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Epimenia arabica spec. nov., a Solenogaster *(Mollusca)* Feeding on the Alcyonacean *Scleronephthya corymbosa (Cnidaria)* from Shallow Waters of the Red Sea

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With 13 figures

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Abstract. The body organization and some biological data of *Epimenia arabica*, a new species of *Solenogastres* of the order *Cavibelonia*, are presented. The species is described based on four large-sized specimens (13–21 cm × 0.7–1 cm) from three different localities off the coast of the Sinai Peninsula (Red Sea). It feeds on *Scleronephthya corymbosa* VERSEVELDT & COHEN *(Octocorallia: Alcyonacea)*, generally at depths of 2–5 meters.

Problem

The *Solenogastres* represent a small class of marine molluscs including some 190 described species classified within four orders. They are laterally narrowed, ciliarily gliding animals and measure between 0.8 mm and 30 cm. *Solenogastres* are still provided with the primitive molluscan mantle organization covered with cuticle and embedded spicules (aplacophoran level, paraphyletically also retained in the *Caudofoveata;* cf. SALVINI-PLAWEN, 1985 b). Other conservative traits in *Solenogastres* include the general configuration of the gut, the musculature, and the circulatory system, whereas their hermaphroditism represents an advanced condition of the reproductive system (cf. SALVINI-PLAWEN, 1985 b, 1988).

Solenogstres almost exclusively feed on *Cnidaria,* and are either free-living or epizoic (SALVINI-PLAWEN, 1981). Except for a few mesopsammic representatives (SALVINI-PLAWEN, 1985 a), they prefer fairly firm substrata (clay, muddy sand, secondary hard bottom, *Cnidaria)* in calm waters; their bathymetric range generally extends from 20 to 6850 meters. Only three described species have

been recorded from shallower localities (cf. SALVINI-PLAWEN, 1971): the interstitial *Biserramenia psammobionta* SALVINI-PLAWEN (8–10 m), the well-known *Neomenia carinata* TULLBERG (20–565 m, but recorded in the Hardangerfjord/Norway already at 10 m: Museum Bergen), and *Dorymenia quincarinata* (PONDER) from New Zealand (14.5 m–238 m).

Because most *Solenogastres* live in greater depth, observations and investigations of living animals are few (PRUVOT, 1891; BABA, 1940 a; SALVINI-PLAWEN, 1968); BABA (1940 a) also conducted some feeding experiments. It was therefore an outstanding discovery when an ongoing collection of *Octocorallia* by the junior author along the coral reefs of the Sinai Peninsula yielded some large-sized *Solenogastres* living among and feeding on *Alcyonacea* at the depth of only a few meters.

Material and Methods

The collected *Solenogastres* specimens were found among colonies of the alcyonacean *Sclerophthya corymbosa* VERSEVELDT & COHEN, 1971, at three different localities along off-shore coral reefs. The records are (Fig. 1):

NS 22060 = Strait of Tiran, Jackson reef, 28°01'N, 34°34'E (26.6.1985), 5 m; two individuals (coll. Y. B.).

NS 22885 = Shag Rock, Gulf of Suez, 27°45'N, 33°55'E (11.7.1986), 2 m; one specimen (coll. Y. B.).

NS 22886 = Ras Muhammad, southern tip of Sinai, 27°48'N, 34°15'E (14.7.1986), 0-25 m; one specimen (coll. Y. B.).

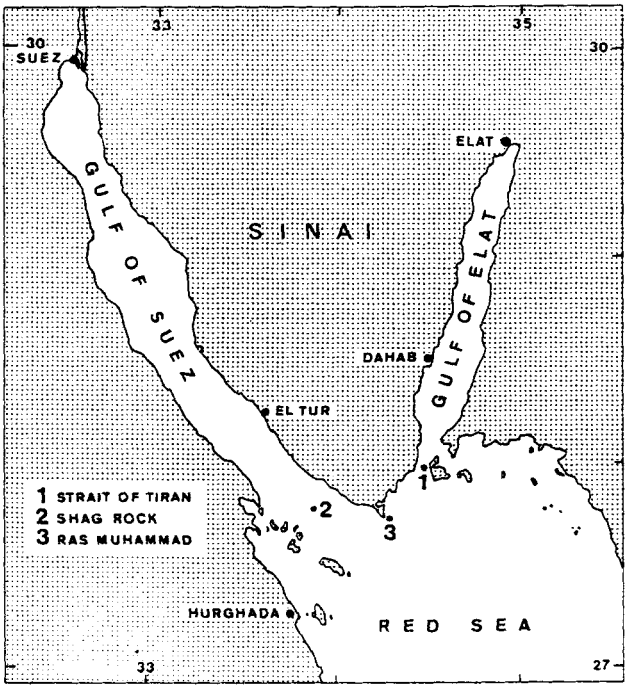


Fig. 1. Map of the study area with finding sites (1–3).

As the body organization and tissue structure are the main tool for species determination in *Solenogastres*, the anterior and posterior ends of two specimens (NS 22060 & NS 22885; alcohol fixation) were cross-sectioned histologically in series of 10 µm and reconstructed (Fig. 2 A, B). AZAN staining was used.

The type specimen (NS 22060; Figs. 3 and 5) is deposited in the Zoological Museum of Tel Aviv University.

