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Four new species and three new records of benthic ctenophores (Family: Coeloplanidae) from the Red Sea

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Abstract During 2012–2013 we surveyed the benthic ctenophore fauna of the Gulf of Aqaba, Red Sea. Four new species, three new records and one known species of benthic ctenophores (family Coeloplanidae) were discovered living as episymbionts on various invertebrates and algae: (1) *Coeloplana loyai* n. sp. (on the mushroom corals *Herpolitha limax* Esper, 1797 and *Ctenactis echinata* Pallas, 1766), (2) *Coeloplana yulianicorum* n. sp. (on the soft coral *Sarcophyton glaucum* Quoy and Gaimard, 1833), (3) *Coeloplana huchonae* n. sp. (on the stems of *Dendronephthya hemprichi* Klunzinger, 1877), (4) *Coeloplana fishelsoni* n. sp. (on colonies of *Xenia umbellata* Lamarck, 1816 and *Paralemnalia* Kukenthal, 1913), (5) *Coeloplana punctata* Fricke, 1970 and (6) *Coeloplana lineolata* Fricke, 1970 – both are new records in the Red Sea (found on colonies of *S. glaucum*), (7) *Coeloplana bannwarthi* Krumbach, 1933 on the spines of the sea urchin *Diadema setosum* Leske, 1778, and (8) *Vallicula multiformis* Rankin, 1956, another member of the family, was recorded for the first time from the Red Sea from brown algae, *Sargassum* seaweed and the holothurian *Pearsonothuria graeffei* Semper, 1868. All four new species of benthic ctenophores are different from other known *Coeloplana* species by their host identity, color, and color pattern. The documentation of *V. multiformis* in the Gulf of Aqaba , Red Sea is a remarkable extension of its geographic distribution, which until now was only reported from the Atlantic and Pacific Oceans. These findings demonstrate the great potential of discovering new species of this understudied group, especially in coral reef ecosystems.

Keywords Platyctenida · Benthic ctenophores · Coeloplanidae · *Vallicula* · Taxonomy · Coral ectosymbionts

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Introduction

Platyctenes (order: Platyctenida) are dorso-ventrally compressed ctenophores. Most ctenophores from this order have secondarily lost the characteristic ctene rows of the order in the adult stage or may not have them at all (Komai 1922). There is only one genus of benthic ctenophores that has ctene rows as an adult – *Ctenoplana* Korotneff, 1886. The order Platyctenida is composed of five different families (Coeloplanidae, Ctenoplanidae, Tjalfiellidae, Lyroctenidae, and Savangiidae), with the Coeloplanidae being the richest in species (Mills 2014). Although Platyctenes resemble nudibranchs and flatworms, they can be distinguished by their thread-like, branched, retractile tentacles. Most species from the family Coeloplanidae are commensal epibionts and live in close association with diverse groups of invertebrates (e.g., octocorals, echinoderms, ascidians) and seaweeds (except *C. meteoris* Thiel, 1968, which dwells on the sediment, *C. mesnili* Dawydoff, 1938 and *C. tattersalli* Devanesen and Varadarajan, 1942, which were collected from the plankton). Yet, the nature of the symbiosis has never been studied and thus is unclear. The degree of specificity between benthic ctenophore species and their hosts is used as a useful taxonomic character. Unlike planktonic ctenophores that reproduce sexually, benthic ctenophores are also known to reproduce asexually by excising fragments from their

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body that can regenerate and form an entire animal. While benthic ctenophores are highly modified compared to their planktonic ancestors of the order Cydippida (Podar et al. 2001), they retain many basic features of those ancestors, especially in their characteristic cydippid larval form.

Traditionally, the taxonomy of benthic ctenophores relies on several morphological characters, including the identity of their hosts. These characters include coloration and pattern, number and arrangement of aboral papillae, maximal length along the tentacular axis, location and shape of tentacular sheath, presence of oral lappets and an oral groove (Gershwin et al. 2010; Matsumoto 1999; Matsumoto and Gowlett-Holmes 1996; Rankin 1956). Some of these characters have been shown to be controversial as they tend to change pattern, shape, and number between live versus fixed specimens, even in the same individual, and also depend on the individual state (e.g., relaxed versus contracted) and environmental conditions (e.g., oxygen level in the surrounding water). For example, Gershwin et al. (2010) reported that live specimens of *Coeloplana mellosa* have 20 aboral simple papillae, while fixed specimens have more than 100. In addition, although color pattern has been useful for distinguishing between species of benthic ctenophores, these pigments are lost post fixation, making it challenging to describe fixed museum samples.

To date, there are 29 described species (including the two spp. varieties of *C. agniae* and the three spp. varieties of *C. gonoctena*) in the family Coeloplanidae. These species belong to two different genera, *Coeloplana* Kowalevsky, 1880 and *Vallicula* Rankin, 1956 (Mills 2014). *Coeloplana* is more speciose compared to the other genus, *Valiculla*, which contains only one species. *Vallicula* differs from *Coeloplana* mainly by the presence of an additional cross-piece in the tentacle sheath, making this structure resemble an anchor (Rankin 1956).

Prior to this study, there were only two known species of benthic ctenophores from the Red Sea: (1) *Coeloplana bannwarthi* Krumbach, 1933 which was described from the Gulf of Suez and was found on the spines of the sea urchin *Diadema setosum* (Krumbach 1933) and also reported from the Jordanian coast of the Gulf of Aqaba (Hulings 1989); and (2) *Coeloplana metschnikowii* Kowalevsky, 1880, described from the Suez canal (near Al-Tur), living on the seagrass *Zostera*.

The present study offers a comprehensive description of coeloplanid taxonomic identification, the first survey of the benthic ctenophore fauna in the Red Sea and a first compilation of the species list in the area.

Materials and methods

Collection and observation

Benthic ctenophore species were collected during 2012–2013 from various invertebrates and algae by scuba diving in three sampling sites along the Israeli shore of the Gulf of Aqaba (29°30′ N, 34°56′ E): (1) North Oil Jetty – NOJ, (2) Underwater Observatory – UO, (3) Interuniversity Institute for Marine Sciences - IUI (Fig. 1). Some specimens were collected together with their hosts, and later dislodged from them in the lab using a pipette with a gentle stream of water. In other cases, the ctenophores were dislodged from their host in situ using a small pipette. Sampling was done mainly at night, as most benthic ctenophore species were easier to locate due to their extended tentacles and better contrast with the dark background water. Each ctenophore encountered was photographed in situ using a Nikon D-90 camera enclosed in a Hugyfot (TM) housing. For each specimen collected, the date, site, depth, and host were registered. Due to the expected difficulties inherent in morphological examination of fixed material, each collected live specimen was inspected in the lab and photographed using a high-resolution camera mounted on a stereoscope. The identification of species was conducted based on all existing Coeloplanidae literature.

Fixation

Following identification and documentation, animals were given museum catalog numbers and were preserved in 4 % (v/v) formalin in filtered seawater and later transferred to 70 % EtOH. Prior to fixation, ctenophores were relaxed, allowing them to fully extend their bodies, using 2.5 % (m/v) $MgCl_2$ in filtered sea-water. Specimens were in good state even after 2 years post fixation. In addition, some whole specimens were preserved in 95 % EtOH for future molecular research, as well as in 2.5 % Glutaraldehyde for electron microscopy.

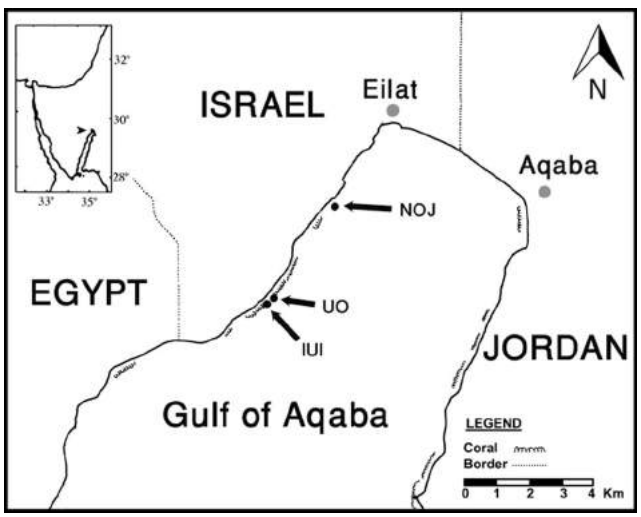

Fig. 1 Map of collection sites: North Oil Jetty (NOJ), Underwater Observatory (UO), Interuniversity Institute for Marine Sciences (IUI)

Scanning electron microscopy (SEM)

Ctenophore samples preserved in 2.5 % Glutaraldehyde underwent dehydration through a graded series of ethanol (30 to 99 %), critically point-dried with liquid CO_2 and then gold-coated. Ctenophores were viewed under a JEOL JSM 840a SEM (Tokyo, Japan) at 25 kV.

Results

Systematic account

Phylum Ctenophora Eschscholtz, 1829

Class Tentaculata Eschscholtz, 1825

Order: **Platyctenida Bourne, 1900**

Family: **Coeloplanidae Willey, 1896**

Diagnosis: Creeping or sessile ctenophores, compressed in oral-aboral axis. Adults lack comb rows, which are present only in the cyddipid larval stage. Two pinnate tentacles with numerous tentilla branching on their ventral side, with colloblasts on their surface. Each tentacle extends from and retracts into a tentacular sheath. Meridional canals are branched and anastomosed. Pharynx is permanently everted. Body length < 6 cm. When resting, the outline is roughly oval, longer in the tentacular axis. However, the shape is extremely fluid, changing by local advances and retractions of the margins. When creeping, the animal becomes elongated and flatworm-like. Statocyst located on the aboral side near the midpoint of the body, appearing as a tiny white granule. Aboral papillae, which are out-growths of the gastro-vascular canals, are usually present. An oral groove along the tentacular axis may be present on the oral side and may be used to form temporary "chimneys". The family comprises two genera: *Coeloplana* and *Vallicula*.

Genus: ***Coeloplana*** **Kowalevsky, 1880**

Diagnosis: Possess the features of the family. *Coeloplana* species have high specificity to their hosts. Tentacle sheath is flask-shaped in aboral view.

Coeloplana loyai **Alamaru and Brokovich, n. sp**.

Material examined: Eilat, Israel, Gulf of Aqaba, Red Sea (Fig. 1). Holotype: TAU-CO35558 (sampled on September 5th 2012 at 6 m depth from the aboral side of the coral *Herpolitha limax* Esper, 1797 at the reef in front of the underwater observatory (UO), preserved in 4 % formalin and later transferred to 70 % EtOH), Paratype 1: TAU-CO35559 (sampled on September 5th 2012 at 6 m depth from the aboral side of *H. limax* coral at the reef in front of the underwater observatory, preserved in 4 % formalin and later transferred to 70 % EtOH). Paratype 2: TAU-CO35560 (sampled on September 5th 2012 at 6 m depth, several specimens on their coral host, *H. limax*, fixed in 4 % formalin). All types were deposited at The National Collections of Natural History at Tel-Aviv University, Israel. In addition, ten specimens collected by A.A. and E.B. were inspected for size measurements. These samples were fixed in 70 % EtOH and later sacrificed for molecular analysis.

