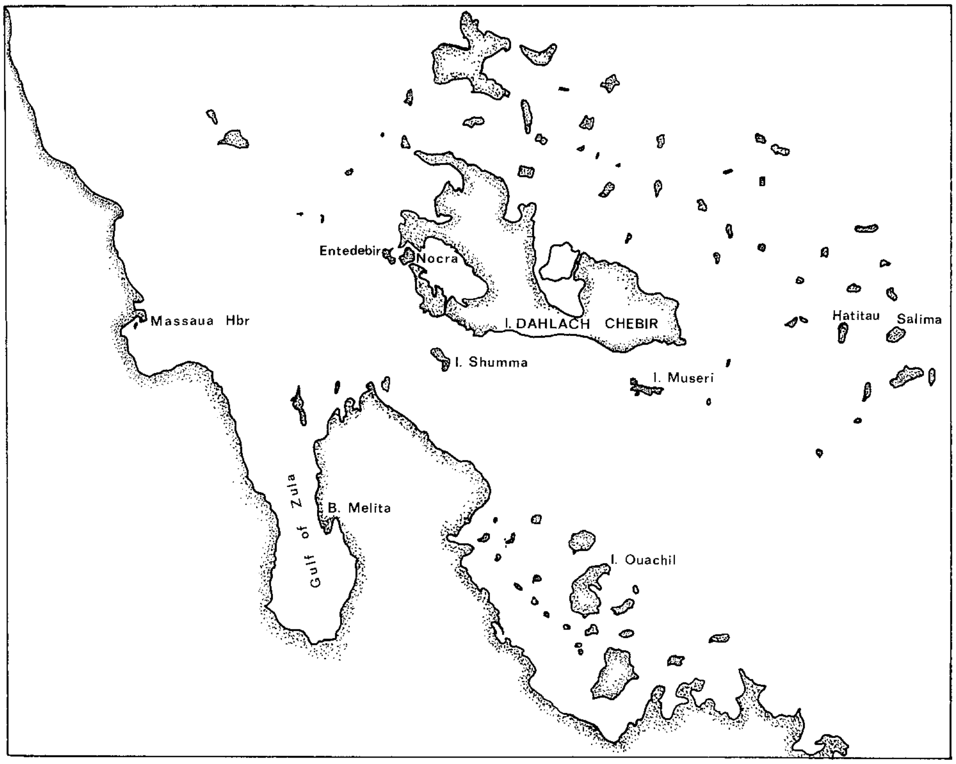

Fig. 2. Dahlak Archipelago, Southern Red Sea

Fig. 3. A typical infra-tidal sandy flat of the Sinai Peninsula, exposed during low tide

the frames of terrestrial vegetation around them. The fossil fauna found on these islands seem not to be conspicuously different from the recent fauna.

On and around the Dahlak Archipelago the littoral investigations were performed in the following 3 different biocoenotic formations:

(1) Sandy and muddy bays of various shapes mostly formed by organogenic marine sediments, with an admixture of terrogenous material brought in by floods. Measurements of the granulometry and chemical composition of these bays are found in NIRS paper (in press). During low tide, large parts of these bays are dried (Fig. 3), exposing a typical psammophilous ensemble of species. The most dominant here are various species of the fiddler-crab genus *Uca*, the small sand crab *Dotilla sulcata* (Fig. 6:1), the amphipod

Thalorchestia mortensi, the acorn worm *Ptychodera flava*, and the sea cucumber *Holothuria arenicola*.

Among the bays investigated, the largest were Abiad Bay, Goliath Bay and Landing Bay of the Entedebir Island; several bays around Musseri Island; and Melita Bay in the Gulf of Zula on the mainland, south of Massawa (Fig. 2).

(2) Vertical cliffs of the fossil coral reefs, facing the sea, deeply eroded and overhanging, which rise to a height of 5 to 8 m above the water level. These limestone walls produce mushroom forms characteristic also on coral islands in other parts of the Indo-Pacific (Macnae and Kalk, 1958). The surfaces of such formations, which descend and terminate in the subtidal region, are populated by typical associations of rock-attaching or rock-boring algae and animals (Fig. 4 and Table 4) and are usually bordered in the water by an extending *Sargassum* zone, and huge colonies of *Zoanthus bertholletii*.

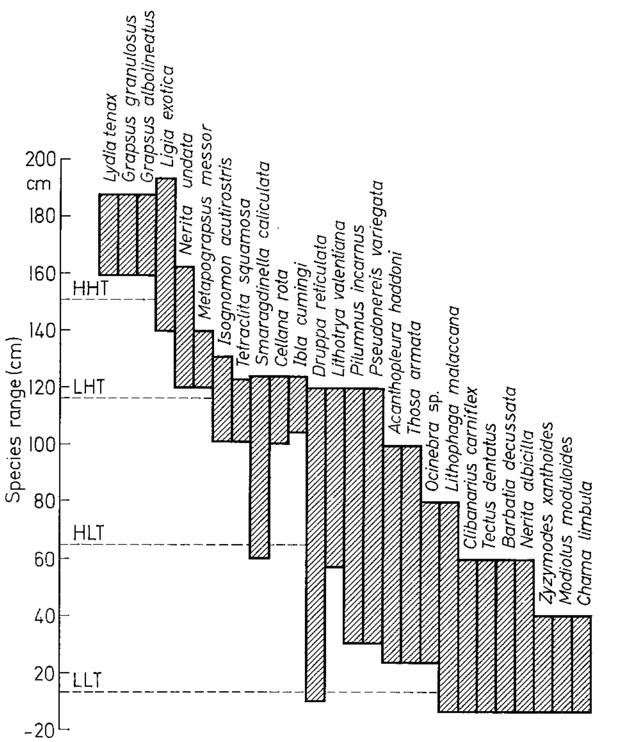

Fig. 4. Distribution of key species in animal communities found on mushroom surfaces and rocky shore (Dahlak Archipelago and Sinai Peninsula)

(3) Mangrove formations were investigated in several places of the Dahlak Archipelago in the vicinity of Massawa as well as on the Sinai Peninsula. Groups of mangrove trees were found growing over shallow muddy bays and lagoons as well as over muddy bottoms underlaid by beach-rock plates. The dominant tree species in the Red Sea is *Avicennia marina* but, on Musseri Island, the second Expedition found groups of *A. marina* together with mangrove trees of the genera *Ceriops* (*tagal*?) and *Rhizophora mucronata*, which were described from the Red Sea by Ascherson (1903), and also mentioned by Macnae (1968).

Other localities investigated in the Dahlak Archipelago were Ouachill Island, close to the mainland, and the Hatitau and Salima Islands on its southeast end (Fig. 2). Collections were also made on the shore of Isola Verde, close to Massawa, on the Dahlak Kebir and Nocra Islands.

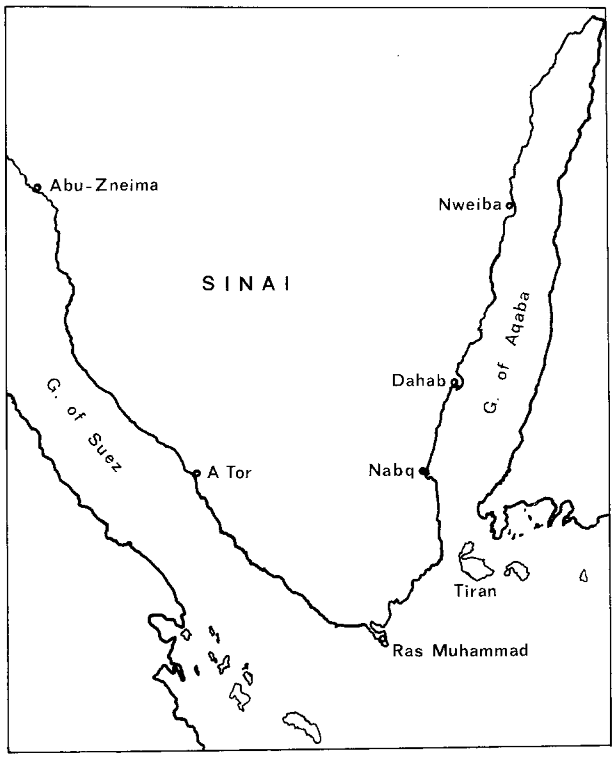

Fig. 5. Gulfs of the Northern Red Sea and Sinai Peninsula

Northern Red Sea (Fig. 5)

The northern part of the Gulf of Aqaba was investigated continuously, from 1951 onwards, in a concentrated effort to understand its general biological character. At the same time, more limited biological-ecological observations on fishes and invertebrates were performed, paying special attention to the ecological distribution and behavior of animals of the following shallow littoral regions: the upper beach-rock and rocky shore, the sandy bays and lagoon of the infratidal and shallow subtidal, or mediolittoral and infralittoral areas as named by PERES and PICARD (1958) and PERES (1967), and the coral-reef formations which border the lagoon towards the sea.

In addition to this, sampling tours of bottom fauna along the Sinai Peninsula coast were performed using rented fishing vessels, as well as landing crafts and cars. Among these tours, 3 two-week expeditions were made along the shallow waters of Sinai: the first expedition, in 1967, started in Eilat and ended at Abu-Zneima on the Gulf of Suez (Fig. 5). During this tour most of the bays, shallow coral reefs and mangrove formations were investigated. The second tour was made in the Gulf of Aqaba in 1968, starting from Nweibe on the Sinai coast and ending along the mangrove formations of Nabq. The third expedition, in 1969, was complementary to the first, but ended at Ras Muhammed in the Gulf of Suez. During all these expeditions most investigations were performed at chosen stations, thus enabling comparison of biota and ecological zonation here with those at Eilat and the Dahlak Archipelago in the southern Red Sea. Special attention was focused on the investigation of the growth of the mangrove *Avicennia marina* found at Ras Muhammed, the tip of Sinai, and at Nabq on the Gulf of Aqaba, which constitute the northernmost populations of this tree in the Red Sea.