Results

1. Description of *Epimenia arabica* spec. nov.

Diagnosis: Reddish animals of large size up to 21 × 1 cm, cuticle with warty elevations, outlets of foregut glands far preradular, distichous radula with six median denticles, paired bundle of six receptacula seminis, mantle cavity with diverticula in symmetrical arrangement. Northern Red Sea, feeding on *Scleronephthya corymbosa* at 2–5 m depth (Figs. 3, 4, 5).

External aspect: The present four animals are elongate and somewhat tapered posteriorly. They measured:

21 cm × 0.8–0.9 cm high × 0.7 cm wide (NS 22885);
16 cm × 0.9–0.6 cm continuously tapering (NS 22060; type);
14 cm × 1.1 cm high × 0.9 cm wide (NS 22060);
13.5 cm × (anterior) 1.1 cm high × 0.9 cm wide to (posterior) 0.7 cm in diameter (NS 22886).

In life, they are reddish, ranging from orange to purple; in air, the body colour darkens (Fig. 3). The mantle surface shows irregular warty and whitish elevations (1–2.5 mm in diameter) scattered over the body (Fig. 3). The narrow foot (mid-ventral groove, Fig. 5) and body openings are generally not conspicuous.

Mantle: The covering cuticle in the studied material ranges in thickness from 200–450 µm ventrally to 500–650 µm dorsally. The wart-like formations are irregularly scattered; they represent a locally thickened cuticle only, attaining 700–1200 µm in height (Fig. 10). As common in *Cavibelonia*, the epidermal papillae protrude from the epithelium through the cuticle to the surface. Their stalks are very slender and the terminal globular enlargements are often crowded close to each other, as in the case of the *Strophomeniidae*. The spicules are not densely arranged, they consist of hollow, needle-like elements as typical for *Cavibelonia* (Fig. 12) and lie in different oblique directions, so that they optically seem to intercross. They measure 150–200 µm × 10 µm, 200–350 µm × 15 µm, or 220–450 µm × 20 µm. The spicules in the mid-dorsal warty thickenings are arranged radially which is not the case in lateral 'warts'. The spicules of the pedal furrow include both large and radial (up to 400 × 20 µm) as well as very small elements (70 × 5 µm), the latter produced by the outer epithelium of the mantle fold (Fig. 6). At both sides of the mantle opening an integumental groove shows solid abdominal spicules (100–120 µm × 7–8 µm) with a short

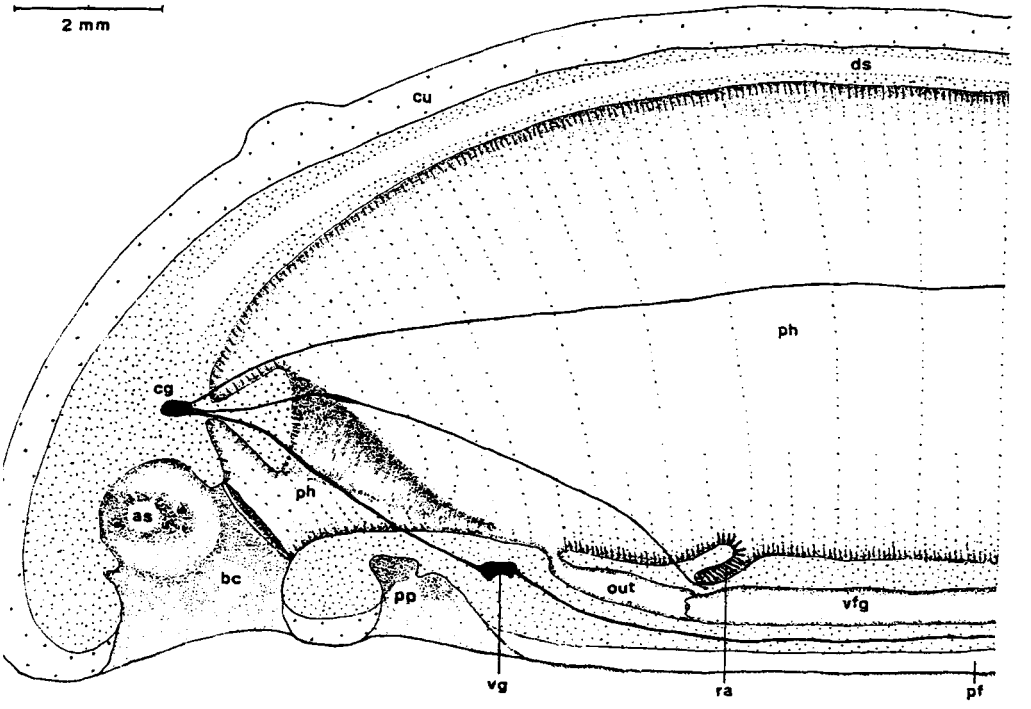
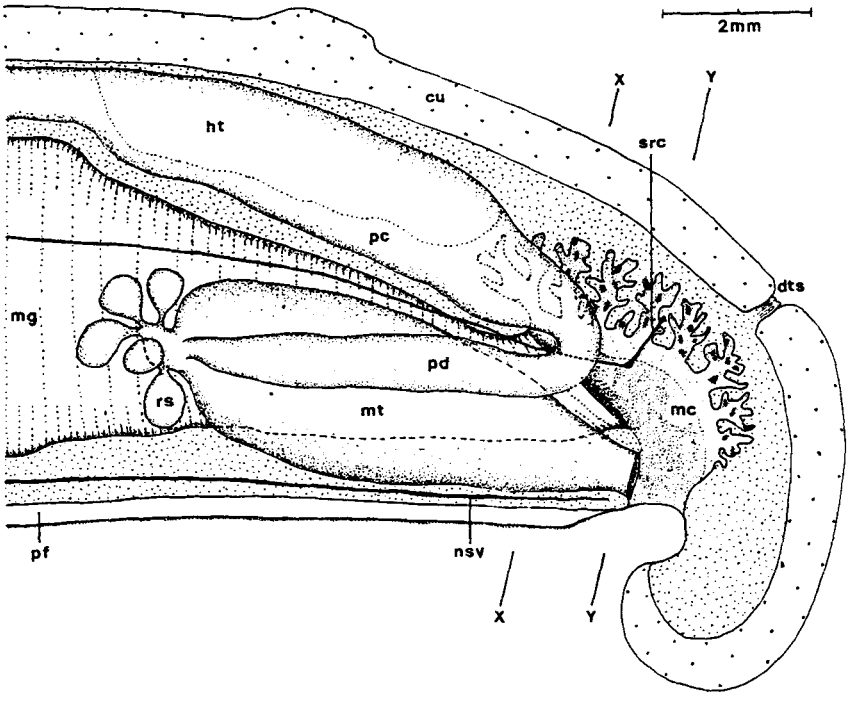