Type locality: Eilat, Israel, Gulf of Aqaba, Red Sea (Fig. 1): 29°30′13.27″N, 34°55′07.50″E.

Etymology: Named in honor of Prof. Yossi Loya, a world-renowned researcher of coral reefs.

Diagnosis: Found on mushroom corals of the genera *Herpolitha* and *Ctenactis*. Transparent cream-colored with light-brown spots, making it look mottled. Unique ruff-like structure surrounding the statocyst on the aboral side may be seen using a stereoscope. Oral groove and oral lappets not apparent.

Description: This is a relatively large *Coeloplana* species, with individuals collected ranging in maximal length between 30–40 mm along the tentacular axis (n=10). Characteristic shape, with the features of the family. Transparent cream-colored with light-brown spots composed of tiny granular pigments, making it appear mottled (Figs. 2 and 3). When the tentacles are retracted into their tentacle sheaths, they form a white line along the tentacular axis, seen as a black line when backlit (Fig. 2b, c). This species was not observed to extend its tentacles in situ either during the day or at night. No apparent papillae observed on the aboral side in situ. However, in the laboratory, after prolonged duration in still water, papillae were observed along the meridional canals (Fig. 3b). *Coeloplana loyai* n. sp. has a unique structure resembling a ruff that surrounds the sensory organ (Figs. 2c and 3). The length of the ruff ranges from 4.5–8.2 mm along the tentacular axis (n=4 measured ctenophores). This structure was present in all specimens examined and is not known from other benthic ctenophore species. The statocyst resembles a granular mass, with a diameter of ~55 μm, located at the center of the aboral sensory organ (Fig. 4a). Due to the transparency of this species, the meridional canals and the reticulations of the gastro-vascular system are clearly visible (Figs. 2c, 3b and 4). As in ordinary planktonic ctenophores, there are eight meridional canals: two tentacular canals, which later split into two canals that surround the tentacle sheath (sub-tentacular canals); and four sub-pharyngeal canals, which are located exteriorly to the sub-tentacular canals (Fig. 3). Oral groove and lappets not present. Extremely thin and delicate species with a tendency to tear when handled.

Reproduction/developmental biology: In samples collected in September 2012, both female and male gonads were observed (Figs. 3a, b, and 4c). The ovaries develop along the meridional canals and the sperm masses develop on both sides of the tentacular sheath and are brownish in color (similar structures were described by Komai 1922). In some of these September specimens, brooded eggs were found on the edges of the oral side, still surrounded by the egg membrane (Fig. 4d).

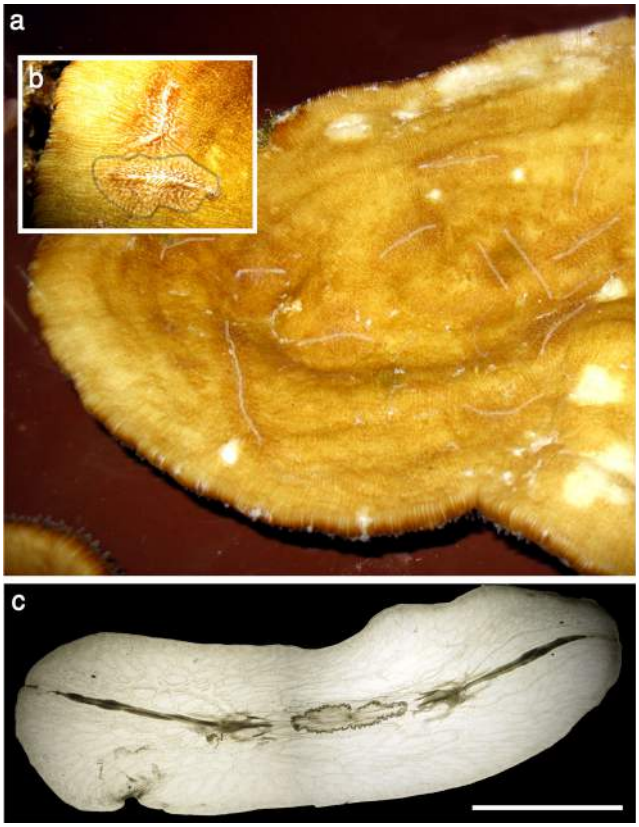

Fig. 2 *Coeloplana loyai* n. sp. from the Gulf of Aqaba, Red Sea. **a** *C. loyai* n. sp. in situ on its host, the stony coral *Herpolitha limax*. The tentacular axis of each individual ctenophore has been highlighted in opaque white line in order to visualize the density of ctenophores on their coral host. **b** Close-up of two specimens showing the color pattern as seen in situ. The outline of one individual is marked in grey. **c** Aboral view of a live specimen ~40 mm in length (scale bar: 10 mm) photographed using rear light transmitted through the specimen. The ctenophore was sedated prior to photographing using cold $MgCl_2$ solution in a small petri dish

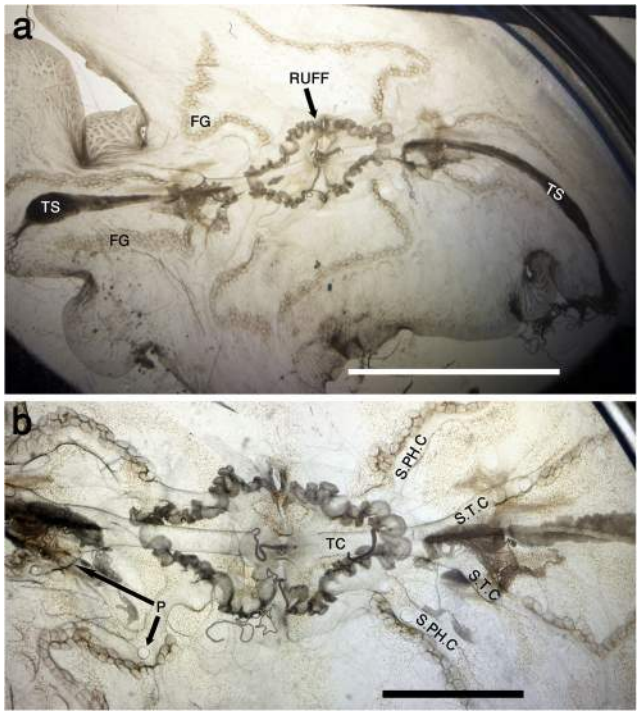

Fig. 3 Aboral view of a live specimen of *C. loyai* n. sp. **a** *Coeloplana loyai* n. sp. showing the unique ruff-like structure surrounding the aboral organ (marked by a black arrow) and the arrangement of female gonads (FG) full of eggs along the meridional canals (scale bar: 1 cm). **b** Close-up showing the canals of the gastro-vascular system, including the tentacular canal (TC), sub-pharyngeal canal (S.PH.C), sub-tentacular meridional canal (S.T.C)), papillae (P), and tentacles enclosed inside tentacle sheaths (TS) (scale bar: 25 mm). Sample preparation was the same as in photograph 2c. Papillae were not observed in normal conditions and protruded only after prolonged duration in a low-oxygenated environment

Distribution and habitat: *Coeloplana loyai* was observed in all three sampling sites between 1–20 m (Fig. 1). The ctenophores were found on the aboral side of the stony corals *H. limax* and *C. echinata*, but were more abundant on *H. limax* (Fig. 2). In most cases, a few individual ctenophores were observed on each coral host (Fig. 2). On rare occasions, a density of over 20 ctenophores was seen on one fungid host. Although the holotype and paratypes were not collected from *Ctenactis*, several other specimens were collected from *C. echinata* corals and inspected for their detailed morphology. During this research, we examined over 200 fungid polyps belonging to the most abundant mushroom coral species of the Gulf of Aqaba. However, *C. loyai* was found only on two species of mushroom corals and was relatively rare.

Ecology and behavior: This benthic ctenophore was never observed to occur on the oral side (upper side) of the mushroom coral polyps. Moreover, this species was not observed to extend its tentacles for feeding either during the day or at night (even though its tentacles were clearly visible when inspected

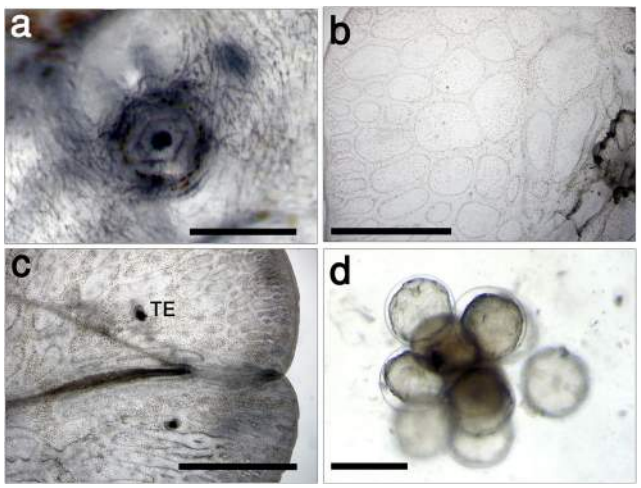

Fig. 4 *Coeloplana loyai* n. sp. **a** Aboral view of the sensory organ showing the granular statocyst in the middle, surrounded by the pole plates (scale bar: 400 μm). **b** Aboral view of the periphery of the animal showing the reticulations of the gastrovascular system, which later converge towards the central area into the main gastrovascular canals. (scale bar: 3 mm). **c** Aboral view showing developed testes (TE) (scale bar: 3 mm). **d** Embryos or fertilized eggs discovered in a specimen in September 2012 surrounded by a membrane (scale bar: 200 μm)

in the lab). Brownish pigmentation raised an hypothesis that this species may host algal symbionts, as does its coral host. However, inspection of specimens under UV light clarified that this was not the case.

Remarks: Although the general structure of *C. loyai* n. sp. resembles that of other *Coeloplana* species, this new species is distinguished from other *Coeloplana* species by several unique characters: (1) coloration pattern: transparent cream-colored with light-brown spots composed of tiny granular pigments, making it appear mottled; (2) a unique ruff-like structure surrounding the aboral sensory organ, which is not known in other *Coeloplana* species; (3) lack of aboral papillae when observed in situ or in well aerated conditions; (4) its host, *C. loyai* n .sp., is the first ctenophore species to be described from the stony corals *H. limax* and *C. echinata* belonging to the family Fungiidae. The association of benthic ctenophores with stony corals was first reported in Hoeksema et al. (2013). In addition to *C. loyai* described herein, Hoeksema et al. reported the association of an undescribed ctenophore species found on *Pleuractis moluccensis* and *Fungia fungites* from Payar Island (Malaysia), *Cycloseris costulata* from Sabah (Malaysia) and *Lithophyllon repanda* from South Sulawesi (Indonesia). Unfortunately, the fixation state of the samples from Malaysia and Indonesia made it impossible to describe them morphologically. Therefore, at this stage we cannot assign a valid name for them and it is not clear if these individuals are in fact *C. loyai*.