Methods

Sandy and muddy bays chosen for investigation were marked by transecting lines running from the shore to the subtidal region and, along these, samples were taken at intervals of 1 m by a special core sampler constructed by the author for this purpose. Horizontal and vertical transects were also performed on infra- and supratidal rocky surfaces, especially on vertical, mushroom-like limestone walls of fossil corals. Together with these methods of collection, additional samples and data were obtained by simply digging with a hoe and sifting the sand through different meshes, or by splintering stones and dead corals.

The third method used for qualitative collection on sandy and rocky shores was poisoning with pronoxfish and anesthesia with quinaldin. This was usually carried out after the first two techniques had been applied. As most of the animals react to these substances by crawling out, it was thus possible to obtain more complete information on the places investigated. In shallow, subtidal zones, the animals were collected by snorkel and SCUBA diving, and from greater depths by bottom-grabs, triangle dredges, and beam-trawls. The observations were completed by divers, who added information about spatial distribution, activity and interaction between animal species.

Approximately 500 animal species are listed in this investigation, and they seem to be the most characteristic for the animal communities of soft-bottoms, beach-rock and rocky shore, and of mangrove growths.

Communities of soft bottoms

The Ocypoda saratan/Dotilla sulcata community

The sandy supratidal and shallow infratidal zone of the Red Sea is populated by the ghost crab *Ocypoda saratan*, and by the land-adapted hermit crab *Coenobita scaevola* (see also MAGNUS, 1960). This pair of species usually occurs along sandy shores slanted not more than 2° to 3°, dispersing from there, widely, along more horizontal places. *O. saratan* forms the outer belt in this community, and its activity can easily be recognized by the high pyramids of sand which the animals gather close to their holes. On the southern Red Sea (Eritrea) where *O. saratan* density is very high, this behaviour produces peculiar "towns" (Fig. 6:*2*) as described also by CARLI (1969) for Migiurtinia. The hermit crab, *C. scaevola*, is found closer to the water line, its numbers are large, and the crabs move around in large herds at low tide (Fig. 6:*3*), especially where scattered rocks are found. Moving landwards, these hermit crabs feed on various terrestrial plant remnants. They may also be observed to climb up high on date-palm trees, feeding on ripe dates. Usually, the sand crab and ghost crab are accompanied by *Talorchestia martensi* and other amphipods from the *Orchestia* group. The infratidal zone, and especially its lower parts, at most places investigated, was found to be inhabited by dense populations of the sand crab *Dotilla sulcata* and various species of the genus *Uca* (such as *U. albimana*). The last 2 species form prominent populations in the more southern parts of the Gulf of Aqaba and the Gulf of Suez, as well as in other parts of the Red Sea. The polychaetes *Perinereis nuntia*, *Naianereis quadraticeps*, *Eunice torquata* and *Lysidice collaris* are also found here, burrowed in the sand. The Mollusca are represented by large numbers of *Venus* spp., *Nassarius clathratus* and *Oliva bulbosa*. Table 1 summarizes part of the typical animal ensemble of such shallow, sandy-bay habitats.

The Hippa picta/Mactra olorina community

This community, being topographically almost parallel to the *Ocypoda/Dotilla* community, is found on more slanted shores with coarser sand or gravel bottom, with an admixture of sand and mud, partly covered by scattered vegetation of the algae *Caulerpa serrulata*, *Cystoseira myrica* and *Padina pavonia*; it extends from the water line or low infratidal region to a depth of 2 to 3 m. A pronounced seasonality is observed in the intensity of development of the algal cover, especially in the more shallow zone: beginning in December their density increases slowly, reaching a maximum in February to March. At this time a decrease of algae occurs, and the bottom becomes more and more exposed. Towards the summer only small remnants of the algal cover remain. The most abundant molluscs at this level are *Mesodesma glabrum*, *Mactra olorina*, *Polynices pyriformis* and *Aglaja cyanea*. *Murex*

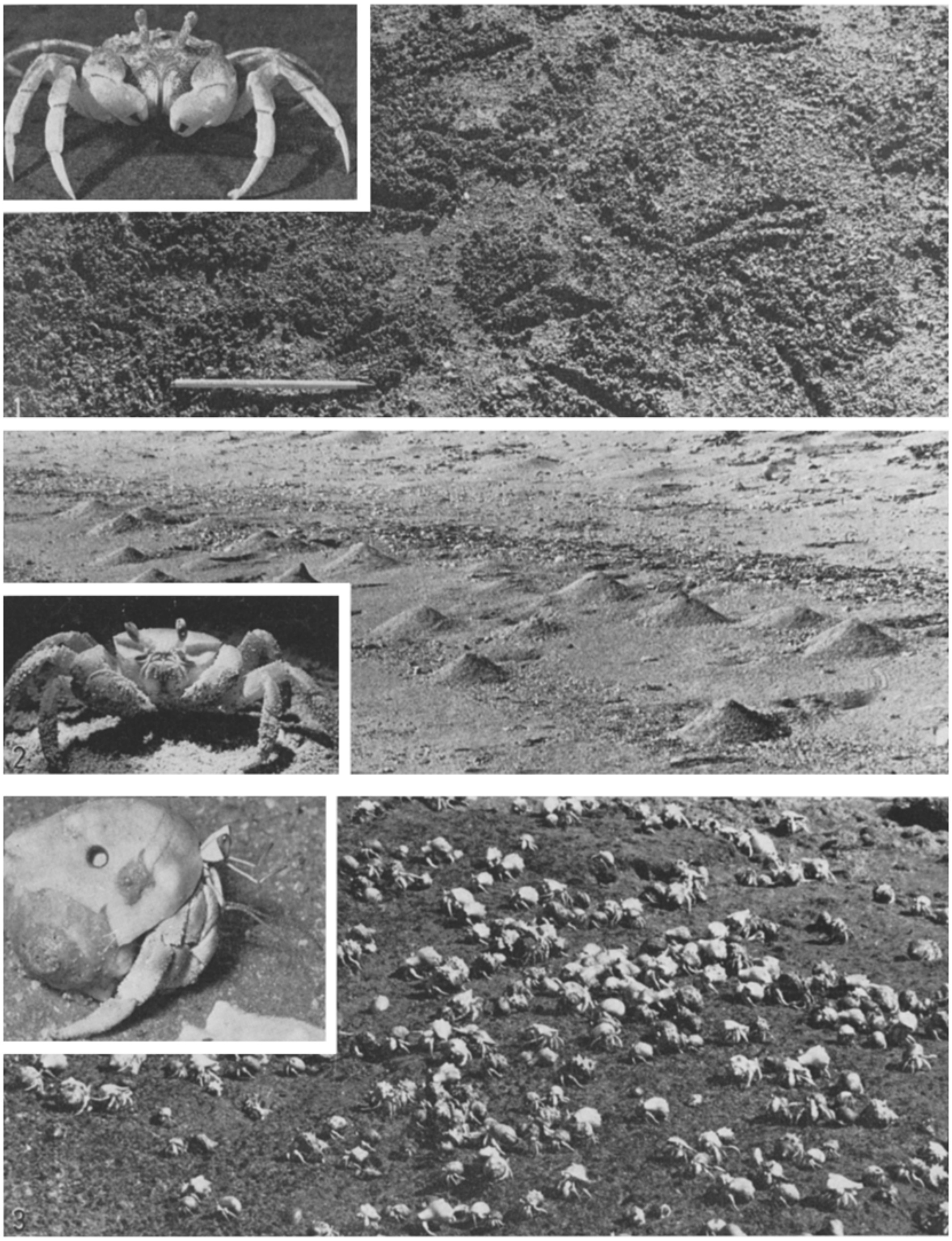

Fig. 6. *1 Dotilla sulcata* (× 2) and the furrows on the sand surface caused by them during feeding; *2 Ocypoda saratan* ($^1/_3$ actual size) and sand hills constructed by them ($^1/_{20}$ actual size); *3 Coenobita scaevola* (actual size) and a herd on the sea shore (Ras Muhammed, Sinai)

tribulus, Strombus fasciatus, Atrina vexillum and occasionally *Oliva bulbosa* are found in the deeper parts, where a greater admixture of more organic materials is found. The polychaetes *Perinereis nuntia, Notomastes latericeus, Dasybranchus caducus, Pectinaria* sp. and *Eunice australis* are common here. The echinoderms are represented by the sea urchins *Lovenia elongata* and *Echinodiscus auritus* (Fig. 7:*1*).

Table 1. *Animals found in sandy bays of the Red Sea*

Polychaeta	
Clymene affinis	*Notopygos variabilis*
Macroclymene monilis	*Chrysopetalum ehlersi*
Hesione pantherina	*Ceratonereis mirabilis*
Polycirrus coccineus	*Notomastes latericeus*
Poecilochaetus serpens	*Dasybranchus caducus*
Eunice australis	*Nianereis quadraticeps*
Perenereis nuntia	*Lysidice collaris*
Mollusca	
Strombus fasciatus	*Conus achatinus*
Strombus mutabilis	*Conus arenatus*
Polynices pyriformis	*Conus lividus*
Monetaria annulus	*Conus quercinus*
Purpuradusta gracilis	*Conus striatus*
Mauritia grayana	*Conus sumatrensis*
Volema pyrum nodosa	*Hastula impage coerulescens*
Nassarius clathratus	*Terebra subulata*
Pleuroploca trapezium	*Arca reticulata*
Oliva bulbosa	*Pinctada imbricata*
Harpa minor	*Mactra olorina*
Crustacea	
Talorchestia martensi	*Leucosia signata*
Gonodactylus chiragra	*Alpheus edwardsii*
Gonodactylus demani	*Alpheus crassimanus*
Gonodactylus smithii	*Athanas djiboutensis*
Acanthosquilla multifasciata	*Callianassa bouvieri*
Protosquilla lenzi	*Penaeus hathor*
Diogenes avarus	*Thalamita savignyi*
Hippa picta	*Portunus longispinnus*
Hippa celaena	*Macrophthalmus telescopicus*
Upogebia sp.	*Calappa hepatica*
Ebalia abdominalis	*Dotilla sulcata*
Ebalia granulata	*Uca albimana*
Philyra variegata	
Echinodermata	
Holothuria vagabunda	*Macrophiotrix hirsuta*
Holothuria arenicola	*Clypeaster humilis*
Holothuria impatiens	*Lorenia elongata*
Holodeima atra	
Pisces	
Conger cinereus	*Bothus pantherinus*
Myrichthys colubrinus	*Samaris cristatus*
Synodus variegatus	

The most abundant crustaceans along the water line are two intermixed species of *Hippa* (*H. picta* and *H. celaena*) which move together with the tide. In usually unexposed deeper and flatter parts are found *Calappa hepatica, Macrophthalmus depressus, M. telescopicus, Gonodactylus chiragra, G. demanii* and *Callianassa bouvieri*. Representing the portunids are *Thalamita savignyi* and *Portunus longispinnus*. The sand-dwelling species of *Octopus aegina* and the sea anemone *Cerianthus mana* which live in mucous tubes penetrating 40 cm into the sand, also occur. As typical sand-dwellers, occur the holothurian *Holothuria arenicola*, the acorn worm *Ptychodera flava* and, above the sand, large colonies of the sponge *Fasciaspongia cavernosa*.