Fig. 2 A. Schematic organization of the anterior body of *Epimenia arabica*. *as* = atrial (preoral) sense organ, *bc* = buccal cavity, *cg* = cerebral ganglion, *cu* = mantle cuticle, *ds* = dorsal blood sinus, *out* = outlet of foregut gland, *pf* = pedal folds, *ph* = pharynx, *pp* = pedal pit, *ra* = radula apparatus, *vfg* = ventral foregut glandular organ, *vg* = (first) ventral ganglion.

proximal hook or a distal bend (Fig. 12). Very small solid spicules surround the dorso-terminal sense organ(s).

Foot and mantle cavity: The foot begins with a shallow pedal pit bearing a ciliated epithelium and intercellular outlets of the anterior mass of mucous cells (pedal gland). Aside from a subdividing transverse bulge, there are no major foldings. At the transition of the pit to the pedal groove, nine longitudinal ciliated folds are formed; within a course of about 10 mm, these successively fuse to a single fold continuing the length of the body. Immediately anterior to the pallial opening the pedal epithelium is covered for a short distance by mantle cuticle (Fig. 11). As usual, the pedal groove is delimited on each side by the mantle fold. The sole glands are dense and open into and beside the pedal fold(s) (Fig. 6).

The mantle cavity opens ventrally. Its space is characterized by two pairs of dorsal longitudinal folds which give rise to branched diverticula (Figs. 10–11). These diverticula extend longitudinally more or less symmetrically through the space between the pericardium and the body end. The epithelium of the entire mantle cavity, including the diverticula, consists of ciliated cells continuous with the hind gut. With respect to the course of the suprarectal commissure of the



B. Schematic organization of the posterior body of *Epimenia arabica*. *cu* = mantle cuticle, *dts* = dorsoterminal (osphradial) sense organ, *ht* = heart, *mc* = mantle cavity, *mg* = midgut, *mt* = spawning duct, *nsv* = ventral nerve cord, *pc* = pericardium, *pd* = pericardioduct, *pf* = pedal fold, *rs* = seminal receptacle, *src* = supra-rectal commissure; X-X = Fig. 10, Y-Y = Fig. 11.

nervous system (Fig. 11), no exact delimitation between rectum and pallial cavity can be defined. The secondary genital outlet discharges ventrally, immediately in front of the mantle cavity opening (Fig. 2 B).

Musculature: The body-wall musculature below the mantle consists of transverse, oblique, and loosely arranged longitudinal fibres. Ventrally and latero-ventrally, the submarginal-longitudinal musculature is formed by several distinct bundles, each embedded in a matrix ("Grundsubstanz"). The serial dorsoventral muscle bands are 1.5–2 mm apart. Other space between body wall and gut (q. v.) or pericardium is provided with a loose arrangement of transverse and other fibres along with connective tissue.

Sensory system: The cerebral ganglion measures 400 µm in length × 600 µm in breadth and 300 µm in height. A frontal and a slight terminal nick indicates its paired nature. Laterally, three or four (?) pairs of cerebral nerves run to the atrial sense organ, and the lateral, ventral, and buccal connectives leave close together termino-laterally. The first pair of lateral ganglia (120 × 100 µm) appears on each side at a distance of 200–400 µm. The elongated first ventral ganglia (600 × 200 × 170 µm) above the beginning of the pedal groove are

connected by two commissures, the anterior one very strong and in part medullary. On each side a strong nerve emerges antero-ventrally from the first commissure and runs laterally to the pedal pit. The buccal connectives are in part medullary (elongate ganglia?); from them a nerve to the anterior pharynx emerges. Subsequently, the connectives run lateral to the anterior foregut and down to the outlets of the glandular organs, where they join below the radula sheath. There are nerves to the outlets themselves, but no distinct buccal ganglia were found. The suprarectal commissure runs among the diverticula of the mantle cavity (Fig. 11).