***Coeloplana yulianicorum* Alamaru, Brokovich and Loya, n. sp.**

Material examined: Eilat, Israel, Gulf of Aqaba, Red Sea (Fig. 1). Holotype: TAU-CO3571 (sampled on September 3rd 2012 at 8 m depth from a colony of the soft coral *Sarcophyton glaucum* at the reef in front of the underwater observatory (UO). Preserved in 4 % formalin and later transferred to 70 % EtOH). Paratypes: TAU-CO35572, TAU-CO35573, TAU-CO35574 (sampled on September 3rd 2012 at 8 m depth from a colony of the soft coral *Sarcophyton glaucum* at the reef in front of the underwater observatory. Preserved in 4 % formalin and later transferred to 70 % EtOH). Two additional samples (TAU-CO35575, TAU-CO35576), each containing five ctenophores, were also deposited. All types were deposited at The National Collections of Natural History at Tel-Aviv University, Israel.

Type locality: Eilat, Israel, Gulf of Aqaba, Red Sea (Fig. 1): 29°30′13.27″N, 34°55′07.50″E.

Etymology: Named after the parents of A.A., Yulian and Anica Alamaru.

Diagnosis: Found on the soft coral *Sarcophyton glaucum*. Color creamy-white with whitish spots and scattered pinkish-reddish dots. Twenty- four dorsal papillae in an X shape (5-7-7-5) surrounding the aboral sense organ. Another 12 papillae, six flanking each tentacular bulb, three on each side. Oral lappets and oral groove present.

Description: Color creamy-white with whitish spots (~500 μm in maximal diameter) and scattered pinkish-reddish dots (~85 μm in diameter), across the entire body on the aboral side (Fig. 5a, b, c). Individuals collected ranged in maximal length between 10.5 and 32 mm (n=23) along tentacular axis. Twenty-four dorsal papillae forming an X shape (asymmetric with 14 on one side and 10 on the other side) were identified in live specimens surrounding the sense organ (Fig. 5c, d). Another 12 papillae were identified, six flanking each tentacular bulb, three on each side (Fig. 5c). On the aboral side, pole plates are not visible, but the sense organ and the statocyst can be clearly seen under a light microscope (Fig. 5e). Reticulations of the gastrovascular system are clearly seen, with radial canals anastomosed, forming a network along the periphery of the animal. Statocyst diameter ~55 μm. Gonads were not observed. On the oral side, lappets and oral groove present and well defined (Fig. 5f). Pharyngeal folds are seen inside the oral opening (Fig. 5f). After fixation in Formalin, the specimens become opaque-cream color

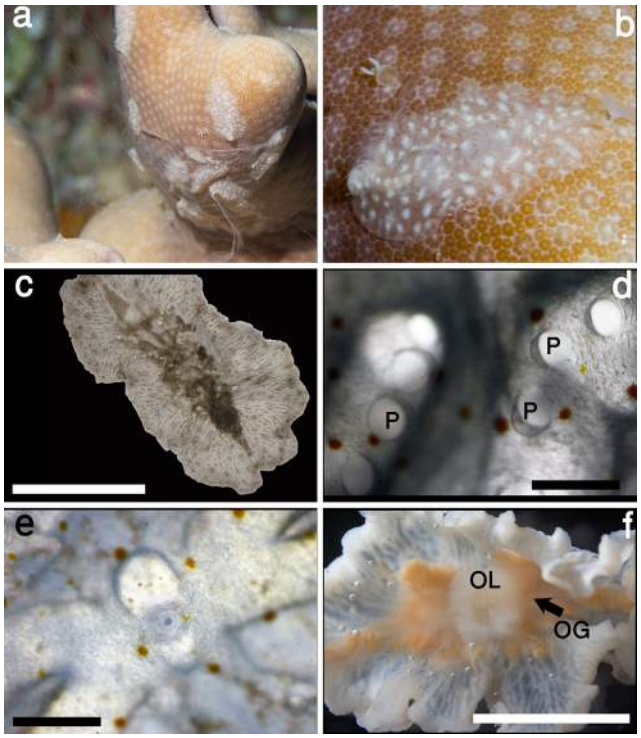

Fig. 5 *Coeloplana yulianicorum* n. sp. from the Gulf of Aqaba, Red Sea. **a** Ten specimens of *C. yulianicorum* n. sp. in situ on their host, the soft coral *S. galucum*, **b** in situ close-up of a single specimen of *C. yulianicorum* n. sp. showing the milky white spots and pink dot markings. **c** Aboral view of live specimen showing the x-shaped arrangement of papillae (scale bar: 1 cm). **d** Close-up of the aboral side showing the simple papillae protruding (scale bar: 500 μm). **e** Aboral view of a live *C. yulianicorum* n. sp. showing the aboral sense organ with the statocyst in the middle and the meridional canals (scale bar: 500 μm). **f** Oral view of a formalin-fixed specimen showing the oral lappets (OL) and oral groove (OG) parallel to the tentacles axis (scale bar: 0.5 cm)

(Fig. 5f), making the internal structure (e.g., gastrovascular system) and papillae challenging to observe, although the fixation was generally good (not like planktonic ctenophores that usually dissolve).

Distribution and habitat: This species is an epibiont found on the inner margins (underside) of the umbrella on colonies of the soft coral *Sarcophyton glaucum* down to a depth of at least 30 m. (Fig. 5a, b). It is one of the most common species of *Coeloplana* found in the Gulf of Aqaba, Red Sea.

Ecology and behavior: Usually, we found several individuals aggregating on each colony (feasibly a result of asexual reproduction, although not observed) (Fig. 5a). *Coeloplana yulianicorum* has two pinnate tentacles, extended both at night and during the day, to capture zooplankton (Fig. 5a). Tentacles seem to be extended farther at night, and may reach a length of at least 20 times that of the maximal animal length.

Remarks: This species differs from all other *Coeloplana* species by its coloration pattern and the identity of its host. To date, four other *Coeloplana* species are known to live on *Sarcophyton*: (1) *C. lineolata* Fricke, 1970, which has a unique patterns of lines parallel to the tentacular axis (2) *C. punctata* Fricke 1970, which is characterized by small green-yellowish dots, (3) *C. wuennebergi* Fricke, 1970, which has large red-violet spots, and (4) *C. mellosa* Gershwin, 2010, which in fact may be the same species as *C. punctata* (see discussion). Out of the four, it appears to be closest to *C. punctata*, which is commensal on *Sarcophyton* colonies and was described by Fricke (1970) from Madagascar. However, *C. yulianicorum* differs from *C. puncatata* Fricke, 1970 by the color of the dots (pink-red in *C. yulianicorum* versus green-yellowish in *C. punctata*), the presence of relatively large (~500 μm) whitish spots in *C. yulianicorum* and by the arrangement and number of papillae (Fig. 5a, b, c, Table 1).

***Coeloplana huchonae* Alamaru, Brokovich and Loya, n.sp.**

Material examined: Eilat, Israel, Gulf of Aqaba, Red Sea (Fig 1). Holotype: TAU-CO35566 (sampled on September 6th 2012 at 6 m depth from a colony of the soft coral *Dendronephthya hemprichi* at the reef in front of the underwater observatory (UO). Preserved in 4 % formalin and later transferred to 70 % EtOH. Paratypes: TAU-CO35567, TAU-CO35568, TAU-CO35569 (sampled on September 6th 2012 at 6 m depth from a colony of the soft coral *Dendronephthya hemprichi* at the reef in front of the underwater observatory. Preserved in 4 % formalin and later transferred to 70 % EtOH). A sample of several ctenophores with their coral host (TAU-CO35570) was also deposited. All types are deposited at The National Collections of Natural History at Tel-Aviv University, Israel.

Type locality: Eilat, Israel, Gulf of Aqaba, Red Sea (Fig. 1): 29°30′13.27″N, 34°55′07.50″E.

Etymology: Named in honor of Dr. Dorothee Huchon, phylogeny and molecular evolution expert, for her endless support, encouragement, and friendship to A.A.

Diagnosis: Found on the soft coral *Dendronephthya hemprichi* (Fig. 6a). Color opaque white with deep scarlet elongated (though small) markings (Fig. 6b, c). No apparent aboral papillae, no oral groove or oral lappets present.

Description: Color of live specimens is opaque white with deep scarlet elongated (though small) markings (Fig. 6b, c). Post fixation the ctenophores become opaque-yellowish with brown tiny markings. No apparent papillae on aboral side (Fig. 6b). Individuals collected ranged in size between 4.6-4.8 mm (n=4) maximal length along tentacular axis. Oral groove not present. Oral lappets visible on oral side, easily seen in fixed animals. When tentacles are retracted inside the tentacular sheath, they resemble white, flask-shaped pouches that are easily recognized on the coral host (Fig. 6a, b). When tentacles are extended, the tentacular sheaths form chimney-like structures (Fig. 6b). The statocyst (~45 microns in diameter) is composed of small granular structures and is located in the middle of the sense organ, between two fleshy plate-like structures (the pole plates) (Fig. 6c). Radial canals easily seen along the periphery of the animal. Gonads not seen.

Distribution and habitat: Found on the stems and branches of the soft coral *Dendronephthya hemprichi* (Fig. 6a). We found this species only on one large colony of *D. hemprichi*. On this colony, the ctenophores reached a density of ~100 specimens on a 20 cm stem.

Ecology and behavior: At night, the extended tentacles form a mesh between the coral branches. In the lab, the ctenophores extended their tentacles and rolled into a ball, making it challenging to measure and photograph them.

Remarks: This species differs from all other *Coeloplana* species by its coloration pattern and the identity of its host. Currently, there are only two other species of *Coeloplana* that were reported to live on *Dendronephthya* colonies: *Coeloplana bocki* Komai, 1920 and *Coeloplana anthostella* Song and Hwang, 2010. *Coeloplana bocki* differs remarkably from the new species found in the Gulf of Aqaba by its color pattern (Table 2). However, *Coeloplana huchonae* n. sp. resembles *C. anthostella* described by Song and Hwang (2010) from Korea. Nevertheless, the new species' scarlet markings are less than half the size of *C. anthostella's* markings and are elongated in shape, versus a star-like shape in the Korean species (Table 2, Fig. 6c, e, f). Moreover, the two species are found on different hosts (*D. spinulosa* and others in Korea versus *D. hemprichi* in the Red Sea) (Table 2, Fig. 6a, d).