Table 2. *Animals in and over shallow muddy bottoms of the Red Sea*

Spongia	
Tethya seychellensis	*Callyspongia spongionelloides*
Fasciospongia cavernosa	*Spirastrella inconstans*
Callyspongia crassa	*Erylus proximum*
Callyspongia viridis	*Cinachyra alba tridens*
Coelenterata	
Cerianthus mana	*Megalactis hemprichi*
Polychaeta	
Driloneries tridentata	*Scyphoproctus steinitzi*
Naianereis quadraticeps	*Polycirrus decipiens*
Glycera cirrata	*Lysidice colaris*
Eunice torquata	*Hermadice carunculata*
Marphysa mossambica	*Lepidonotus clava*
Chrysopetalum ehlersi	*Sabella porifera*
Arabella iricolor	
Mollusca	
Cerithium columna	*Conus quercinus*
Cerithium marus	*Conus textile*
Strombus tricornis	*Conus virgo*
Strombus fasciatus	*Terebra cerithina*
Strombus mutabilis	*Terebra maculata*
Lambis truncata seabe	*Aglaja cyanea*
Natica macrochiensis	*Aplysia oculifera*
Polynices pyriformis	*Modiolus auriculatus*
Murex tribulus	*Perna (Parviperna) nucleus*
Vassum turbinellus	*Pinna muricata*
Conus geographus	*Gafrarium pectinatum*
Crustacea	
Lembos podoceroides	*Dardanus lagopodes*
Cymadusa filosa	*Dardanus tinctor*
Elasmapus pectenerus	*Alpheus djiboutensis*
Parhyale hawaiensis	*Thalamita savignyi*
Philyra variegata	*Portunus sanguinolensis*
Gonodactylus chiragra	*Portunus pelagicus*
Gonodactylus demani	*Macrophthalmus depressus*
Gonodactylus falcatus	*Chloridiella nigra*
Gonodactylus spinosus	*Uca tetragonon*
Manningia amabilis	*Uca inversa*
Galathea brevimana	*Uca albimana*
Echinodermata	
Luidia savignyi	*Echinodiscus auritus*
Luidia maculata	*Lovenia elongata*
Stellasteropsis fooadi	*Brissopsis luzonica*
Astropecten polyacanthus	*Holothuria albiventer*
Ophiolepis superba	*Holothuria hilla*
Clypeaster humilis	*Holothuria pardalis*
Pisces	
Amblygobius albimaculatus	*Uranoscopus fuscomakulatus*
Cryptocentrus caeruleopunctatus	*Synanceia verrucosa*
Synodus variegatus	*Inimicus fillamentosus*
Platycephalus indicus	*Syngnathus brevirostris*

The fish fauna is represented here by *Bothus pantherinus, Trachinocephalus myops, Synodus variegatus, Platycephalus indicus, Conger cinereus* and *Myrichthis colubrinus*. Among the gobis occur *Ambly-*

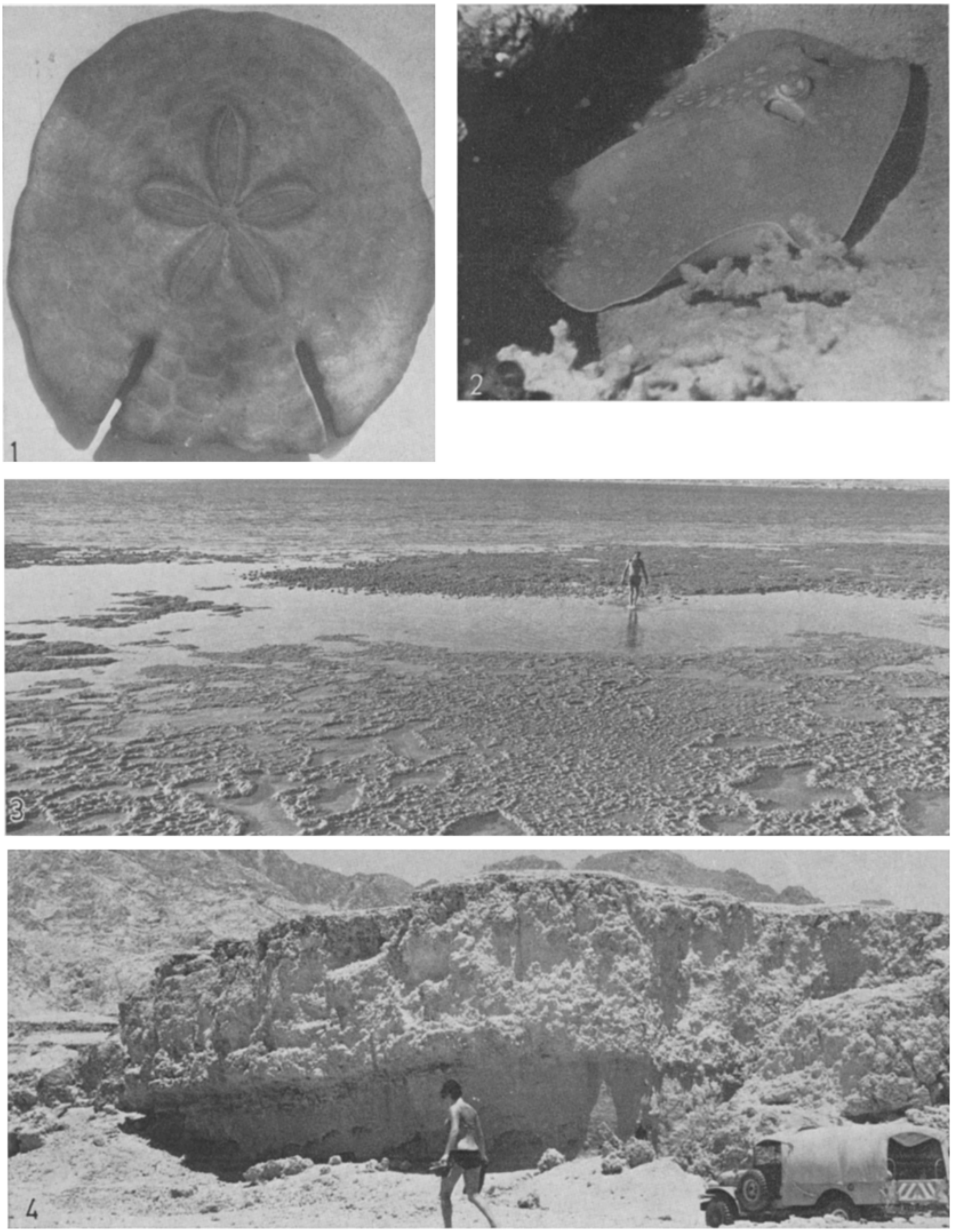

Fig. 7. *1 Echinodiscus auritus* (actual size); *2 Taeniura lymma* in its natural habitat ($^1/_5$ actual size); *3* rocky surface exposed during low tides (Southern Sinai); *4* fossil coral platforms near Dahab (Fig. 5)

gobius albimaculatus, *Cryptecontrus caeruleopunctatus* and other species living in symbiosis with *Alpheus djiboutensis* and closely related pistol shrimps. Around small rocky pieces occurring here and there are scattered groups of the apogonids *Ostorhichus cyanosoma*, *O. angustatus*, *Paramia bipunctata*, and juvenile specimens of *Cheilodipterus lineatus*; there are also groups of the small lion fish *Dendrochirus brachyptera*, which feed on them. The bathoids are represented here by *Taeniura lymma* (Fig. 7:2). Additional species found in this habitat are listed in Table 2.

The Ptychodera flava/Radianthus koseirensis community

This community, usually a continuation of the *Ocypoda/Dotilla* community, extends between the shore and the subtidal rocky habitats. The bottom of this zone is composed of calcareous-muddy sediment of the lagoon continuing to a depth of 1.0 to 3.0 m. Together with various algae, the first groups of the grass *Cymodocea ciliata* are also found here. The community includes mostly digging animals which find food and shelter in this region. The benthic fauna of this region seems to be especially rich in crepuscular animals, active during the night. The most prominent among the sandy infauna is *Ptychodera flava*, which forms a dispersed population burrowed to a depth of 40 cm in the sediment. The digging sea anemone *Radianthus koseirensis* also occurs here; its foot is attached at a depth of 20 to 30 cm to a pebble or stone. This anemone also serves as shelter for groups of young specimens of the clown fish *Amphiprion bicinctus* (Fishelson, 1965, 1970). Scorpion fishes are common, hiding among the stones, especially the species *Parascorpaena aurita, Scorpaenodes guamensis* and *Dendroscorpaena cirrosa.*

Other large animals dwelling here are: *Ochetostoma erythrogrammon* (Echiuridae), *Holothuria arenicola, Lovenia elongata, Clypeaster humilis* (Echinodermata), *Conus textile, Cerithium columne, Strombus* spp., *Nassarius* spp. (Mollusca). The large gastropod *Lambis truncata* occurs, crawling on the bottom, together with the pencil-like *Terebra subulata, T. cerithina* and others. From among the Bivalvia, this sandy bottom is well populated by *Mactra olorina* and *Tellina virgata*, extending from here also to deeper regions. The most common among the polychaetes are *Polycirrus coccineus Hesione pantherina, Drylonereis tridentata, Notopygos variabilis* and *Macroclymene monilis.* The Crustacea occur profusely, especially the *Alpheus* species (*A. crassimanus, A. edwardsi, A. sublucanus*) as well as the symbiotic *A. dijboutensis. Penaeus hathor, Thalamita poissonii* and *T. savignyi, Callianassa bouvieri* and several species of *Gonodactylus* are also present. The sponges typical here are *Tethya seycheilensis* and *Spirastrella inconstans*, the latter form a very peculiar econiche for numerous endozoic and epizoic animals (Fishelson, 1966b).