The number of dorso-terminal (osphradial) sense organs varies. Specimen NS 22885 has a single organ innervated by four small and two larger nerves. The other sectioned specimen possesses four sense organs, one behind other; each is provided with one to four nerves. The preoral or atrial sense organ is delimited by a horseshoe-shaped, 350–500 µm wide ciliary tract. Posteriorly this tract bends dorsally to form bulges or folds which do not unite in front of the anteriormost point of ciliation. The atrial papillae are short and clustered in groups of 5–9 elements.

Alimentary tract: The mouth opens posterior to the dorsal folds of the atrial ciliated tracts (common atrio-buccal opening). This region and the adjacent pharyngeal portion appear to be capable of considerable expansion and contraction by musculature and blood pressure. There are dense muscle fibres but no distinct buccal sphincter exists. A large transverse pharyngeal bulge separates a blind dorsal space from the buccal cavity. It continues on each side of the pharynx as a fold leading midventrally to the openings of the foregut glands. The lateral folds appear to be due to hydrostatic pressure, and are not a constant structure. The pharynx itself is a wide space filling most of the body cavity of that region. Posteriorly it is attached to the body wall by muscle fibres and connective tissue. The pharyngeal epithelium is uniform and provided with a weak cuticle. Approximately at the midpoint of the pharynx are the ventral openings of the foregut glands followed by the radula.

The two ventral foregut glandular organs lead into tube-like outlets 2000 µm apart. Into each of these ducts of pharyngeal epithelium a gland opens on a small, approximately 2 mm long papilla. Both glands themselves are of epithelial nature and are surrounded by a weak sheath of musculature (type C in SALVINI-PLAWEN, 1978, 1985). The radula is situated above the region where the papillae open into the outlets (Fig. 6). The position of the radula sheath is unusual as it takes an anterior-posterior to posterio-dorsal course (see Fig. 2 A): the free teeth thus protrude into the pharynx somewhat behind the sheath itself. There is no subradular pocket (ventral radula sac). The radula consists of a 150–200 µm wide, laterally thickened band (pre-ribbon, Fig. 13 B) with about 25 rows of distichous hooks, 70–80 µm apart; these teeth are up to 250 µm long, with six median denticles each (Fig. 13 A). As documented in *Aesthoherpia* (SALVINI-PLAWEN, 1988: 312–313 and 356–358), there is a direct structural continuity between the interconnecting band (pre-ribbon) and the protruding teeth (Figs. 7 and 13).

The transition of the pharynx to the midgut is recognized by histological features: there is only a slight change in dimension and no constriction. The

Fig. 3. Living specimen of *Epimenia arabica* (NS 22060; type), about 16 cm long and darkened in air, together with contracted *Scleronephthya corymbosa*.

midgut has a thin epithelium with densely arranged, short, branched diverticula (Fig. 9; "villi" *sensu* BABA, 1940 a). Midventrally the diverticula are few and small, and dorsally there is the usual ciliated tract. All cells contain several granular bodies and/or vacuoles. The midgut is surrounded by a weak muscularis and is a consistent 0.4–1.2 mm from the body wall (see *E. verrucosa* in BABA, 1940 a: Figs. 1–3). Accordingly, the dorsoventral musculature causes only slight ventrolateral constrictions ("outpouchings") every 1.5–2 mm. The dorsal ciliated tract is wide and formed of high, cylindrical cells. Posteriorly the midgut diminishes in diameter (as it passes the pericardium and the spawning ducts), and the dorsal ciliation spreads out to form the rectum. Due to the postpericardial diverticles and the position of the suprarectal commissure, no exact delimitation between hindgut and mantle cavity (q. v.) is recognizable.

Circulatory system: The heart is in its entirety an invagination of the pericardium and is dorsally delimited by the pericardial musculature or, anteriorly, by the subintegumental musculature. The single atrium joins the voluminous ventricle obliquely. The ventricle connects with the mediodorsal sinus, which runs from between the gonads to the cerebral region where it opens. The muscle fibres of the dorsoventral system delimiting the ventral sinus are weak.

There are two types of blood cells, viz. elongated-oval to lacrimous, slightly light-refracting elements (17–25 µm × 5–8 µm) and round to oval granulocytes (Ø 5–11 µm).

Reproductive system: The medial walls of the paired, hermaphroditic gonad generate the yolky eggs which attain a diameter of 300–350 µm. Each sperm cell possesses a rod-like headpiece (10–13 µm) and a long tail. The ciliated gonopericardial ducts are short and fuse medioventrally as they pass into the voluminous, elongate pericardium. The pericardium is weakly ciliated throughout and in the studied animals contains passing eggs. It continues posteriorly in paired "horns" which bend into the pericardioducts (Fig. 10). The pericardioducts have a regularly folded, strongly ciliated epithelium surrounded by musculature. They join the spawning ducts anteriorly. At each junction there opens a bundle of six short-necked receptacula seminis (400–800 µm × 400–500 µm). The spawning ducts are spacious and lined with high prismatic gland cells. They are fused for the posterior fourth of their course (Fig. 11). Terminally, the epithelium becomes simple and ciliated, forming a short outlet.