***Coeloplana fishelsoni* Alamaru, Brokovich and Loya, n. sp.**

Material examined: Eilat, Israel, Gulf of Aqaba, Red Sea (Fig. 1). Holotype: TAU-CO35561 (sampled on September 6th 2012 at 6 m depth from a colony of the soft coral *Xenia umbellata* at the reef in front of the underwater observatory

Table 1 All known species of the family Coeloplanidae, including their morphological characters (size, color, aboral papillae, tentacle sheath location), based on the original descriptions of the species. In cases where additional descriptions, different from the originals, were reported in the literature, we added a citation next to the addition. Geographical distribution and identity of hosts is compiled based on all available literature. *As stated in the text, the validity of this species should be re-assessed

	Organism	Reported by	Host	Size in MM (no. of organisms examined)	Color	Oral Groove and lappets, aboral papillae and other characters	Distribution
1a	*C. agniae* Dawydoff, 1930	Dawydoff 1930c; Dawydoff 1938b	*Sinularia polydactyla* (Octocorallia)	Up to 60, usually 40–50 (?)	Clear milky white (or gray) with quite varied opalescent shades: yellow, pink, brown or even slightly purplish. brown , green, red , white, yellow tiny pigments may be present, never, however, forming well-defined stains.	4 distinct rows of 8–12 simple papillae each in an X-pattern through the statocyst, plus 3–4 each in 4 more rows, 2 flanking each tentacle bulb	Bay of Nhatrang, Gulf of Annam, Vietnam
1b	*C. agniae var. striata* Dawydoff, 1938	Dawydoff 1938b	*Sinularia polydactyla* (Octocorallia)	Same as *C. agniae*	The general color of the aboral face is the same as in *C. agniae*: very clear, yellowish-white, with different nuances among which dominates brown. But while coloring *C. agniae* is uniform, the aboral surface of the variety has a sharp longitudinal striation	Same as in *C. agniae*	Côn Sơn Island (previously named Paulo-Condor), south China sea, Vietnam
2	*C. anthostella* Song and Hwang, 2010	Song and Hwang 2010	*Dendronephthya spinulosa* and other Dendronephthyans (Octocorallia)	1–4 (many)	Milky white with many tiny deep scarlet star-shaped markings	Not observed	Jejudo Island, Korea
3	*C. astericola* Mortensen, 1927	Mortensen 1927; Dawydoff 1938b; Dawydoff 1955	*Echinaster luzonicus* (Asteroidea)	Up to 10 according to Mortensen. Up to 16 according to Dawydoff	Deep red or scarlet with large irregular spots of creamy-yellow. Another color morph has an inverse color pattern	4 crescentic rows of 4 simple papillae, emanating from the statocyst in a figure eight pattern	Ambon Island, Indonesia; Côn Sơn Island, south China sea, Vietnam; India; Great Barrier Reef, Australia
4	*C. bannwarthi* Krumbach, 1933	Krumbach 1933; Hulings 1989; Eeckhaut et al. 1997; Coppard and Campbell 2004; Current study	*Diadema* spp. (Echinoidea)	NA	Dark purple/brown	Not described	Gulf of Suez, Gulf of Aqaba, Red Sea; Singapore; Fiji
5	*C. bocki* Komai, 1920	Komai 1920; Komai 1922; Song et al. 2011	*Stereonephthya japonica*, *Dendronephthya spinulosa*, *D. dendricata* (Octocorallia), Hydroids, Algae, Echinoderms	5–15, rarely 30 (many)	Branching and anastomosing strip patterns that run along the tentacular axis, and may be dark vermilion, dark red, brick red, pinkish, orange or greyish. Song et al. added a blue striped color variant.	Not described (7–13 paratentacular; 4–8 simple papillae)	Misaki, Japan Munseom Island, Korea
6	*C. duboscqui* Dawydoff, 1930	Dawydoff 1930a; Dawydoff 1938b; Matthews 1954	*Pteroides* (Octocorallia) and *Hypnea* (Red Algae)	8–15 (many)	Intense orange or vermillion to orange. In Hawaii, yellowish-green	Not observed	Gulf of Siam, Thailand; Hawaii
7	*C. echinicola* Tanaka, 1932	Tanaka 1932		10–30 (?)			Seto, Japan

Table 1 (continued)

	Organism	Reported by	Host	Size in MM (no. of organisms examined)	Color	Oral Groove and lappets, aboral papillae and other characters	Distribution
			Toxopneustes pileolus (Echinoidea)		The aboral side is yellowish-brown with white dots. Periphery is green.	32 simple papillae, 8 larger, 24 smaller	
8	*C. fishelsoni* Alamaru, Brokovich and Loya	Current study	*Xenia umbellata*, *Paralemnalia* (Octocorallia)	4–9	Opaque white with numerous tiny white dot markings	Oral groove not present No apparent papillae	Gulf of Aqaba, Red Sea
9a	*C. gonoctena* Krempf, 1920	Krempf 1920; Krempf 1921; Dawydoff 1938b; Pople 1960	*Alcyonia krempfi and A. pahyclados* (Octocorallia)	20–50 (many)	Milky white or grey with brown circular spots surrounding the large aboral papillae	5 simple papillae in each of 4 rows forming an X-shape in a figure eight pattern with the distal most in each row larger	Coast of Annam, Vietnam
9b	*C. gonoctena var. natalensis* Pople, 1960	Pople, 1960	*Sphaerella krempfi* (Octocorallia)	Up to 10 (many)	Milky white or grey with one or two brown spots in the middle of the tentacular axis, between the tentacle sheath and sense organ	No large dorsal papillae from the parastomal canal. Up to 7 dorsal papillae in a single row from each paratentacular canal	Natal, South Africa
9c	*C. gonoctena var. rosea* Dawydoff, 1938	Dawydoff, 1938b	*Alcyonium* sp. (Octocorallia)	Up to 20 (12)	Uniformly intense pink. No spots present. Oral side white-grayish	Similar to *C. gonoctena*	Côn Sơn Island, south China sea, Vietnam
10	*C. huchonae* Alamaru, Brokovich and Loya	Current study	*Dendronephthya hemprichi* (Octocorallia)	4.6–4.8	Opaque white with deep scarlet elongated (though small) markings	No apparent aboral papillae and oral groove. Oral lappets present	Gulf of Aqaba, Red Sea
11	*C. indica* Devanesen and Varadarajan, 1942	Devanesen and Varadarajan 1942	NA	NA	Grey	8 papillae	Krusadai Island, Gulf of Mannar, India
12	*C. komaii* Utinomi, 1963	Utinomi 1963	*Cladiella digitulata* (Octocorallia)	5–15 (58)	Uniformly milky white or seashell pink with yellow tentacle bases	5–6 pairs of simple papillae	Sagami Bay, Japan
13	*C. krusadiensis* Devanesen and Varadarajan, 1942	Varadarajan 1934; Devanesen and Varadarajan 1942	*Pentaceros hedemanni* (Asteroidea)	28 (many)	Red	6–20 simple papillae	Krusadai Island, Gulf of Mannar, India
14	*C. lineolata* Fricke, 1970	Fricke 1970	*Sarcophyton* (octocorallia)	40–50 (many)	Transparent brown with lines parallel to the tentacular axis	60–70 papillae (9-7-7-9)	Madagascar
15	*C. loyai* Alamaru and Brokovich	Current study	*Herpolitha limax and Ctenactis echinata* (Hexacorallia)		Transparent cream-colored with light-brown spots, giving it a speckled appearance, tentacular axis white	No apparent papillae in normal state. Papillae may appear after prolonged duration in still water. Oral groove and oral lappets not apparent. Unique ruff-like structure surrounding the sense organ	Gulf of Aqaba, Red Sea
16	*C. mellosa* Gershwin, Zeidler and Davie, 2010	Gershwin et al. 2010	*Sarcophyton* (Octocorallia)	10–25 (4)	Whitish with hundreds of tiny brown dots. Close-up, body brownish with cream colored ectodermal reticulations	20 simple papillae arranged in an X-shape when alive. Preserved samples have over 100 papillae in 16 rows, 3 sizes and two types	GBR Townsville, Queensland, Australia
17	*C. mesnili* Dawydoff, 1938	Dawydoff 1938b	Planktonic/free living	NA	Transparent pale green with bright orange statocyst and papillae	12 simple orange papillae (2-4-4-2)	Gulf of Tonkin, Vietnam
18	*C. meteoris* Thiel, 1968		Free living on soft sediments	25–35 (?)			

Table 1 (continued)

	Organism	Reported by	Host	Size in MM (no. of organisms examined)	Color	Oral Groove and lappets, aboral papillae and other characters	Distribution
		Thiel 1968; Venkataraman et al. 2012			Clear with yellow-white reticulations covering body and red pigmentation around canals, tentacle sheaths and papillae	4 rows of simple papillae, 3–4 per row	Somalia; North Queensland Australia; India
19	*C. metschnikowii* Kowalevsky, 1880	Kowalevsky 1880; Haas 1942;	*Zostera* (Seagrass)	4–6 (1)	Grey on dorsal side, white on ventral side	Not described	Red Sea, near A-Tor; Jaffa,Mediterranean
20	*C. mitsukurii* Abbott, 1902	Abbott 1902; Abbott 1907b	*Melobesia* (red algae) and *Sargassum* (brown algae)	< 10, usually ~ 5 mm (?)	Brown to brownish yellow, with yellow white cells around margin and two bands of yellow around statocyst	4 curved rows of 6–8 papillae per row with 2–5 digitate processes, radiating around the sense organ in a figure eight (10–20 aboral papillae, each with digitate processes)	Misaki, Japan
21	*C. perrieri* Dawydoff, 1930	Dawydoff 1930b; Dawydoff 1938b	*Posidonia* (seagrass) or free living on rocks	Up to 10 (many)	Deep olive green with sepia spots, with narrow yellow orange margins: tentacles yellow-brown	10 simple papillae (2-3-3-2) Oral lappets present	Phú Quốc Island, Gulf of Siam, Cambodia
22	*C. punctata* Fricke, 1970	Fricke 1970	*Sarcophyton* (Octocorallia)	Ca. 30 (many)	Milky white with green yellowish dots	70–100 simple papillae (1012-12-10)	Madagascar
23	*C. reichelti** Gershwin, Zeidler and Davie, 2010	Gershwin et al. 2010	Variety of red and green algae and seagrasses	4–10 (6)	Transparent pale yellowish body with hundreds of ectodermal and endodermal green specks with frosty white cells on papillae and margins	8–20 large, branched, permanent papillae, plus 8 smaller cylindrical, ephemeral papillae midway to margins	GBR Townsville, Queensland, Australia
24	*C. scaberiae* Matsumoto and Gowlett-Holmes, 1996	Matsumoto and Gowlett-Holmes 1996	*Scaberia agardhii* (algae)	Up to 25 (many)	Solid dark orange or vivid red without spots of any kind	4 rows of simple papillae in a figure eight pattern and also along margins	Yorke Peninsula, South Australia
25	*C. sophiae* Dawydoff, 1938	Dawydoff 1938b	*Solenocaulon jedanensis* (Octocorallia)	10 (1)	Cadmium red with white spots	4 rows of 3–5 simple papillae. Oral groove present	Tourane Bay, Vietnam
26	*C. tattersalli* Devanesen and Varadarajan, 1942	Devanesen and Varadarajan 1942	Planktonic/free living	12 (many)	Translucent, suffused with green	8 simple papillae; sometime with secondary papillae which may appear branched	Krusadai Island, Gulf of Mannar, India
27	*C. thomsoni* Matsumoto, 1999	Matsumoto 1999	*Jania* (coralline algae)	Up to 10 (12)	Pale green or white with yellow white cells scattered over dorsal surface	Green morph has 16 papillae (8 rows of 2), 4 branched, other simple. White morph with 4 large permanent papillae and 12 small ephemeral papillae	Rottnest Island, Western Australia
28	*C. weilli* Dawydoff, 1938	Dawydoff 1938b	*Heterocentrotus mammillatus* (Echinoidea)	3–4 (?)	Pigmentless to deep chocolate brown	Lacking papillae	Réarn , Cambodia
29	*C. willeyi* Abbott, 1902	Abbott 1902; Abbott 1907b; Matthews and Townsley 1964; Gordon 1969; Tokioka 1969;	*Zostera*, *Caulerpa*, *Saragassum* (seagrass and algae) and *Echinothrix diadema*, *Echinothrix calamaris*,	10–60 (many)	Deep purple, red or orange fading to pink with white spots along the margins. Yellow blotches at the base of papillae	Simple or club-shaped papillae	Misaki, Japan; Turkey, Mediterranean; Hawaii; Pakiri, New-Zealand; Fiji