The Halophila stipulacea/Asymmetron (lucayanum?) community

This specific habitat extends down along gentle slopes, starting from 2 to 5 m to a depth of about 40 m. The vegetation of this common angiosperm, which occurs on several occasions together with the other closely related species *Cymodoce ciliata, Diplantera uninervis* and *Thallassia hemprichi*, extends over a dark brown, muddy bottom with a high percentage of vegetal detritus. This vegetation also includes several species of algae of the genus *Caulerpa* (*C. serrulata* and *C. peltata*) and of other genera. On all these plants is a rich cover or Foraminifera, Hydrozoa (such as *Dynamena cornicina*), serpulid worms and Bryozoa: among these occur typical fishes such as *Aeoliscus punctatus, Hippocampus hystrix, Syngnathus brevirostris, Solenostomus cyanopterus* and *Tripterygium trigloides* which hide and feed on minute animals, mostly Crustacea, which are common here. The flatfishes *Samaris cristatus* and *Bothus pantherinus* are also common. The sand-dwelling fish *Hemipteronotus* and *Trichonotus niki* (Clark and Schmidt, 1966) form dense populations; normally they swim close above the sand surface, reacting to every strange stimulus by quick dives into the sand. Also digging in the sand are eel-fishes such as *Pantonora tenuis, Callechelys striatus, Conger cinereus, Muraenichthys gymnotus* and *M. schultzei*, as well as the garden eel *Gorgasia sillneri.* This latter fish species seems to prefer muddy flats bordering steep slopes; it feeds on passing planktonic organisms.

The *Asymmetron* population found in this region (Steinitz, 1962) is mostly concentrated in the upper zone, between depths of 3 to 10 m. Living half-buried in the upper sandy layer, these chordates are very active at night, swimming with quick undulating movements close to the bottom (observations from aquaria).

The ophiurids *Ophiactis savignyi, Amphiodia microplax, Macrophiotrix hirsuta*, the sea-urchins *Laganum depressum, Clypeaster humilis* and *C. rarispinus*, several species of the sea-star genus *Astropecten*, the polychaetes *Notopygos variabilis, Arabella iricolor, Polycirrus decipens* and *Chrysopetalum ehlersi* occur here. Sipunculids are also common in the upper part of the region. From among the Crustacea, the most common here are *Gonodactylus smithi, Pseudosquilla ciliata, Alpheus crassimanus, A. diadema, Arete iphianassa*; the hermit crab *Dardanus tinctor*, and *Thenus orientalis.* Even small colonies of corals, especially of the genus *Stylophora* are found here, growing on small stones. Additional animal species common in shallow parts of this region are listed in Table 3. The interstitial and interalgal microfauna is very rich in amphipods, tanaidaceans, harpacticoid copepods, nematodes and cumaceas (Por and Lerner-Seggev, 1966). The dense population of the foraminifer *Operculina gaimardi* appears to be typical for the deeper parts of this zone.

The Operculina gaimardi/Turritella terebra community

The bottom of this zone is composed of gravel and parts of shells intermixed with large amounts of silt

Table 3. *Animals found on and around rocks in the shallow waters of the Red Sea*

Spongia	
Thosa armata	*Suberites clavatus*
Dimiriana schmidti	*Phyllospongia foliascens*
Tethya seychellensis	*Cliona orientalis*
Spirastrella cunctatrix	*Cacospongia* sp.
Geliodes incrustans	
Coelenterata	
Thyroscyphus fruticosus	*Favia favus*
Plumularia halecioides	*Platygyra lamellina*
Dynamena cornicina	*Porites lutea*
Dynamena crisioides	*Acropora scandens*
Tubularia sp.	*Stylophora pistillata*
Aqabaria pulchra	*Goniastrea pectinata*
Tubipora musica	*Anthopleura eilatensis*
Parerythropodium fulvum	*Radianthus (Antheopsis) koseirensis*
Heteroxenia fuscescens	*Radianthus ritteri*
Athalia fishelsoni	*Thalassianthus aster*
Cladiella leptocheles	*Triactis producta*
Lithophytum arboreum	*Megalactis hemprichi*
Lobophytum pauciflorum	*Macrodactyla aspera*
Pocillopora hemprichi	*Cryptodendrum adhesivum*
Sipunculidea	
Phascolosoma pacificum	*Aspidosiphon elegans*
Phascolosoma scolops	*Aspidosiphon klunzingeri*
Golfingia vulgaris	
Polychaeta	
Ceratonereis erythraensis	*Dasychone cingulata*
Pareulepis geayi	*Dasychone lucullana*
Lovenia medusa	*Sabellastarte indica*
Spirobranchus jousseaumei	*Terebella lapidaria*
Eurythoe complanata	
Mollusca	
Phacellozona laqueata	*Cypraea pantherina*
Acanthochiton curvisetosus	*Erosaria nebrites*
Tonicia suezensis	*Erosaria turdus*
Chiton olivaceus var. *affinis*	*Leptoconchus striatus*
Clanculus pharaonis	*Conus flavidus*
Trochus erythraeus	*Conus quercinus*
Trochus virgatus	*Aglaja cyanea*
Magelus anthiqus	*Cavolina uncinata*
Cerithium columna	*Glossordoris quadricolor*
Cerithium morus	*Kentrodoris annuligera*
Strombus gibberulus	*Barbatia ovata*
Mauritia arabica	*Modiolus auriculatus*
Lyncina camelopardalis	*Tridacna elongata*
Lyncina carneola	*Sepioteuthis lessoniana*
Pteria imbricata	*Sepia pharaonis*
Pteria spadicea	*Octopus aegina*
Plicatula ramosa	*Octopus macropus*
Lima saverbyi	
Crustacea	
Creusia spinulosa secunda	*Cryptodromia granulata*
Cyproidea ornata	*Camposcia retusa*
Mesacturus brevisquamatus	*Myra pugax*
Gonodactylus spinosus	*Thalamita crenata*
Gonodactylus chiragra	*Thalamita savignyi*
Galathea brevimana	*Lybia leptochelis*
Dardanus lagopodes	*Alpheus frontalis*
Dardanus woodmasonis	*Alpheus microstylus*
Petrolistes leptocheles	*Alpheus diadema*
Petrolistes rufescens	*Athanas djiboutensis*
Dardanus tinctor	*Aretopsis aegyptiaca*
Clibanarius carnifex	*Arete iphianassa*
Calcinus latens	*Hymenoceros pictus*
Chlorodiella nigra	*Saron neglectus*
Pachygrapsus minutus	
Pilummus incanus	
Echinodermata	
Gomophia aegyptiaca	*Holothuria impatiens*
Echinaster purpureus	*Bohadchia cousteani*
Echinaster callosus	*Holodeima flavomaculata*
Asteropsis carnifera	*Sinaptula reciproquans*
Asterina burtoni	*Stichopus variegatus*
Fromia ghardaqana	*Culcita coriacea*
Linckia multifora	*Diadema setosum*
Ophiocoma erinaceus	*Echinometra mathaei*
Ophiolepis superba	*Echinotrix calamaris*
Ophiolepis cincta	*Tripneustes gratilla*
Ophiotrix savignyi	*Prionocidaris baculosa*
Mactophiotrix hirsuta	*Lamprometra klunzingeri*
Holothuria pardalis	*Heterometra savignyi*
Holothuria vagabunda	
Ascidia	
Phallusia nigra	*Symplegma viridis*
Phallusia arabica	*Didemnum candidum*
Amaroucium lobatum	*Polycarpa mytiligera*
Pisces	
Taeniura lymma	*Gobiodon rivulatus*
Escenius gravieri	*Cirripectes variolosus*
Escenis nalolo	*Dinematichthys ilnocoeteoides*
Halmoblennius flaviumbrinus	*Haliophis guttatus*
Istiblennius bistriatus	*Conger cinereus*
Istiblennius edentatus	*Siderea geometrica*
Hirculops cornifex	*Callechelys marmoratus*
Tripterigion abeli	*Myrichthys maculosus*
Cryptocentrus caeruleopunctatus	*Myrichthys colubrinus*
Bathygobius fuscus	*Lycodontis undulatus*
Paragobiodon echinocephalus	

and mud in its upper layers. Deeper parts are composed of light yellowish sediments. Starting approximately at a depth of 30 to 40 m, this community extends to the shallow parts of the subphotic zone, down to about 200 to 260 m.

Most prominent here are molluscs of the genus *Xerophora*; *Phalium* (*Semicassis*) *faurotis*, *Strombus p. plicatus* and *Murex tribulus*. In the deeper parts the gastropod *Turritella terebra* is dominant, together with the clams *Aloidis modesta*, *Chione* sp. and the scaphopod *Dentalium* sp. Crustaceans found here are *Podophthalmus vigil*, *Harpiosquilla harpaxi*, *Squilla gilesi* and the hermit crabs *Nematopagurus diadema*, *Trizopagurus shebae* and *Cestopagurus pectinipes* (LEWINSOHN, 1969). The echinoderms of this region are the serpent star *Ophiactis parva*, *Ophiotrix* (*Acanthophiotrix*) *purpurea*, *Ophiomasa cacaotica* and the sea urchins *Clypeaster reticulatus*, *C. rarispinus* and *Palaeostoma mirabile*; polychaetes are represented by *Petaloproctes terricola*, *Hyalinoecia tubicola*, *Platynereis dumerilii*, *Glycera cirrata* and *G. tesselata*; the latter extend also into deeper waters (FISHELSON and RULLIER, 1969). The most typical benthic fishes are *Champsodon omanensis* and *Bregmaceros maclellandi*.