2. Habitat and feeding

The *Epimenia arabica* specimens from the three localities (Fig. 1) attain a maximum size of 21 × 1 cm and feed on the alcyonacean coral *Scleronephthya corymbosa* VERSEVELDT & COHEN (1971), which generally occurs at depths between two and five meters (Fig. 4). This coral species is very often found attached upside down on overhanging reef substrata mainly in underwater caves. In some Red Sea localities, *S. corymbosa* forms a monospecific, dense coverage in mats of a few square meters, with colonies reaching a height of 20–25 cm. Very often the colonies occur in clear reef water with strong tidal currents. *Epimenia arabica* specimes are difficult to find while diving since they are hidden by the dense branches of the alcyonaceans. The present *E. arabica* were found while sorting out the *Scleronephthya* colonies. Nevertheless, in a recent field trip to the coral reefs of Ras Muhammad, southern tip of Sinai, careful underwater examination of *S. corymbosa* patches revealed additional individuals of *E. arabica* foraging *in situ*.

Discussion

1. Systematics

Only one species of *Solenogastres* has been previously described from the Red Sea, viz. *Forcepimenia protecta* SALVINI-PLAWEN, 1969. It was recorded in the Strait of Gubal at the southern end of the Gulf of Suez off Al-Ghardaqa/ Hurghada, Egypt (Fig. 1) at 30 m depth. This small species (2 mm), with distichous radula and ventral foregut glands of type A, belongs to the *Cavibelonia-Pararrhopaliidae* and is quite different from the specimens described here (cf. SALVINI-PLAWEN, 1969, 1978).

The thick cuticle and multi-layered hollow needles (Fig. 12) place the present animals in the order *Cavibelonia;* the distichous radula, the ventral foregut glands with epithelial arrangement of glandular cells (type C), and the presence of several receptacula seminis on each side define them as *Epimeniidae* (cf.

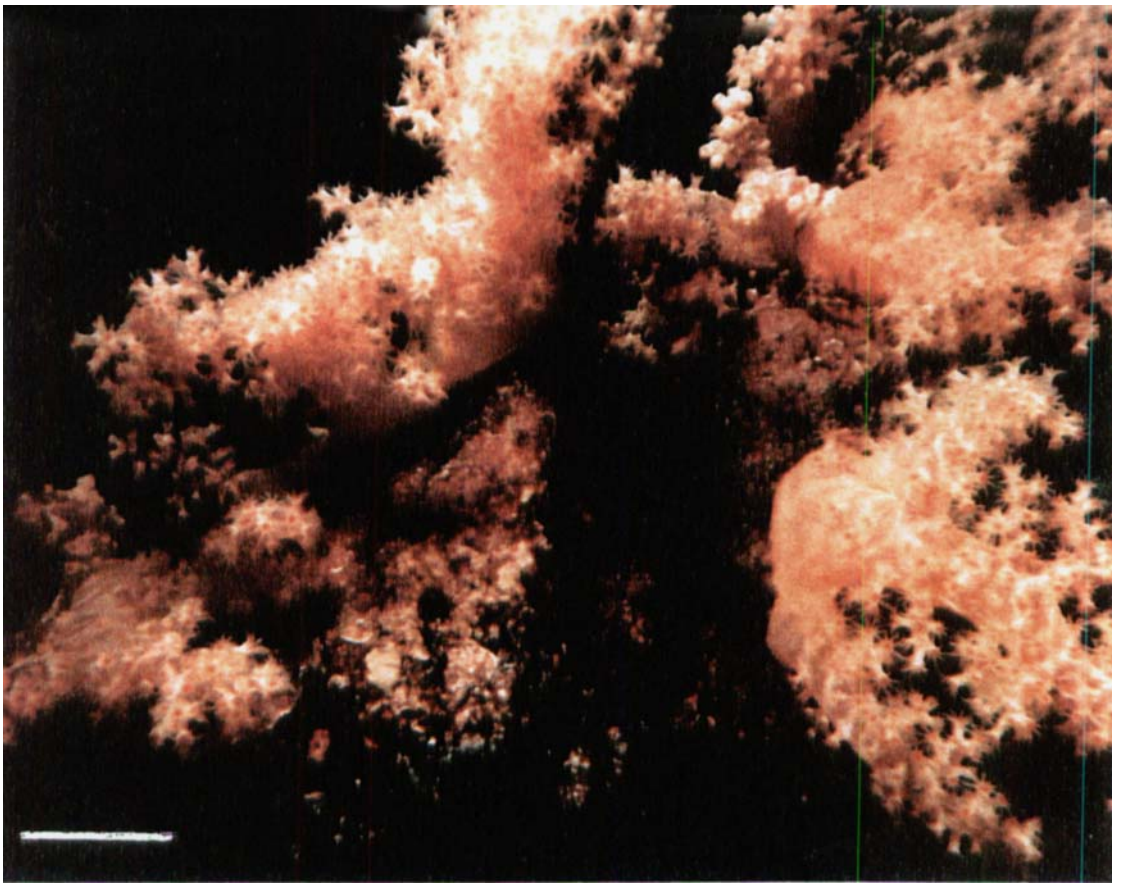


Fig. 4. Living colonies of *Scleronephthya corymbosa (Alcyonacea);* bar = 20 mm.