Table 1 (continued)

	Organism	Reported by	Host	Size in MM (no. of organisms examined)	Color	Oral Groove and lappets, aboral papillae and other characters	Distribution
		Coppard and Campbell 2004; Cavas and Yurdakoc 2005;	*Heterocentrotus mammilatus* (Echinoidea)				
30	*C. waltoni* Glynn, Bayer and Renegar, 2014	Glynn et al. 2014	Various species of shallow water gorgonians from the genera *Eunicea*, *Plexaurella*, *Muricea*, *Gorgonia*, *Pseudoplexaura*, *Pseudopterogorgia*, *Pleaxaura*, *Muriceopsis* (Octocorallia)	Up to 5 (many)	Translucent, pale yellowish tint or yellowish brown and darker in the central area. Fine irregular reticulations of white on all individuals. Most individuals have brown pigment granules, sometimes forming a reticulation coarser than the white pattern	Oral groove present. No apparent papillae	South Florida
31	*C. wuennenbergi* Fricke, 1970	Fricke 1970	*Sarcophyton* (Octocorallia)	50–60 (many)	Whitish to grey with dark red violet spots	40 simple papillae (3-7-7-3)	Madagascar
32	*C. yulianicorum* Alamaru, Brokovich and Loya	Current study	*Sarcophyton* sp. (Octocorallia)	10.5–32	Creamy-white with whitish large spots and scattered small pinkish-reddish dots	Twenty- four dorsal papillae in an X shape (5-7-7-5) surrounding the aboral sense organ. Another 12 papillae, 6 flanking each tentacular bulb, 3 on each side. Oral lappets and oral groove present	Gulf of Aqaba, Red Sea
33	*Vallicula multiformis* Rankin, 1956	Rankin 1951; Rankin 1956; Marcus 1957; Freeman 1967; Emson and Whitfield 1991; Eldredge and Miller 1995; Wirtz 1998; Mills and Haddock 2007; Carlton and Eldredge 2009; Moro et al. 2010; Oliveira et al. 2007; Glynn et al. 2014; Prasade et al. 2015; Current study	Found on various organisms including marine algae and invertebrates. In this study: Seagrasses, algae, *Pearsonothuria graeffei* (Holothurian)	1–13 (many)	Transparent, either colorless with whitish markings or lightly colored on aboral surface with brown, pink or green pigment, color being most pronounced in the areas surrounding the apical organ, tentacle sheath and around the periphery. Red pigments occurring in small green and brown cells that resemble chromatophores		Discovery Bay, Jamaica; Brazil; Bermuda; Hawaii, Madeira, Portugal; California; Canaries; Cuba; Florida; Gulf of Kutch, West coast of India; Gulf of Aqaba

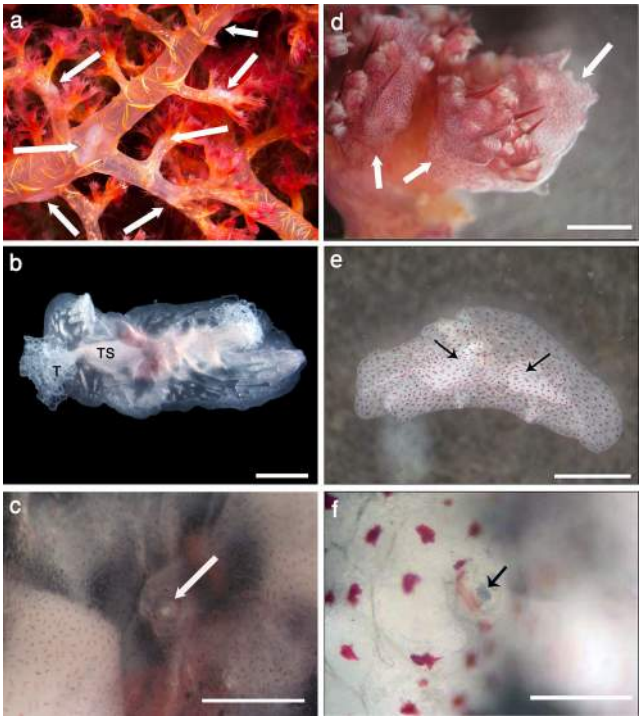

Fig. 6 *Coeloplana huchonae* n. sp. (on the left column) *vs. Coeloplana anthostella*, (on the right column, adopted from Song et al. (2011). **a** *Coeloplana huchonae* n. sp. from the Gulf of Aqaba, Red Sea in situ on its host, the soft coral *Dendronephthya hemprichi*. White arrows indicate ctenophores on the stem of the coral colony. **b** Aboral view of a live specimen of *C. huchonae* n. sp. showing the tentacles (T) and the tentacle sheath (TS) (scale bar: 1 mm). **c** Close-up of the aboral sense organ of *C. huchonae* n. sp. showing the statocyst in the middle (white granular mass indicated by the white arrow) (scale bar: 1 mm). Note the tiny pink elongated markings. **d** *Coeloplana anthostella* on a colony of *Dendronephthya spinulosa* collected in Japan (scale bar: 2 mm). White arrows indicate ctenophores on the stem of the coral colony. **e** Live specimen of *C. anthostella*, arrows show the tentacle sheaths (scale bar: 1 mm). **f** Close-up of the aboral sense organ showing the statocyst of *C. anthostella* (scale bar: 0.5 mm). Note the difference in size and shape of the pink markings of *C. huchonae* n. sp. from the Red Sea versus *C. anthostella* from Japan.

(UO). Preserved in 4 % formalin and later transferred to 70 % EtOH). Paratypes: TAU-CO35562, TAU-CO35563, TAU-CO35564 (sampled on September 6th 2012 at 6 m depth from a colony of the soft coral *Xenia umbellata* at the reef in front of the underwater observatory. Preserved in 4 % formalin and later transferred to 70 % EtOH). Additional sample of two ctenophores on their coral host, *X. umbellata* (TAU-CO35565) were also deposited. All types are deposited at The National Collections of Natural History at Tel-Aviv University, Israel.

Type locality: Eilat, Israel, Gulf of Aqaba, Red Sea (Fig. 1): 29°30′13.27″N, 34°55′07.50″E.

Etymology: Named in the honor of the late Prof. Lev Fishelson, a world-renowned marine biologist who passed away in 2013.

Diagnosis: Found on the soft corals *Xenia umbellata* (Fig. 7a) and *Paralemnalia* sp. (Fig. 7b). Color opaque white with white dot markings (Fig. 7c, d). No apparent papillae on aboral side.

Description: Color opaque white with small white dot markings creating a uniform cover (Figs. 7c, d and 8a). No apparent papillae on aboral side (Fig. 8a). Individuals collected ranged in maximal length between 4 and 9 mm along tentacular axis (n=10). Oral groove and lappets not present. Although gonads were not found, samples collected in September 2012 were observed to brood embryos or fertilized eggs (~200 microns) under the margins of the oral side (Fig. 8b). Statocyst size is ~30 μm (Fig. 8c).

Distribution and habitat: Found on the stems of the soft corals *Xenia umbellata* and *Paralemnalia* sp. at shallow depths of ~6 m (Fig. 7).

Ecology and behavior: During the night, the ctenophores crawl on top of the polyps towards the exterior part of the colony and extend their tentacles into the water column in order to capture food (Fig. 7a, b).

Remarks: This species differs from all other *Coeloplana* species by its coloration pattern and the identity of its host. To date, there are no Coeloplanidae species that are known to live in association with *Xenia* and/or *Paralemnalia* soft corals. However, it is known that *C. agniae* Dawydoff, 1930 lives on *Sinularia* colonies, which resemble *Paralemnalia*. Nevertheless, *C. agniae* differs from *C. fishelsoni* by its opalescent colors and variety of pigments, whereas *C. fishelsoni* is opaque white with white dots (Table 1). Moreover, *C. agniae* has four distinct rows of papillae forming an X-pattern through the statocyst and four additional rows of papillae flanking the tentacle sheaths—*C. fishelsoni* n. sp. does not have aboral papillae.

***Coeloplana punctata* Fricke, 1970 – NEW RECORD**

Material examined: Eilat, Israel, Gulf of Aqaba, Red Sea (Fig. 1). Sample: TAU-CO35585, (sampled on September 5th 2012 at 4 m depth from a colony of the soft coral *Sarcophyton glaucum* at the reef in front of the underwater observatory (UO). Preserved in 4 % formalin and later transferred to 70 % EtOH). Sample is deposited at The National Collections of Natural History at Tel-Aviv University, Israel.

Diagnosis: Epibiont on colonies of the soft coral *Sarcophyton* (Fig. 9a). Greenish-yellowish dots on aboral side (Fig. 9b). Extremely high number of aboral papillae (70–100) arranged in 10-12-12-10 pattern (Fig. 9c).

Description: Color milky white with brown-yellowish round spots across the entire body and green-yellowish dots (much smaller, but more numerous than the spots) scattered across the entire body surface (Fig. 9a, b). Only three individuals were collected, therefore few data are available on their size range. Length along tentacular axis ranged between 10.4 and 21.3 mm, and width ranged between 5.46 and 10.8 mm (n=3). Papillae arranged in four rows creating an X-shape around the statocyst (Fig. 9c). Eleven papillae in each row (parastomial papillae). Four rows of paratentacular papillae,

Table 2 Comparison between species of *Coeloplana* that live on *Dendronephthya* corals: *Coeloplana huchonae* n. sp., *Coeloplana anthostella* Song and Hwang, 2010 and *Coeloplana bocki* Komai, 1920

	Coeloplana huchonae n. sp. Current study	*Coeloplana anthostella* Song and Hwang, 2010	*Coeloplana bocki* Komai, 1920
Host	*Dendronephthya hemprichi* (Octocorallia)	*Dendronephthya spinulosa*, *D. decussatospinisa*, *D. dendricata*, *D. gracillima* (Octocorallia)	*Stereonephthya japonica*, *D. spinulosa*, *D. dendricata* (Octocorallia), Hydroids, Algae, Echinoderms
Color and pattern	Opaque white with deep scarlet elongated markings (size: ~20 μm in length)	Opaque white with deep scarlet star-shape markings (size: ~100 μm in length)	Dark red to orange with stripes
Size of body (L X W, mm)	4.6–4.8×1.9–2.7	1-4×0.5–3	30×15
Aboral papillae	None	None	10–20 club shape
Gonads	Not observed	Not observed	Summer–Autumn
Depth	10 m	25–32 m	Littoral
Localities	Coral reefs of Eilat, Gulf of Aqaba, Red Sea	Munseom, Jejudo Island, Korea	Sagmi Bay, Misaki, Japan
References	Current study	Song et al. 2011; Song and Hwang, 2010	Komai, 1920

14 papillae in each row. Total of 100 papillae (14-11-11-14) (Fig. 9c). This extremely high number of papillae in live organisms is in agreement with the original description of Fricke (1970). Reticulations of the gastrovascular system easily seen. Meridional canals branch repeatedly and form a reticulated network towards the periphery of the body. Individuals collected in Madagascar by Fricke (1970) were ~ 30 mm in length. Statocyst seen as a granular mass located at the middle of the aboral sense organ ~ 45 μm (Fig. 9d). Gonads were not observed.