The littoral rocky and beach-rock communities

Extending along most of the coasts of the investigated areas, the rocky surfaces form a belt, the width and slope of which widely differ in various places. In Eilat (the northernmost point within the Gulf of Aqaba) this belt is approximately 1.5 to 5.0 m wide, being a conglomeration mostly composed of colorful magmatic stones glued by organic materials with a small addition of concrete organogenic components. Here and there, within this conglomerate, fossil coral colonies may be found. During low tides, and under the thermal and light conditions of this region, these belts, rich in rocky pools, are partly dissolved and destroyed by activity of algae as well as the rise in acidity of the surroundings. As this type of activity continues over long periods of time, the result is that, instead of beach rock, piles of stones and gravel are found along the water line.

Further south, along the Sinai coast of the Gulf, this shore line becomes wider and the beach-rock belt produces table-like formations which, along the coast, form a 20 to 80 m wide plate, nearly horizontal and usually exposed during low tide (Fig. 7:*3*). Thus, the inner lagoons which occur between the shore rocky-plates and the fringing coral reefs, so typical along the northern part of the Gulf of Aqaba, become less and less pronounced, terminating completely along the southern part of Sinai and at other places of the Red Sea. Here, the animal world typical of the lagoon is displaced by populations characteristic of muddy beach-rock surfaces. This phenomenon seems to be connected with the various times of immersion of the different parts of the Gulf of Aqaba during the past, or with the transgressions of the terrestrial blocks along the Red Sea which are now being investigated by Israeli geologists. The occurrence of pleistocenic and evidently older fossil corals above the beach-rocks, close to or further from the recent shore line is evidence of such transgressions. Preliminary observations have shown that, in Eilat, parts of beach-rock belts with fossil corals are immersed below the infratidal region or within it (FRIEDMAN, 1965), but that there is no evidence of fossil corals above the extreme highest water line. Further south, 30 to 40 miles (60 km) from Eilat, blocks of pleistocenic coral reefs occur over the water line, growing on beach-rocks or even over sand flats. Near Dahab on the Sinai coast the fossil corals appear above the water line, as well as 20 to 50 m from the sea shore, reaching a height of 2.5 to 5.0 m (Fig. 7:*4*). Sixty km further south, at Ras-Atantur, these coral remnants are much further from the sea and rise 5 to 10 m high. At the tip of Sinai, at Ras-Muhammed which faces the Red Sea proper, the fossil reefs are 32 to 40 m high. The structure of all these fossil reefs closely resembles that of the coral islands of the Dahlak Archipelago (HOROWITZ, 1968; NIR, *in* press), and those lying within the tide range form characteristic coast lines with vertically shaped mushroom structures (Fig. 8:*1a*). On various islands of the Dahlak Archipelago in the southern Red Sea, the height of these usually undercut and shadowed rocky walls ranges from 5 to 8 m, whereas, along the southern part of the Sinai coast in the Gulf of Suez, they are 0.5 to 1.0 m high (Fig. 8:*1b*). They are almost entirely absent along the Sinai coast of the Gulf of Aqaba. The variability in extension of the horizontal beach-rock shore line and the vertical mushroom surfaces undoubtedly influences the distribution and composition of the animal population inhabiting this habitat.

Starting from the supralittoral region seawards, several zones and animal communities have been determined:

The Tectarius armatus/Tetraclita squamosa rufotincta community

This community begins in the high supratidal region, a site only sporadically washed, and is exposed to the high thermal conditions of this desert region: the community extends seawards, together with the extending beach-rock plate. In the highest parts, except for filamentous endolithic algal species such as *Brachytrychia balani* and *Homaeotrix rubra*, the most abundant organisms here are the littorinids *Tectarius armatus* and *Littorina novaezelandae*. These two species have been observed to be active only during the night or in stormy, colder periods of winter. On the same level, but on the surfaces of the mushroom undercuts, they are accompanied by the typical boring organisms of rocky subsurfaces: the barnacle *Lithotrya valentiana*, and the ascothoracic *Lithoglyptes indicus*. Together with these, very dense populations of the gastropod *Nerita undata* and the crustaceans *Ligia exotica* and *Grapsus albolineatus* occur.

Lower down, towards the water line, appear the barnacle *Chthamalus depressus* and, in holes and crevices, specimens of the crab *Metopograpsus messor*. Here also are found the first groups of the giant barnacle *Tetraclita squamosa rufotincta* (Fig. 8:*2*), which form a belt extending along the high- and midinfratidal zones. These highest *Tetraclita* groups mark the uppermost line influenced by the tidal rhythm; they are usually submerged and exposed twice a fortnight. The activity of the *Tetraclita* is thus interrupted twice a day. Preliminary observations showed that, during exposure, *Tetraclita* seem to be able to regulate their inner temperatures and to withstand the high temperatures of their surroundings. Measurements during the highest August ambient temperature of 36 °C showed a difference of 5 °C between the temperature of the animals and that of the air. During the measurement procedure, it was observed that specimens of *Tetraclita* contracted within their shell from time to time, expelling over their body drops of water which eva-

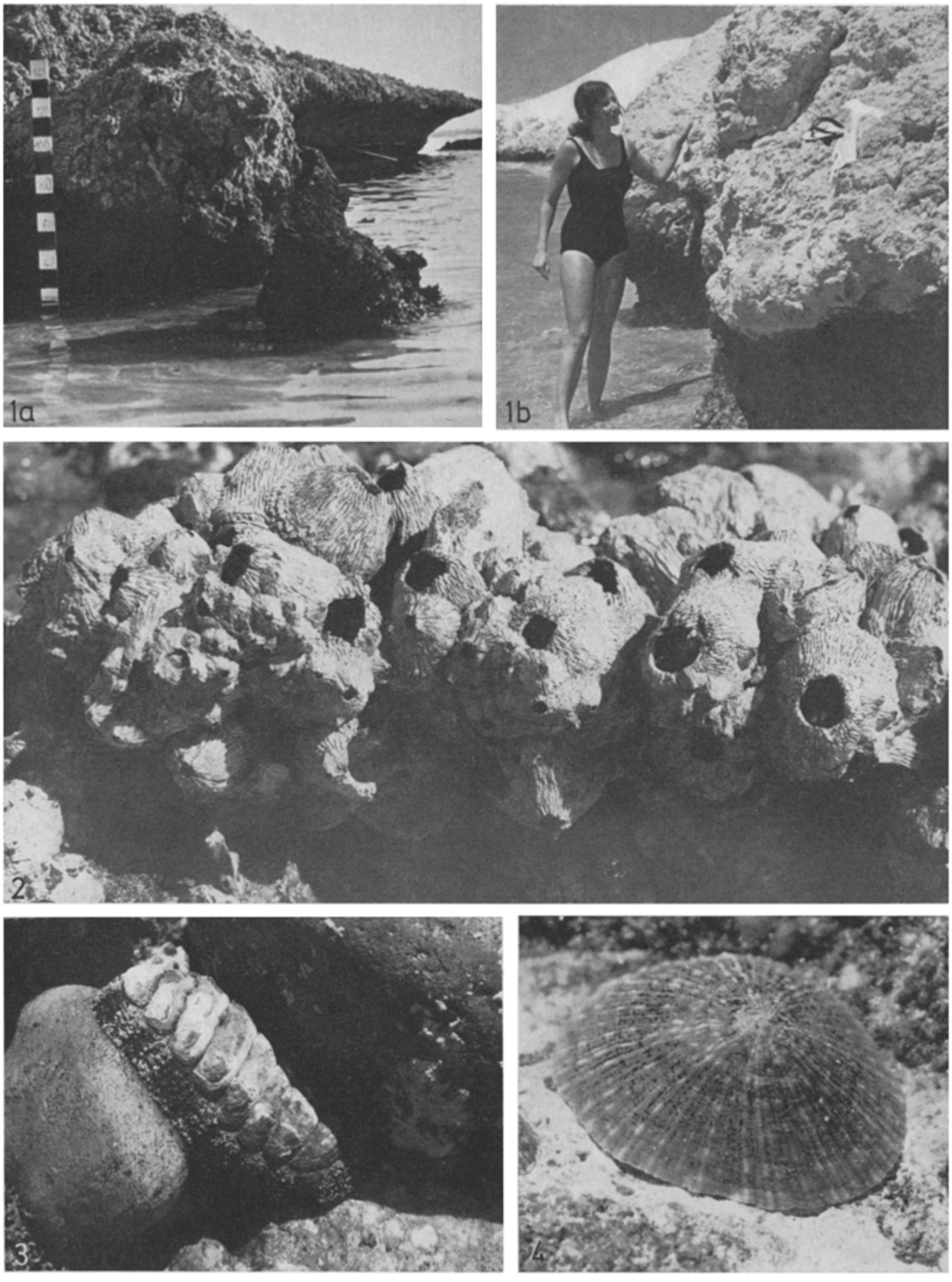

Fig. 8. *1* Mushroom structure of pleistocenic coral rocks (a) at Dahlak Archipelago, (b) near Ras Muhammad (Sinai); *2* *Tetraclita squamosa* along infratidal beach-rock at Eilat, Red Sea ($^1/_2$ actual size); *3* *Acanthopleura haddoni* moving over from a stone (actual size); *4* *Cellana rota* (× 2)

porated immediately. The *Tetraclita* population extends together with the seaward extension of the beach-rock plate, as described for the more southern parts of the Sinai coast in the Gulf of Aqaba. Thus, groups of them may be found immediately above the fringing coral reefs.