SALVINI-PLAWEN, 1978). The currently known single genus *Epimenia* NIERSTRASZ is characterized by a common atrio-buccal opening, by a terminal sense organ, by midgut pouches, by a single, fused secondary genital opening, and by the absence of copulatory stylets as well as of respiratory plicae. Accordingly, the present species likewise belongs to *Epimenia,* which includes four species, viz. *Epimenia australis* (THIELE, 1897) from the Sea of Timor, *E. verrucosa* (NIERSTRASZ, 1902) from Indonesia and Japan, *E. ohshimai* BABA, 1940 a, b from Japan, and *E. (?) vixinsignis* SALVINI-PLAWEN, 1978 from the Ross Sea (Antarctic). All these species are of large size when mature, while *E. verrucosa* holds the record in length among the *Solenogastres,* attaining a maximal size of 30 × 1 cm (BABA, 1939).

Epimenia arabica is clearly distinguished from other *Epimenia* species by several characters: (1) The tubular outlets of the foregut glands are far anterior to the radula (which coincides with *E. australis* but is in contrast to *E. verrucosa, E. ohshimai,* and *E. vixinsignis*). (2) The diverticula elaborated in the mantle cavity are unique; the capacious, incompletely paired, dorsal chamber of the mantle cavity in fully mature *E. verrucosa* (see BABA, 1940 a) has a different configuration. (3) The size and particular shape of the radula (Fig. 13) differs from the other species (but not including *E. verrucosa*). (4) There is a significant relation between body size (which parallels maturity) and the number of

receptacula seminis. This excludes *E. arabica* from conspecifity with one of the already known species: even if of smaller body size (*i. e., E. verrucosa* 3–9.8 cm, *E. australis* 9 cm, *E. ohshimai* 9–12 cm), they all possess more than 2 × 6 receptacula (cf. THIELE, 1902: 255–261; NIERSTRASZ, 1902: 14–18; BABA, 1939, 1940 a, b). (5) The external appearance differs in colour and/or cuticular thickenings: only *E. verrucosa* also possesses 'warts', yet it is generally rusty or dark brown with blue markings. Finally (6), the geographical distribution also underlines the specific independence of *Epimenia arabica* spec. nov.

The name refers to the Roman term for the Red Sea, viz. to the *sinus arabicus*.

2. Biology

Little direct information is available on feeding of *Solenogastres in situ*. An epizoic habit does not necessarily infer nourishment on the hypobiont (as discussed in SALVINI-PLAWEN, 1981: 379/385). The above observation on foraging, however, is supported by the presence of a piece of the *Scleronephthya* colony in the buccal opening of the type specimen (NS 22060; Fig. 5). Moreover, a fairly intact portion of an alcyonacean prey was found in the pharynx of one of the sectioned animals (NS 22885; Figs. 8–9). In addition, the anterior midgut of this specimen contains numerous warty, straight or curved sclerites (spindles) measuring between 300 µm × 30–50 µm (without warts) and 1000 µm × 90 µm;

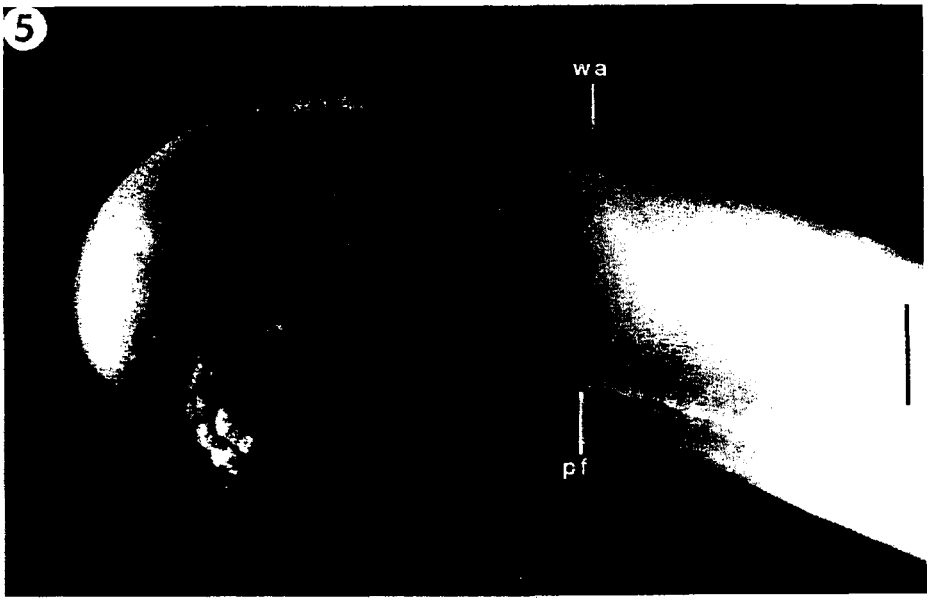


Fig. 5. Anterior end of preserved type specimen (NS 22060) of *Epimenia arabica* with swallowed portion of *Scleronephthya corymbosa* (see Fig. 3). *pf* = pedal groove, *wa* = wart-like thickening of mantle cuticle; bar = 3 mm.