Distribution and habitat: Found on colonies of the soft coral *Sarcophyton glaucum* (Fig. 9a).

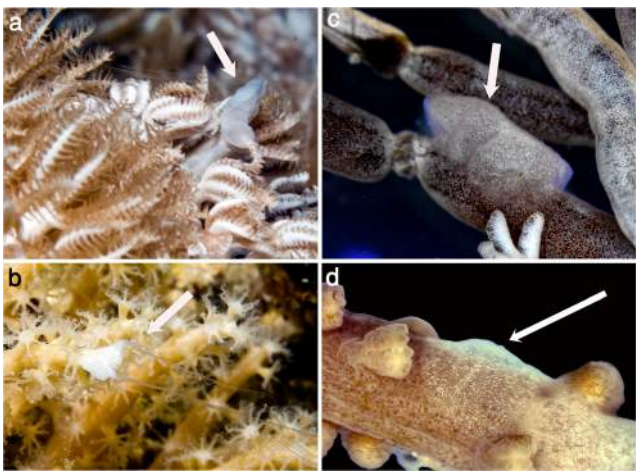

Fig. 7 *Coeloplana fishelsoni* n. sp. from the Gulf of Aqaba, Red Sea. **a** One *Coeloplana fishelsoni* in situ on its host, the soft coral *Xenia umbellata* **b** One *Coeloplana fishelsoni* n. sp. in situ with its tentacles extended on its host, the soft coral *Paralemnalia* sp. **c** Aboral view of a live specimen on the stem of the *Xenia* coral. **d** Aboral view of a live specimen on the stem of *Paralemnalia*. White arrows indicate the ctenophore

Ecology and behavior: *Coeloplana punctata* could be found together with *C. lineolata* on the same coral colony.

Remarks: In the original description of the species, Fricke 1970 described two color variants which differ by the size of the aboral dots and the body background color (whitish or greenish). Unfortunately, the accompanying black and white photos do not seem to fit the description of both variants. As the samples collected in the Red Sea and described herein fit

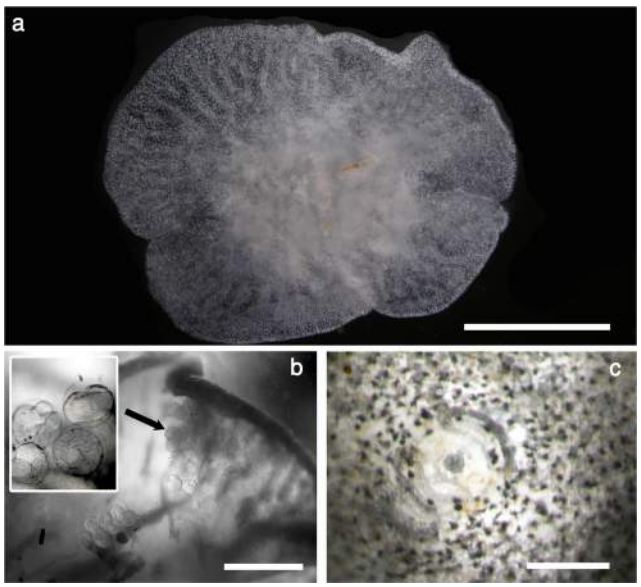

Fig. 8 *Coeloplana fishelsoni* n. sp. **a** Live, fully extended specimen showing the tiny white markings covering the entire body, oral view (scale bar: 3 mm). **b** Oral view of a specimen sampled in September 2012 showing brooded embryos or fertilized eggs on the margins of the animal (scale bar: 1000 μm). Blowout shows the embryos/fertilized eggs surrounded by a membrane. **c** Aboral view of the sense organ showing the granular statocyst in the middle surrounded by two pole plates (scale bar: 100 μm)

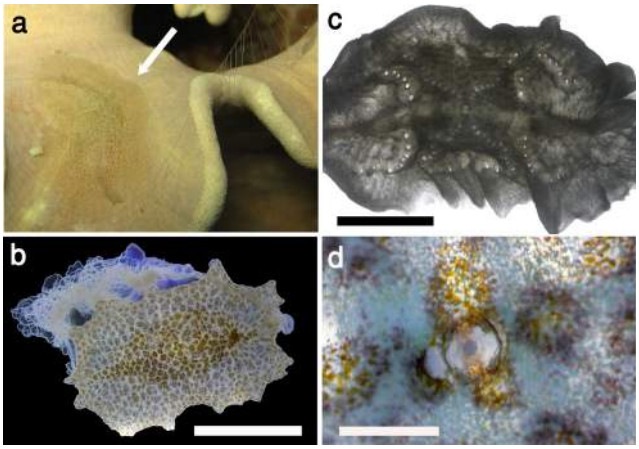

Fig. 9 *Coeloplana punctata* from the Gulf of Aqaba, Red Sea. **a** In situ *C. punctata* on a colony of the soft coral *Sarcophyton glaucum*. Note extended tentacle and tentilla to the right of the ctenophore. Ctenophore indicated by a white arrow. **b** Live specimen of *C. punctata*, with the left tentacle extended, showing the round brown marking pattern (scale bar: 0.5 cm). **c** Live, fully-extended specimen showing the x-shaped arrangement of aboral papillae crossing the aboral organ (scale bar: 2.5 mm). **d** Close- up of the aboral sense organ showing the statocyst (scale bar: 300 μm)

all the characters described in Fricke's paper (but not the photo), we assign them the name *C. punctata*. It should be noted that during our literature review, we noticed that the Red Sea specimens resemble the pictures of *Coeloplana mellosa* Gershwin, Zeidler, and Davie, 2010 from Australia. However, they differ greatly in the number of aboral papillae present in live specimens (20 versus 100). Therefore, at this point it is unclear whether *C. mellosa* is in fact a synonym of *C. punctata*. Support for this hypothesis is that Gershwin et al. reports observing 100 papillae in preserved specimens of *C. mellosa*, which is in agreement with the original description of Fricke. Obtaining samples of *C. mellosa* from Australia and comparing them to our samples may resolve the issue.

***Coeloplana lineolata* Fricke, 1970 – NEW RECORD**

Material examined: Eilat, Israel, Gulf of Aqaba, Red Sea (Fig. 1). Sample: TAU-CO35584 contains two ctenophore specimens, (sampled on May 27th 2012 at 10 m depth from a colony of the soft coral *Sarcophyton glaucum* at the reef in front of the Interuniversity Institute of Marine Sciences of Eilat (IUI). Preserved in 4 % formalin and later transferred to 70 % EtOH). Sample is deposited at The National Collections of Natural History at Tel-Aviv University, Israel.

Diagnosis: Found on the soft coral *Sarcophyton glaucum* (Fig. 10a, b). Characteristic pattern of brownish parallel lines parallel to the tentacular axis on aboral side (Fig. 10b, c). There are 60–70 aboral papillae arranged in 9-7-7-9 pattern (Fig. 10d).

Description: Transparent yellowish-brown with unique pattern of brownish lines parallel to the tentacular sheaths (Fig. 10b, c). Lines (~185 μm in width) are composed of multiple tiny brown pigment granules (Fig. 10b, c). The width of gaps between adjacent lines is ~300 μm. Individuals collected ranged in maximal length from 9 to 35 mm (n=7) along tentacular axis and from 6 to 13.6 mm maximum width. To date, this is the largest species of all three *Coeloplana* species found on the soft coral *Sarcophyton glaucum* in the Red Sea. Thirty-six dorsal papillae in an X-shape were identified in live specimens surrounding the aboral sense organ (Fig. 10d). An additional 20 papillae were identified, ten flanking each of the two tentacular bulbs, arranged in two rows of five (one row on each side, 9-5-5-9). After examining several specimens, it seems that the total number of aboral papillae ranges between 38 and 56. Statocyst diameter is ~50 μm (Fig. 10e). Oral lappets present surrounding the mouth, oral groove is present but narrow (Fig. 10f). Reticulations of the gastrovascular systems are seen; however, the structure of the meridional canals was not observed. Gonads were not observed.

Distribution and habitat: Found on the inner margins (underside) of the umbrella of *S. glaucum* colonies. The unique pattern of parallel brownish lines seen on the aboral surface of the animal match the underside of the *Sarcophyton* colonies (Fig. 10a).

Ecology and behavior: This species was observed to be on the underside during the day, when it needs to be camouflaged, while during the night it crawls to the upper parts of the colony to feed (Fig. 10a, b). *Coeloplana lineolata* may be found on the same coral colony with individuals of *C. punctata*.

Remarks: The individuals of *C. lineolata* found in the Gulf of Aqaba match the original description by Fricke (1970) with regards to color and pattern, and are identical to the photographs included in the original manuscript. There are small differences in the number of papillae (64 in the original description by Fricke vs. 38–56 in this research), which may be attributed to natural variation. It is important to note that another striped Coeloplanid, *Coeloplana agniae var striata* Dawydoff, 1938, was identified as a variant of *C. agniae*, as individuals were found on the same host and differed only in color pattern. Fricke did not compare his species to that of Dawydoff and it may well be that they are the same species.

***Coeloplana bannwarthi* Krumbach, 1933**

Material examined: Eilat, Israel, Gulf of Aqaba, Red Sea (Fig. 1). Samples: TAU-CO35581 contains five ctenophore specimens, TAU-CO35582 contains seven specimens, TAU-CO35583 several specimens on the spines of the host (sampled on May 27th 2012 at 3 m depth from the spines of the sea urchin *Diadema setosum* (Leske, 1778) at the reef in front of the Interuniversity Institute of Marine Sciences of Eilat (IUI). Preserved in 4 % formalin and later transferred to 70 % EtOH). Sample is deposited at The National Collections of Natural History at Tel-Aviv University, Israel.

Diagnosis: Found on the spines of the sea urchin *D. setosum* (Fig. 11). Characteristic dark purple / brown color. No aboral papillae present.