In all the localities observed. the belt of *Tetraclita squamosa rufotincta* is richly inhabited by algae

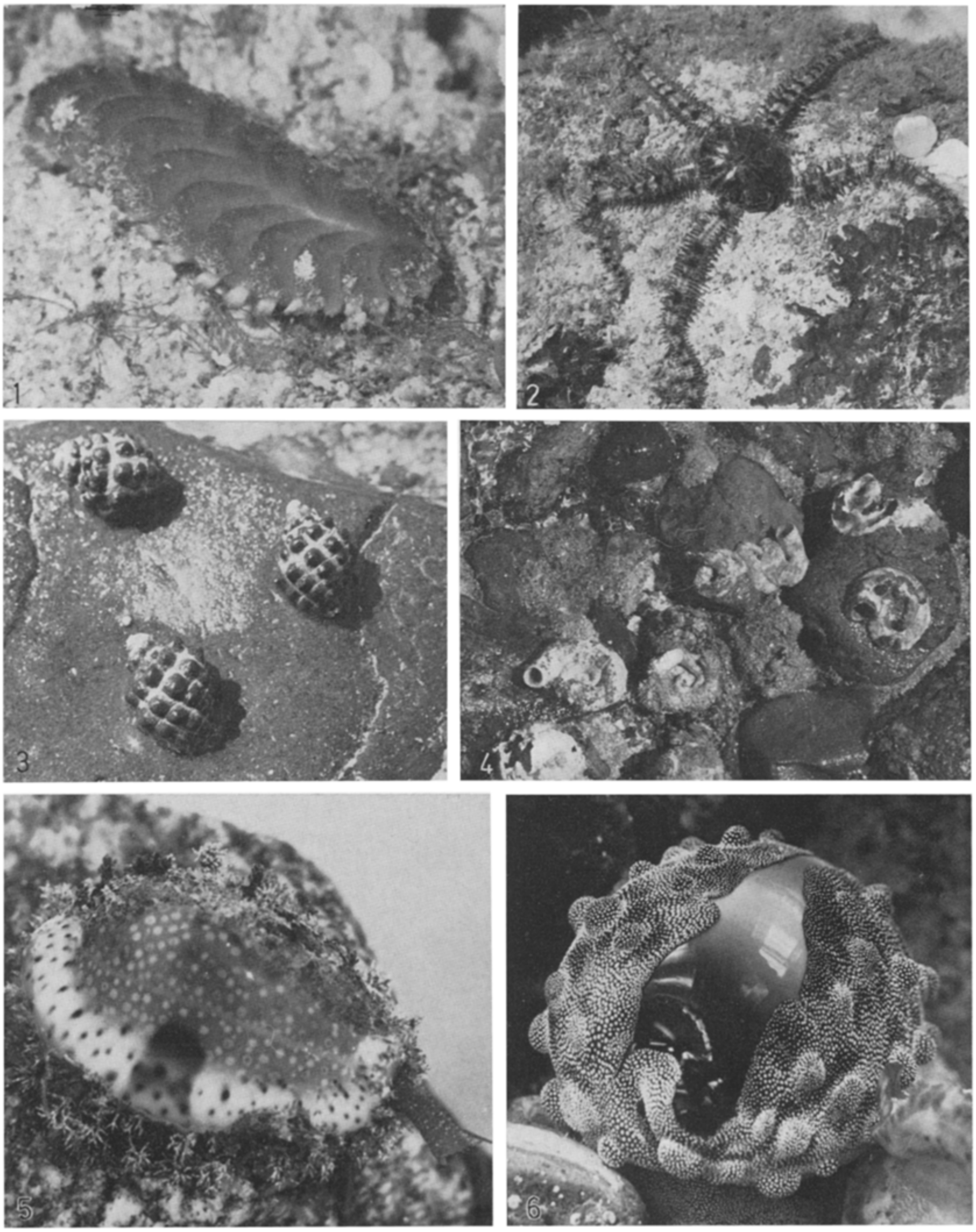

Fig. 9. *1* Scaled brittle-worm *Iphione muricata* (× 2); *2 Ophiocoma scolopendrina* ($^1/_2$ actual size); *3 Drupa tuberculata* (actual size); *4* vermetid *Serpulorbis innoperta* ($^1/_2$ actual size); *5* cowri *Erosaria nebrites* (× 2); *6 Talparia talpa* partly covered by mantle (enlarged)

(*Sphacelaria tribuloides, Sphyridia filamentosa* and *Jania rubens*) as well as different animal species. The most abundant are the large chitons *Acanthopleura haddoni* (Fig. 8:*3*), the gastropod *Cellana rota* (Fig. 8:*4*) and the bivalve *Ostrea cucullata*. Together with these are found *Planaxis sulcatus, Nerita polita, N. forskali, Monodonta dama, Littorina scabra* and *Thais hippocastaneum*. In crevices of this region are found the chiton-like *Iphione muricata* (Polychaeta) (Fig. 9:*1*), *Ibla cumingi* (Cirripedia) and the ophiurids *Ophiocoma erinaceus* and *O. scolopendrina* (Fig. 9:*2*). The latter 2 species feed on plankton and organic particles, collecting them from the water surface during low tide, as observed also by MAGNUS (1962). On the extended infratidal beach-rock plates of the southern part of the Gulf of Aqaba, the density of these serpent stars may reach 150 to 200 specimens/m^2, forming here the dominant part of a community. In the northern part of the Gulf and at Eilat, where the rock platform formations are limited along the upper part of the infratidal, the *Ophiocoma* population occurs in the form of a belt along the infratidal *Tetraclita* colonies. The lowest part of this belt, covered by a dense growth of low algae (*Caulerpa serratula, Calpomenia sinuosa, Cystoseira myrica, Digenea simplex*), is mainly characterized by the molluscs *Conus taeniatus* and *Drupa* (*Morula*) *tuberculata* (Fig. 9:*3*). The density of *C. taeniatus* may reach 25 to 55 specimens/m^2, and it seems that, during low tides, they hide by penetrating into the algae cover. Along this habitat the vermetid *Serpulorbis inopertus* is also very common (Fig. 9:*4*), forming a typical belt.

Table 4. *Animal species found along the infratidal rocks of the Red Sea*

Polychaeta	
Iphione muricata	*Pseudonereis variegata*
Lepidonotus glaucus	*Hydroides heteroceros*
Nicomache lumbricalis	
Mollusca	
Acanthopleura haddoni	*Drupa tuberculata*
Cellana rota	*Thais hippocastaneum*
Monodonta dama	*Volema pyrum*
Tectus dentatus	*Conus flavidus*
Turbo argyrostomus	*Smaragdinella calyculata*
Lunella coronata	*Barbatia decussata*
Nerita forscali	*Anadara maculata*
Nerita polita	*Arca (Navicula) avelana*
Nerita undata	*Modiolus moduloides*
Littorina scabra	*Lithophaga malaccana*
Tectarius armatus	*Isognomon acutirostris*
Cerithium clypeomorus	*Spondylus ducalis*
Planaxis sulcatus	*Ostrea cucullata*
Mauritia grayana	*Chama limbula*
Chicoreus ramosus	
Crustacea	
Tetraclita squamosa rufotincta	*Grapsus albolineatus*
Tetrachthamalus oblitteratus	*Grapsus granulosus*
Chthamalus stellatus	*Geograpsus crinipes*
Ibla cumingi	*Pachygrapsus minutus*
Lithotrya valentiana	*Lydia tenax*
Lygia exotica	*Pilumnus incarnus*
Clibanarius siganus	*Atergatis roseus*
Clibanarius carnifex	
Echinodermata	
Ophiocoma picta	*Ophiotrix savignyi*
Ophiocoma erinaceus	*Ophiolepis cincta*
Pisces	
Istiblennius rivulatus	*Bathygobius fuscus*
Salarius fasciatus	

Within the infratidal rocky region are found the first sea anemones, namely the digging *Anthopleura eilatensis* (FISHELSON, 1970), as well as the crabs *Pilumnus incanus, Geograpsus crinipes, Clibanarius signatus* and *Paguristes ciliatus.* This belt is also very rich in blenniid fishes; especially numerous here are *Salarias fasciatus* and *Istiblennius rivulatus.* A list of other animal species found in this habitat is given in Table 4.

The Gena varia/Echinometra mathaei community

Occurring below the infratidal, this community is found around and below stones, dead coral parts or burrowed in the muddy-sand sediment. From among the molluscs, *Gena varia* (Trochidae) is typical here, living in aggregates on the undersurfaces of stones, sometimes 25 to 30 specimens together. This photophobic species feeds on algae; it reacts to every strong touch by autotomy of the posterior part of the foot, which can be regenerated (FISHELSON and KIDRON, 1968). On the same sites are also found numerous aggregations of the small *Planaxis lineolatus* as well as *Heliotis pustulata, Serpulorbis inopertus, Modiolus auriculatus, Erosaria nebrites* (Fig. 9:*5*), *Mauritia grayana, Talparia talpa* (Fig. 9:*6*), *Conus arenatus, C. vexillum, C. textile*, various species of *Cerithium* and *Strombus mutabilis*, and the tectibranch *Berthella citrina* (Fig. 10:*1*). Additional opisthobranch molluscs, such as *Aplysia oculifera, Notarchus indicus* and *Pleurobranchus forskàli* are found around stones and in crevices. The polychaetes *Eunice afra, Loimia medusa, Eurythoë complanata, Lepidonotus clava, Hermodice carunculata* and *Sabellastarte indica* (Fig. 10:*2*) are common in this zone. Echinodermata are represented here by the sea urchins *Echinometra mathaei, Tripneustes gratilla* and large populations of *Diadema setosum* (Fig. 10:*3*). All 3 species of sea urchins are active during the night; at sunset they leave their crevices and start moving and feeding. The typical sea stars here are *Asterina burtoni, Astropecten polyacanthus* (Fig. 10:*4*), *Linkia multifora* and *Fromia ghardaqana*. Here are also found the first specimens of the crinoid *Lamprometra klunzingeri*, which, in its distribution, extends up to a depth of 2 to 3 m. Very typical for this habitat as well as along infratidal beach-rock plates are the echiuroids *Ochetostoma erythrogrammon* and (to some extent) *Bonellia viridis*, which live in sediments accumulated within crevices. The Holothuroidea are mostly found on the bottom of the lagoon, covered by sediments, algae or shells. Among them the most abundant are *Holothuria vaga-*