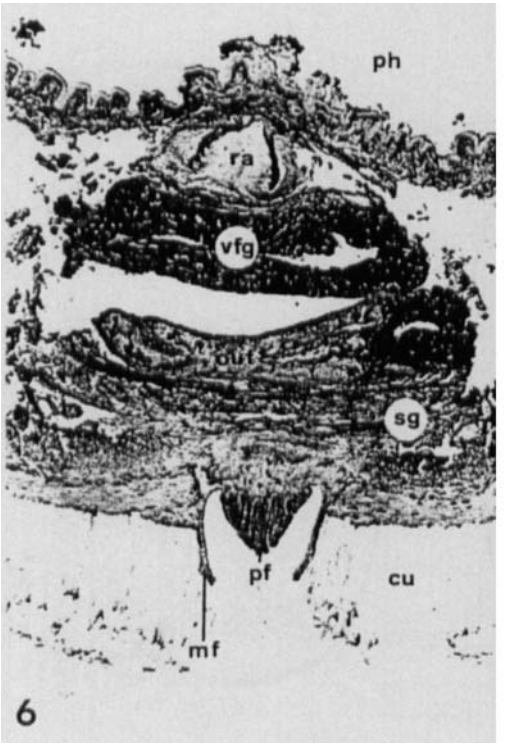
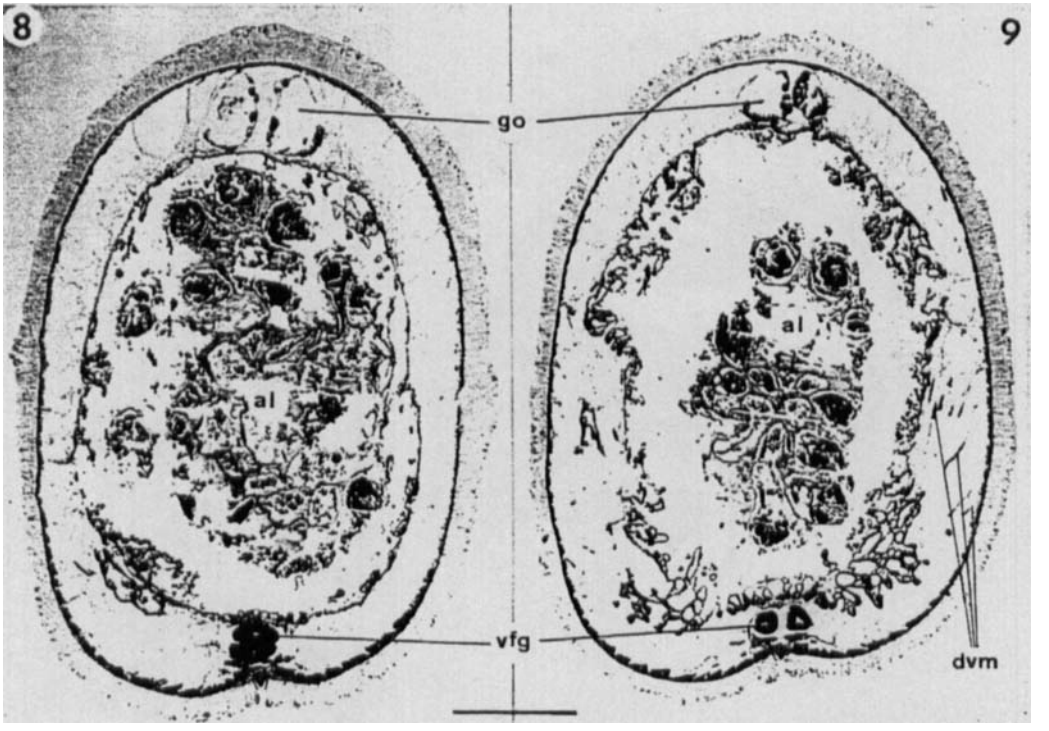


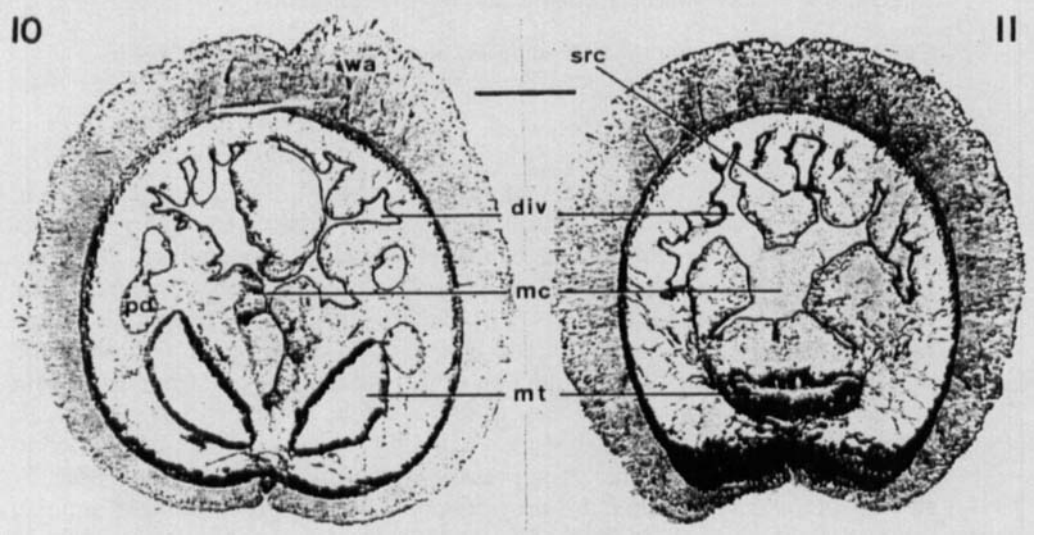
Fig. 6. Cross section through radula region of *Epimenia arabica* (NS 22060). *cu* = mantle cuticle with embedded spicules, *mf* = mantle fold, *out* = outlet of foregut gland, *pf* = pedal folds, *ph* = pharynx, *ra* = radula in sheath, *sg* = sole glands, *vfg* = foregut gland.