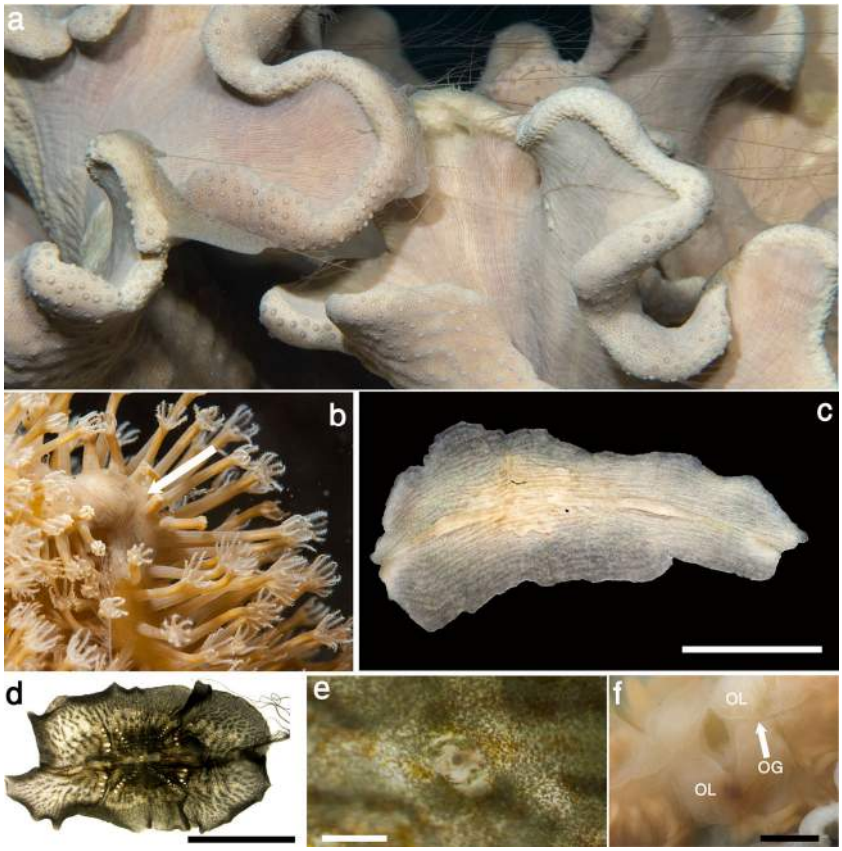

Fig. 10 *Coeloplana lineolata* from the Gulf of Aqaba, Red Sea. **a** Two *C. lineolata* specimens in situ on their soft coral host (*Sarcophyton glaucum*), extending their tentacles for feeding at night. **b** *C. lineolata* in situ on *S. glaucum*, showing the color pattern of parallel brown lines. **c** Aboral view of a live specimen of *C. lineolata* (scale bar: 1 cm). **d** Aboral view of a $MgCl_2$ treated backlit specimen showing the papillae arrangement (scale bar: 1 cm). **e** Close-up of the aboral sense organ showing the granular statocyst in the middle (scale bar: 300 μm). **f** Oral view of a fixed specimen showing the oral opening surrounded by oral lappets (OL). White arrow indicates the oral grove (OG) (scale bar: 1 mm)

Description: Aboral side dark brown in color (Fig. 12a). When the ctenophores are seen in situ, attached to the spines of the urchin, they may seem black in color (Fig. 11a, b). Oral side is milky white in live specimens. Ramifications of gastrovascular system are not clearly visible in either live or fixed animals. In some $MgCl_2$ treated specimens, the meridional canals are visible (Fig. 12a). When the animal is contracted, the area surrounding the sense organ resembles a six-lobed inflated cushion (Fig. 12b). Pole plates are visible in live specimens only after treating the animal with $MgCl_2$ for relaxation. Statocyst is granular and ranges in diameter between 32 and 72 μm (Fig. 12c), and its diameter increases with the animals maximal length. In normal state, no apparent papillae are visible. However, in specimens that were kept for several hours in petri dishes, ephemeral papillae started to emerge on the aboral side (Fig. 12d). Individuals collected ranged in size from 1.5 to 16 mm (n=23) maximal length along tentacular axis, and 0.98 to 6.96 mm in width. In fixed specimens, oral lappets are clearly seen surrounding the oral opening (Fig. 12e). Pharynx with many pharyngeal folds (Fig. 12e).

Distribution and habitat: Found on the spines of the sea urchin *D. setosum* in shallow water reefs in the Gulf of Aqaba (Fig. 11). According to Dafni (2008), this benthic ctenophore species was not seen in the Gulf of Aqaba for at least a decade. However, during our survey, we found it to be very common across several sites.

Ecology and behavior: During the day, the ctenophores are concentrated near the sea urchin's test and are difficult to see. During the night they crawl to the upper parts of the spines and extend their tentacles for feeding (Fig. 11). Infestation rate of the sea urchin may exceed 100 individuals per urchin (Fig. 11a).

Reproduction /developmental biology: Several early stage embryos were observed in the petri dish with an individual ctenophore collected on September 6th 2012. The average diameter of the embryos was 285 μm. In addition, asexual

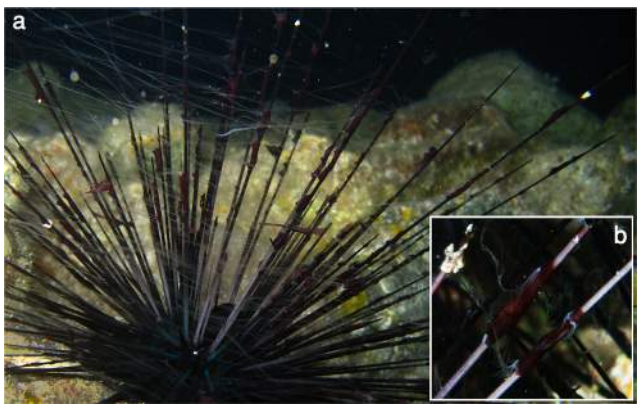

Fig. 11 *Coeloplana bannwarthi* (**a**) In situ on the spines of the sea urchin *Diadema setosum*, (**b**) close-up of two *C. bannwarthi* on white spines of *D. setosum* with their tentacles extended

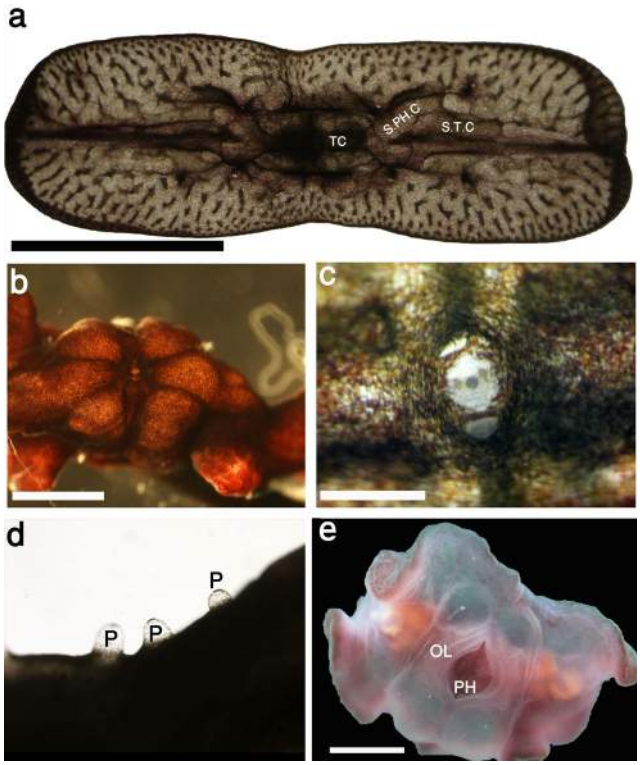

Fig. 12 *Coeloplana bannwarthi* morphology. **a** $MgCl_2$ treated fully extended backlit *C. bannwarthi* specimen showing the meridional canals arrangement. TC – tentacular canal, S.PH.C – Sub pharyngeal meridional canal, S.T.C – subtentacular canal (scale bar: 5 mm). **b** Aboral view of a contracted specimen demonstrating the six-lobed cushion shape of the polar area (scale bar: 2 mm). **c** Close-up of the aboral sense organ showing the granular statocyst in the middle (scale bar: 200 μm). **d** Side view of a specimen showing three ephemeral papillae that emerged after keeping the specimen for several hours in a petri dish. **e** Oral view of a formalin fixed *C. bannwarthi*. Note the well-developed oral lappets surrounding the mouth. Oral groove not present (scale bar: 2.5 mm)

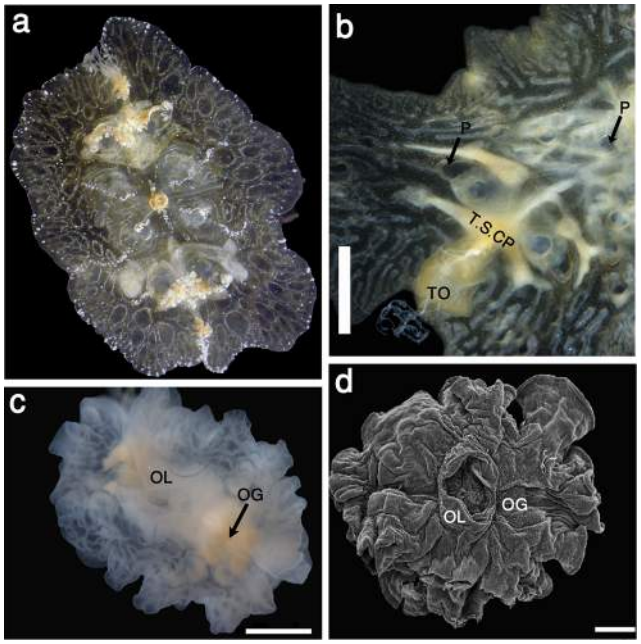

Fig. 13 *Vallicula multiformis* from the Gulf of Aqaba. **a** Live specimen of *V. multiformis*, showing coloration pattern, unique tentacle sheaths and the ramifications of the gastrovascular system. **b** Close-up of the tentacle sheath area showing the cross-piece structure, which is unique to the genus (scale bar: 2 mm) P – Pappilae, T.S.CP – Tentacle sheath cross-piece. TO – Tentacle opening with white tentacle tip protruding out. **c** Oral view of a preserved specimen of *V. multiformis* showing oral lappets (OL) and oral groove (OG) (scale bar: 1 mm). **d** Scanning electron micrograph of *V. multiformis* (scale bar 500 μm) OG – Oral Groove; OL – Oral lappets

reproduction was inferred, as some of the specimens collected were small and lacked some of the structures.

***Vallicula* Rankin, 1956**

Diagnosis: Possesses the characters of the family. Body flattened in oral-aboral axis with pharynx extended for creeping on the oral surface, or body folded in two along tentacular axis and floating or similarly folded and sessile on brown algae, hydroids, or ascidians. Comb plates absent. Oral grooves extending from mouth along tentacular axis to opening of tentacular sheaths on aboral surface with oral edges in central region, either produced as a pair of lappets, or further extended to form an accessory creeping sole. Anchor-shaped tentacle sheaths with extensible tentacles up to 20 or 30 times the length of the body. Branching and anastomosed gastrovascular system with aboral papillae capable of altering their position and shape and with well-marked spherical chambers near each tentacle sheath.

***Vallicula multiformis* Rankin, 1956 – NEW RECORD**

Material examined: Eilat, Israel, Gulf of Aqaba, Red Sea (Fig. 1). Samples: TAU-CO35577 three specimens, TAU-CO35578 six specimens, TAU-CO35579 few specimens, TAU-CO35580 three ctenophores on their *Sargassum* sp. host (all specimens were sampled on May 27th 2012 at 8 m depth from a colony of the algae *Sargassum* at a sandy-rubble patch located between the Interuniversity Institute of Marine Sciences of Eilat (IUI) and the Underwater observatory (UO). Preserved in 4 % formalin and later transferred to 70 % EtOH). Sample is deposited at The National Collections of Natural History at Tel-Aviv University, Israel.

Diagnosis: Unique anchor shape of tentacles sheath with a distinct "cross piece" (this character discriminates between the genera *Coeloplana* and *Vallicula*) (Fig. 13a, b). Transparent, either colorless with whitish markings or lightly colored on aboral surface, with brown, pink, or green pigments (Fig. 13a). Color is more pronounced in area immediately surrounding the apical organ, along tentacular axis and around periphery.