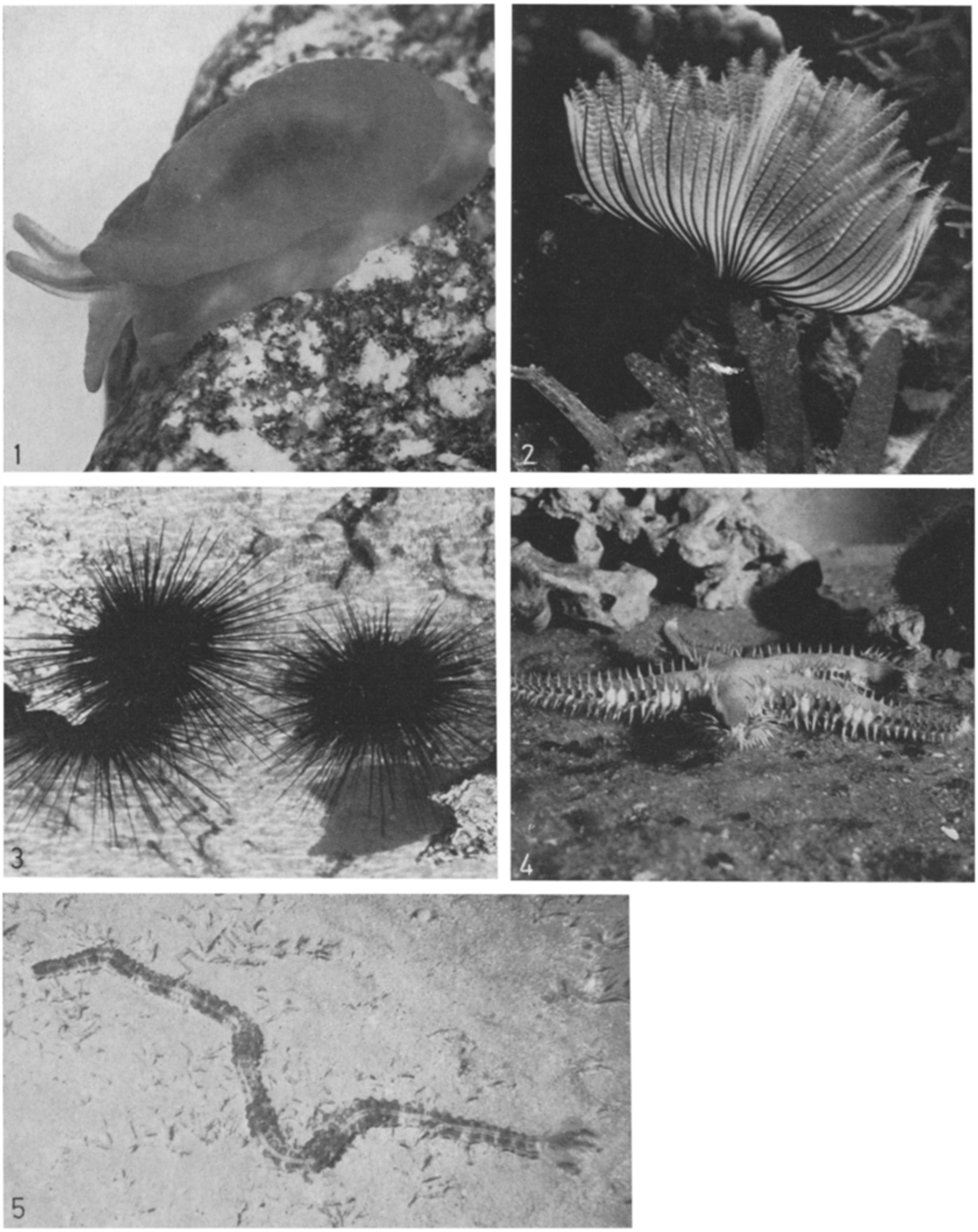

Fig. 10. *1* Tectibranch *Barthella citrina* (× 2); *2 Sabellastarte indica* (actual size); *3 Diadema setosum* in its natural habitat ($^{1}/_{2}$ actual size); *4 Astropecten polyacanthus* ($^{2}/_{3}$ actual size); *5* synaptid sea-cucumber *Opheodesma grisea* ($^{1}/_{10}$ actual size) at Eilat, Red Sea

bunda, H. impatiens, Holodeima atra and Stichopus variegatus, as well as large specimens of the synaptid *Opheodesma grisea* (Fig. 10:*5*). The typical serpent stars are *Ophiolepis superba, Ophiotrix savignyi* and *Ophiocoma erinaceus*. The crustaceans are very richly represented and the most peculiar of this community are: the boxer crab *Lybia leptochelis,* which holds in each of its chela small specimens of the sea anemone

Triactis producta, and the pistol crab *Alpheus frontalis* which lives in tubes attached under stones and prepared by itself from the algae *Oscillaria* (FISHELSON, 1966a). Other crustaceans common here are *Gonodactylus demanii*, *G. falcatus*, *G. mesactura*, *G. brevisquamata*, *Cryptodromia granulata* and *C. canaliculata*. The lobster *Scyllaroides tridacnophaga*, which feeds mostly on large bivalves, is also found. Topographically in the same habitat, but in places with more compact beach-rock plates (Gulf of Aqaba), are found quite large populations of another lobster — *Panulirus penicillatus* — which is extensively hunted by the local bedouins. There are also several species belonging to Xanthidae (*Epixanthus frontalis, Etisus laevimanus*). From among the fishes which occur here, the most typical are various eleotrid species, *Trypterigion* spp., the congrigadid *Haliophis guttatus*, the murei eels *Siderea geometrica* and various species of the genus *Lycodontis*.

Mangrove growths

The investigated areas of the mangroves are those of Melita Bay in the Gulf of Zula (Ethiopia); Musseri Island of the Dahlak Archipelago; Ras Muhammed at the tip of Sinai; Shurat-a-Mankata and Nabq on the Sinai coast of the Gulf of Aqaba. At these stations, except for Musseri Island, *Avicennia marina* is the only species forming the mangrove growths. On Musseri Island the *Avicennia* are accompanied by *Rhizophora* and *Ceriops* (Fig. 11:*1*).

Preliminary analyses of the abiotical conditions in the shallow waters of the mangrove lagoons showed that, at midday, the temperature of the water can rise to 34 °C, while the amount of dissolved oxygen drops to 0.32 ppm, giving a saturation of 3.5%, compared with a value of 120% saturation which was measured at the same time in an open bay. Undoubtedly, these extreme conditions modulate a very hard habitat, suggesting a poor animal association. Thus, from among the fishes collected on such occasions, only a few specimens of *Aphanius dispar* and *Therapon jarboa* were found here.

In several of the investigated areas, *Avicennia marina* grows on extensive submerged rock plates covered by a thick layer of dark muddy sediment rich in organic material. This forms a very peculiar habitat — a kind of flat covered by stagnating sediments, densely interrupted by protruding rocks or small eroded lagoons, pools and water passages. At several places, this more or less horizontal habitat extends from 100 to 150 m, remaining uncovered during most of the low tide. Towards the shore, these mangrove growths are framed by terrestrial halophytes such as *Sueda* spp., *Salvadora persica*, and others. Only in Melita Bay and some places of Musseri is this biotope typical, and the trees, which are much higher and denser, grow on a deep soft layer of mud. Also only in Melita was the mangrove fish *Periophthalmus koelreuteri* found. This fish needs

Table 5. *Animals found among mangroves of the Red Sea*

Spongia	
Heteronema erecta	*Tedania anhelans fassabensis*
Bajulus laxus	*Biemna fortis*
Spirastrella inconstans	*Suberites clavatus*
Coelenterata	
Cytaeis nassa (on *Nassarius*)	*Boloceroides macmurichi*
Zoanthus bertholetti	*Cryptodendrum adhesivum*
	Aiptasia (diaphana?)
Polychaeta	
Clymene lombricoides	*Glycera tesselata*
Loimia medusa	*Armandia melanura*
Marphysa mossambica	*Ceratonereis erythraensis*
Eunice torquata	*Petaloproctes terricola*
Mollusca	
Haliotis pustulata	*Strombus erythraensis*
Trochus erythraeus	*Strombus gibberulus*
Nerita polita	*Strombus mutabilis*
Nerita undata	*Nassarius clathratus*
Littorina scabra	*Conus arenatus*
Terebralia palustris	*Conus tesselatus*
Cerithium punctatus	*Modiolus auriculatus*
Planaxis sulcatus	*Ostrea cucullata*
Crustacea	
Exirolana orientalis	*Alpheus rapax*
Parelasmopus suluensis	*Alpheus sublucanus*
Cymaduse filosa	*Callianassa madagassa*
Acasta porata (in sponge)	*Metapograpsus thukuar*
Balanus a. amphitrite	*Metapograpsus messor*
Chthamalus stellatus	~~*Grapsus*~~ *granulosus*
Pseudosquilla ciliata	*Pseudograpsus erythreus*
Manningia amabilis	*Iliograpsus paludicola*
Mesacturus brevisquamatus (in sponge)	*Paracleistostoma leachii*
	Sarmatium crassum
Gonodactylus demani (in sponge)	*Portunus granulatus*
	Thalamita poissonii
Gonodactylus chiragra	*Ebalia abdominalis*
Protosquilla lenzii	*Macrophthalmus depressus*
Clibanarius longitarsus	*Calappa hepatica*
Diogenes avarus	*Uca inversa*
Diogenes gardinieri	*Uca tetragonon*
Penaeus hathor	*Dotilla sulcata*
Echinodermata	
Echinometra mathaei	*Ophiolepis cincta*
Echinotrix calamaris	*Ophiocoma scolopendrina*
Diadema setosum	
Ascidia	
Ecteinascidia conclini f. *minuta*	*Metrocarpa nigrum*
Phallusia nigra	*Didemnum candidum*
Pisces	
Istiblennius rivulatus	*Myrophis uropterus*
Salarius fasciatus	*Bothus pantherinus*
Haliophis guttatus	*Aphanius dispar*
Conger cinereus	

Fig. 11. *1* Growths of *Rhizophora* and roots of *Avicennia* on Musseri Island, Dahlak Archipelago; *2* and *3* *Periophthalmus koelreuteri* and its nest; *4* *Uca tetragonon*

a thick layer of mud for the preparation of its burrows (Fig. 11:*2*, *3*).