Fig. 7. Cross section through radula sheath (photo upside down for comparison with Fig. 13 A) of *Epimenia arabica* (NS 22060). *pr* = pre-ribbon in direct continuation with the teeth, *vfg* = foregut gland.

these coincide with the sclerites of *Scleronephthya corymbosa* (cf. Fig. 9 in VERSEVELDT & COHEN, 1971). Both observations fit the statements by BABA (1940 a: 161) on *E. verrucosa* in which freshly-taken specimens were often packed with a voluminous piece of the prey *(Nephthya* and *Dendronephthya)*. In contrast to the supposed food-uptake of the latter species by bringing the radula to the foremost end of the protruded pharynx and cutting off a portion of the prey (BABA, 1940 a: 161), such function of the radula in *E. arabica* must remain doubtful. It is fairly small with respect to the extent of the pharynx, the size of the whole animal, and the size of the engulfed prey, and thus no such function can be credited to the radula. The present species probably nourishes itself by ripping off and swallowing the prey fragments by muscular foregut actions, rather than by feeding with help of the radula. The latter may, however, have a pushing function for the transport of prey within the pharynx. The differences in the bucco-pharyngeal configuration encountered in the two sectioned specimens (see p. 144) indicate a flexible foregut and support this interpretation.



Figs. 8–9. Cross sections (1000 µm apart) through anterior body region at beginning of midgut (out of picture in Fig. 2 A) of *Epimenia arabica* (NS 22885) showing swallowed piece of *al* = alcyonarian colony; *dvm* = dorsoventral musculature, *go* = gonad, *vfg* = ventral foregut gland; bar = 2 mm.



Figs. 10–11. Cross sections through posterior body of *Epimenia arabica* (NS 22885) corresponding to lines X-X and Y-Y in Fig. 2 B. *div* = diverticula of mantle cavity *mc*, *mt* = spawning duct, *pd* = pericardioduct, *src* = suprarectal commissure, *wa* = wart-like thickening of mantle cuticle; bar = 1 mm.

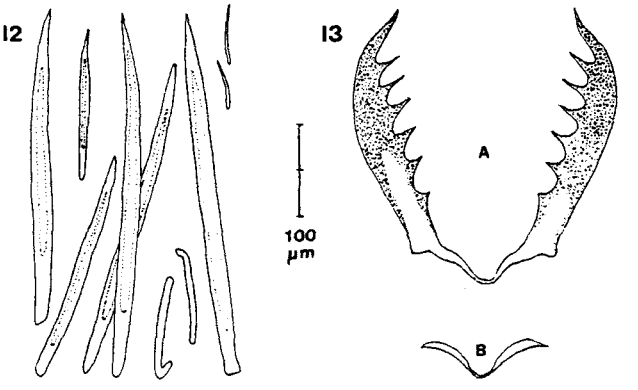


Fig. 12. Mantle spicules of *Epimenia arabica*.

Fig. 13. Radula of *Epimenia arabica*: A. reconstruction of one transverse row of teeth (cf. Figs. 7 and 8); B. cross section through continuous radula band (pre-ribbon).

The pharynx of one sectioned specimen (NS 22885) contains dissolved, granular material (chyle). Amongst it, however, an intact errant polychaete of 3 mm length is preserved (it shows about 25 segments with uniramous parapodia including long vermiform dorsal and short ventral cirri); this underlines the swallowing uptake of food. In contrast to the findings in most cnidariavorous species, where the ingested nematocysts remain fully intact (cf. SALVINI-PLAWEN, 1972, 1981), no distinct nettle capsules were discerned in the gut of either sectioned specimen. *E. arabica* may thus be one of few cases in which nematocysts become dissolved and digested (SALVINI-PLAWEN, 1988: 316).

E. arabica has only been found together with *S. corymbosa* at 2–5 m depth but never among other Red Sea coral species such as *Scleronephthya lewinsohni* VERSEVELDT & BENAYAHU (1978), a congener inhabiting in deeper waters in 55–82 meters. Therefore, at least in the studied reef, we suggest a species-specific association between *E. arabica* and its prey (hypobiont/host) alcyonacean *S. corymbosa*. No detailed investigations of the octocorallian fauna from other regions of the Red Sea are known. It is, however, expected that *Epimenia arabica* will be found with *Scleronephthya corymbosa* in other Red Sea reefs.

Summary

Investigations on the *Octocorallia* fauna off the Sinai Peninsula led to the finding of the new solenogaster *Epimenia arabica*. This large-sized representative fits well into the generic definition of *E. australis* (Sea of Timor) and *E. verrucosa* (Indonesia – Japan), but is distinguished from them in external appearance, the position of the pharyngeal opening of the foregut glands, the elaboration of the mantle cavity, and geographical provenance. Due to the association with the alcyonacean *Scleronephthya corymbosa* from shallow waters of the Red Sea, but not with the deeper occurring *S. lewinsohni* or with other corals, feeding could be confirmed by ingested portions of the prey and *in situ*. *Epimenia arabica* thus inhabits the shallowest depths of all *Solenogastres* recorded to date. The geographical distribution might well include the coral reefs of the entire Red Sea.

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