From among the algae, *Centroceras clavellatum*, *Lyngbya majuscula*, *Dictyosphaeria cavernosa*, *Valonia aegagrophila*, *Bryopsis hypnoides*, *Cladophora albida*, *Laurencia obtusa* and *Digenea simplex* occur here. Growths of the sea grass *Cymodocea serrulata* are also found frequently. A special econiche is formed by the vertical roots and submerged parts of the mangroves; submerged and bared during the tides, they form a substrate for typical infratidal animals such as *Ostrea cucullata*, *Nerita polita* and *Planaxis sulcatus* from among the molluscs, and *Tetraclita squamosa* and *Tetrachthamalus oblitteratus* from among the barnacles. Living colonies of the coral *Stylophora pistillata* were found hanging onto the roots of *Avicennia marina* in the Gulf of Aqaba. Other animals which were collected and seem to be typical of all the investigated mangrove areas are: from among the Polychaeta — *Marphysa mossambica*, *Armandia melanura*, *Petaloproctus terricola*, *Clymene* (*Euclymene*) *lombricoides*, *Ceratonereis erythaeensis*; from among the Crustacea — *Alpheus rapax*, *Metapograpsus thukuhar*, *Sarmatium crassum*, *Sesarma guttatum*, *Macrophthalmus telescopicus*, *Paracleistostoma leachii*, *Thalamita crenata*, *Callianassa madagassa* and *Callianassa novaebritanniae*. Together with these are usually found several species of the fiddler crab, especially *Uca albimana* and *U. tetragonon* (Fig. 11:*4*). Animals found here are listed in Table 5.

Discussion

Soft bottoms

Observations showed that the shallow-water bays investigated, although of different granulometric and chemical composition, are populated by a typical, mostly homogeneous animal population, strongly resembling invertebrate populations described from similar habitats in Madagascar (Pichon, 1966, 1967; Thomassin, 1969). The metric distribution of these populations in their habitats is mostly dependent upon the angle of the bottom slope (Fishelson, in preparation) and this remains in strict accordance with wave action and submergence-emergence rhythms. The gentler the angle, the weaker the wave forces, and the more the substratum remains unchanged. This allows a constant layering of sand particles, forming stable conditions for a permanent series of substrate-dwelling animals. On the other hand, the strength of the wave action is also dependent upon the morphology of the surroundings: gentle slopes allow the incoming waves to "free" themselves slowly from their mechanical force, enabling also a gradual dispersion of passing sedimentary particles all along the slope. Such a wave returning towards the sea is unable to draw with it the sunken sediments. Thus, a differential granulometric composition is formed, which comprises the living conditions for most of the psammobiotic inhabitants occurring here. As all the bays investigated were topographically located close to the openings of wide collecting wadis or on one of their shoulders, thus forming the margin of a delta or a part of it, it seems that the sediments which are brought in during the floods of these wadis contribute directly to the formation of the bays.

Most of the species found here feed on detritus and micro-organisms which inhabit the tiny spaces among the sand particles and accumulate over the sand. Only in stable conditions can the populations of these micro-organisms develop and form the food chain for the above mentioned species, and doubtless for many more.

Thus, starting from the geomorphology of the shore slope, we are dealing with a chain of factors which seem to be connected in the following sequence: gentle bottom angle → reduced wave force → regular distribution of sediments → stable environmental condition → development of micro-organisms in fauna and flora → succession of bottom dwellers. From the above it seems that, if the basic factor involved — appreciable bottom slope — occurs, then all the others will consequently develop, thus enabling the bottom community to form and establish itself.

Continuing with this line of reasoning, it seems that the mangrove flats represent in most cases the end product of this development. Apparently, the first fixation of soft bottoms for mangrove growths begins by development of bottom filamentous algae which stabilize and adhese the sand granules. Together with this, floating mangrove saplings, which accidentally take root here, adhere and attempt to grow. If they succeed, they also contribute to the fixation of the bottom layers, and to the stabilization and accumulation of sediments. Such conditions were observed on the Shumma Island of the Dahlak Archipelago, where sparse and probably young growths of *Avicennia marina* were found growing over white calcareous sand, with only a little black detritus concentrated around their barks. Such a mangrove growth develops constantly, forming underneath the typical black muddy bottom: it thus eliminates the sand-dwelling fauna of calcareous sandy flats and leaves the specific and more adapted muddy-bottom species.

In addition, new econiches are formed, such as the surfaces of the mangrove barks and roots. Protruding over the water from the midtidal to the supratidal, these support the occurrence of a typical *Ostrea-Planaxis-Tetraclita* zone, well developed along the entire rocky shore fringe in the Red Sea. As mentioned, even branched colonies of the scleractinian genus *Stylophora* were found to grow hanging on mangrove roots in the Gulf of Aqaba (Nabq).

However, it seems that sometimes, by the above process, mangrove flats can again be covered by sand and return to their starting point: on Melita Bay and Isola Verde near Massawa it was observed that, perhaps by changes in wave directions or by human construction activities, calcareous and siliceous sand was brought in between the mangroves which covered the old muddy bottom formation together with the mangrove roots and formed high belts and ridges protruding into the sea. On these occasions the typical "clean" sand fauna returns between the high, mature mangrove trees. Thus, clearly sand-dwelling amphipods and isopods are found here, as well as crabs of the genera *Dotilla*, *Coenobita*, *Ebalia*, *Nassarius*, *Polynices* and *Cypraea* from among the gastropods and others, bordering in lower horizons with the typical mangrove fauna such as various *Uca* species, *Sesarma*, alpheids and, from among the fishes, *Periophthalmus koelreuteri*.

Rocky shore

All the rocky habitats extending along the investigated parts of the Red Sea have highly uniform inhabitants. This seems to be due to the fact that the most common substrate found here is pleistocenic limestone remnants. These remnants are porous and easy to bore, and prove ideal for all the organisms, especially those occurring above the average tide level, insofar as they provide crevices or burrows in which to hide. In general, 2 characteristic habitats can be recognized: the undercut mushroom surfaces and the horizontal beach-rock flats. The mushroom structures are especially rich in animals. They are usually shadowed by the overhanging coral platform, constituting a much cooler and humid environment than the general surroundings. Therefore, we find here various algae, large populations of *Acanthopleura haddoni* and *Nerita undata*. The endolithic barnacle *Lithothrya valentiana* extends here up to 1.5 m above water level, a phenomenon not observed at any place where these animals are exposed to insulation. It is clear that the spatial and vertical distribution of this rocky surface community is primarily correlated with the form of the substratum. This type of habitat seems to be very common along shore lines in different geographical regions, described from the Great Barrier Reef of Australia as well as from Inhaca Island (MACNAE and KALK, 1958).

In most parts of the Southern Red Sea, the beach-rock surfaces are covered by a thick layer of muddy sediments and seem to serve as a substratum for mangrove growths with their typical fauna. Only at several places along the Sinai coast in the northern Gulf of Aqaba, not reached by mangroves, a peculiar beach-rock fauna has developed. Rich in crevices, small lagoons and caves, this habitat is populated by different eel fishes of the genera *Conger*, *Lycodontis* and *Murenichthys*, several species of blennis and gobis, crabs and stomatopods and various polychaetes. The most characteristic of all, however, is the densely and regularly distributed population of the serpent star *Ophiocoma erinaceus*. During low tide, the whole rocky surface looks like a network of *O. erinaceus* arms, bending in all directions or pointing towards the water surface, collecting food in the manner described by MAGNUS (1962) in Ghardaga, Egypt. With the rising tide the ophiurids retreat and disappear into their holes. This seems to prevent their being preyed upon by the numerous fishes which invade the region with the rising water. Observations published by MAGNUS (1962) and observed by us indicate that these serpent stars are territorial animals, each of them occupying a nest-crevice, and using their arms to push away other specimens. Because of this behaviour, the distribution pattern of the population remains more or less constant, density being limited by the length of the arms of the specimens involved.

Below this infratidal line, marked by the lowest groups of *Tetraclita squamosa*, begins the dense fauna of typical obligatory marine forms such as the sea anemone *Anthopleura eilatensis*, the leparid *Ibla cumingi*, groups of Nemertea worms, flatworms and polychaetes, large columns of hydrozoans and bryozoans, as well as numerous species of crustaceans. Here also occur the first *Bathygobius fuscus*, *Isthiblennius rivulatus* and other blennis. Deeper, below the low tide marks, where more dead corals and stones are found above the sediment (making the habitat more complex), the number of animal species per unit of space increases continuously. These numbers are, of course, greatly increased when the infauna of stones and dead coral pieces are included.

Summary

1. The ecological and bathymetrical distribution of the Red Sea shallow infra- and subtidal benthic fauna is described, and briefly discussed. An attempt is made to divide this fauna into a number of communities, according to the habitats from which they were collected.

2. In connection with the above, the following groups were described for the soft bottoms: *Ocypoda saratan* — *Dotilla sulcata*; *Hippa picta* — *Mactra olorina*; *Ptychodera flava* — *Radianthus koseirensis*; *Halophila stipulacea* — *Asymmetron* (*lucayanum?*); and *Operculina gaimardi* — *Turritella terebra*.

3. For the rocky infra- and shallow subtidal the following communities are mentioned: *Tectarius armatus* — *Tetraclita squamosa*, and *Gena varia* — *Echinometra mathaei*. These communities usually terminate within the lagoon, between the rocky shore and the fringing reef.

4. Below the tidal range, the *G. varia* — *E. mathaei* community becomes very rich in species, because of animals which group below and around dead corals and stones.

5. The mangrove growths of the Red Sea are briefly discussed and their most common animal species described.

Acknowledgements. This is a welcome opportunity to thank all the scientists who have been cooperating with us for years along the Red Sea, identifying and describing the collected material. Thanks are also due to the colleagues, students and technicians who helped during different stages of the field work. Special thanks go to Mr. A. SHOOB for taking the photographs; to Mr. R. KALEF for preparation of the figures, and to Mrs. R. MANNEBERG for help in the final preparation of the manuscript.

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Date of final manuscript acceptance: March 8, 1971. Communicated by O. KINNE, Hamburg