Description: Color ranges from colorless to transparent green to transparent yellow, depending on its host. Small white granular pigments concentrated along the animal's perimeter and surrounding the aboral sense organ (Fig. 13a). In some specimens, light orange pigmentation is concentrated around the sense organ (Fig. 13a). All specimens have brown pigments located in cells that resemble chromatophores.

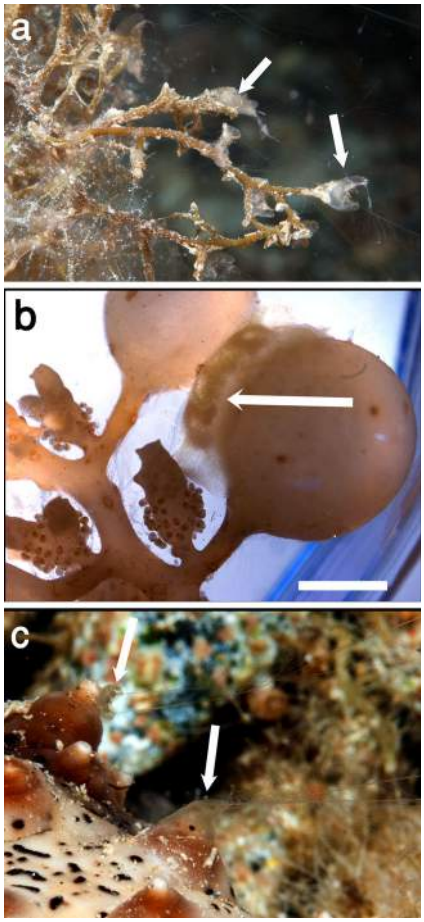

Fig. 14 *Vallicula multiformis* from the Gulf of Aqaba, Red Sea on different hosts. **a** *V. multiformis* on an unidentified brown alga. Note extended tentacles in the flow, **b** *V. multiformis* on the seaweed *Sargassum*. Note the aboral papillae from a lateral view (marked by white arrow) (scale bar: 2 mm). **c** Two *V. multiformis* (marked by white arrows) on the sea cucumber *Pearsonothuria graeffei*

Tentacle sheath differs from that of *Coeloplana* by having an additional cross-piece, resembling an anchor (Fig. 13a, b). Individuals' (n=28) maximal length ranges between 3 and 32 mm along tentacular axis, and their width ranges between 1 and 19 mm. Individuals have eight large club-shaped papillae, four flanking each tentacle bulb, two from each side (Fig. 13b). When tentacles are contracted and packed into the tentacle sheath, the tentacle sheaths look greenish in color. Aboral sense organ resembles a four-leaf clover, having four large papillae, one on each lobe. Statocyst diameter ~60 μm. Oral lappets and a well-defined oral groove present (Fig. 13c, d). Reticulations of the gastrovascular system are clearly visible (Fig. 13a). Gonads were not observed

Distribution and habitat: Found on unidentified brown algae (Fig. 14a), on the vesicles of *Sargassum* seaweed (Fig. 14b) and on the spines of the holothurian *Pearsonothuria graeffei* (Fig. 14c). This is a generalist species with a variety of hosts, ranging from algae to invertebrates, in many global locations.

Ecology and behavior: This species was found to be prevalent in the Gulf of Aqaba mostly during the winter, when the water column is mixed and there is a massive algal bloom. During this period *Vallicula* reached densities of hundreds of individuals per *Sargassum* algae. This is in agreement with previous observation in Hawaii of over 3000 *V. multiformis* per square meter (Carlton and Eldredge 2009).

Discussion

This study presents the first survey of the benthic ctenophore fauna in the Gulf of Aqaba. We have found four new species of benthic ctenophores (*C. loyai* n. sp., *C. yulianicorum* n. sp.; *C. huchonae* n. sp. and *C. fishelsoni* n. sp.) and three new records for the Gulf of Aqaba (*C. lineolata* Fricke, 1970, *C. punctata* Fricke, 1970 and *Vallicula multiformis* Rankin, 1956). The fact that half of the species documented in this study are new species demonstrates that this group holds great potential for uncovering new, unknown species. Moreover, because benthic ctenophores are epibionts on various algae and invertebrates that are common in coral-reef areas throughout the world, it may indicate that the biodiversity of this group is expected to be high in coral-reef ecosystems. This hypothesis is corroborated by the frequent documentation of these animals in coral-reef areas by amateur underwater photographers, as revealed when searching the keywords "benthic ctenophores" on Google.

Geographic range of *Vallicula*

Our new record of *V. multiformis* in the Red Sea represents an extension of the species' geographic distribution, which was known until recently only from the Atlantic ocean and Hawaii. The first record from the Indian Ocean was recently reported by Prasade et al. (2015), who collected specimens in the Gulf of Kutch, West coast of India. *Vallicula multiformis* was originally described from Jamaica (Rankin 1956) and later recorded from Brazil (Marcus 1957; Oliveira et al. 2007), Bermuda (Freeman 1967), Hawaii (Eldredge and Miller 1995), Madeira Island in Portugal (Wirtz 1998), California (Mills and Haddock 2007), Canarias Islands, Cuba (Moro et al. 2010) and Florida (Glynn et al. 2014). At this point, we are unable to determine whether *Vallicula* is a circumglobal species or an easily transported invading species, dispersing through shipping routes (either by ballast water or as part of fouling organisms). The ability of *Vallicula* to live on a variety of hosts gives it an advantage and probably enables its large geographic distribution, whether invasive or not.

Morphological identification of benthic ctenophores

The seven main morphological characters traditionally used for benthic ctenophore identification are: color, pattern, size, papillae number, shape of tentacle sheath and the presence or absence of an oral groove and oral lappets. Oral groove presence and the shape of the tentacular sheath originally distinguished between the two genera in the family (*Coeloplana* vs. *Vallicula*), but these characters were not used to distinguish between different species from the genus *Coeloplana*. The use of these morphological characters in benthic ctenophore species identification is complicated and may not be unequivocal. The reason is that these characters are altered post chemical fixation, rendering taxonomic revisions based on existing museum records challenging.

Discrimination between Vallicula and Coeloplana

Although Rankin (1956) suggested that *Vallicula* should be considered as a new genus due to the presence of an oral groove, oral lappets and anchor-shape tentacle sheaths that are not found in *Coeloplana*, we argue that an oral groove and oral lappets do in fact occur in some species of *Coeloplana*, but not in all. For example, *C. lineolata* and *C. yulianicorum* n. sp., the new species found on *S. glaucum*, both have an oral groove, although in *C. lineolata* it is very narrow. Moreover, an oral groove is known to be present in two other species described from Australia: *C. scaberiae* and *C. thomsoni*, both designated as new *Coeloplana* species by Matsumoto (Matsumoto 1999; Matsumoto and Gowlett-Holmes 1996). Also, oral lappets were observed in the framework of this study in *C. bannwarthi* collected from the spines of the urchin *Diadema setosum* (Fig. 12e). We conclude that the only morphological character that is valid for identifying the genus *Vallicula* is the unique anchor-shape of the tentacle sheaths (having an additional cross-piece, Fig. 15). The fact that only the anchor shape distinguishes between *Vallicula* and *Coeloplana* raises a doubt regarding the standing of *Vallicula* as a separate genus. However, recent molecular evidence based on 18S and ITS sequences supports the validity of *Vallicula* as a separate genus (Simion et al., 2015).

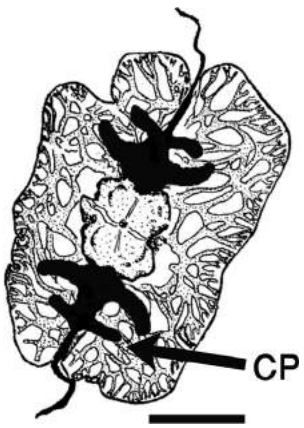

Fig. 15 A drawing of *Valiculla multiformis* showing the unique anchor-shape of tentacles sheath with a distinct additional cross-piece (CP)

Reviewing recent literature on Coeloplanidae, we noticed in the original description (Gershwin et al. 2010) that *C. reichelti* appears to have an anchor-shape tentacle sheath with a distinct cross-piece (see Fig. 2F in Gershwin et al. 2010). Moreover, comparing Fig. 2e from Gershwin et al. (2010) to Fig. 13a in the current manuscript (and other photos in our possession) shows that there are similarities in color, pigmentation and general morphology between the specimens. Therefore, it is possible, even likely, that *C. reichelti* may be in fact *Vallicula*. We suggest that the issue may be easily resolved applying molecular methods as shown in Simion et al. (2015).

Discrimination between Coeloplana species

Color and pattern Based on our observations, the color and pattern of Coeloplanidae species does not change in live specimens, even after detaching them from their host and keeping them for a few weeks in the laboratory. Transparency may change as a result of the animal's state (i.e., relaxed versus contracted). However, based on existing literature, there seem to be several color morphs for certain species (e.g., *C. gonoctena var. rosea*, *C. gonoctena var. natalensis* and *C. agniae var. striata*). We cannot rule out that these varieties are in fact different species. At least for the species described here from the Gulf of Aqaba, color and pattern are useful and descriptive and allow species differentiation.

Size Size measurements are challenging, as these animals are very flexible and tend to change shape constantly. In addition, size measurements are also affected by the animal's state (e.g., relaxed *vs*. contracted) and also change greatly post fixation, as both formalin and ethanol dramatically alters the body shape. However, based on a comparison of length between all known species of Coeloplanidae (Table 1), it is clear that there are species that are generally smaller (e.g., *C. anthostella*, *C. duboscqui*, *C. perrieri*), while others may reach almost 60–70 mm when mature (e.g., *C. willeyi*, *C. loyai*, *C. lineolata*).

Aboral papillae Historically, the number of aboral papillae was used to distinguish between coeloplanid species. However, we argue that the aboral papillae are not informative for distinguishing between species as their number can vary greatly, even in the same individual as reported here for *C. loyai* and also noted by Gershwin et al. (2010). Several authors have hypothesized that these protruding extensions of the gastrovascular system are involved in gas exchange, and therefore, papillae number will increase when placing an individual in a low oxygenated environment (Abbott

1907a, b; Rankin 1956). This hypothesis was corroborated by our observations on various species found within the framework of this study. After placing the animals in small petri dishes for observation, the number of papillae increased. This even happened in species with no observed papillae when initially examined, whereas after several hours these structures appeared (e.g., as seen in *C. bannwarthi*). In addition, the number of these papillae changes post fixation. For example, Gershwin et al. (2010) reported that live specimens of *C. mellosa* have 20 simple papillae, whereas post fixation in formalin solution they seem to have > 100 papillae.

Oral groove and lappets Although the presence of oral groove and lappets cannot be used to discriminate between *Vallicula* and *Coeloplana*, they may be used as supporting characters when identifying *Coeloplana* species. Some *Coeloplana* species exhibit both structures (e.g., *C. yulianicorum*, Fig. 5f and *C. lineolata*, Fig. 8e), some have only oral lappets (e.g., *C. bannwarthi*, *C. huchonae*) or only the oral groove (e.g., *C. sophiae*) and other do not show any of these characters at all (e.g., *C. loyai*). These characters are better seen in fixed animals than in live ones.

Host specificity as an identifying character

The association between ctenophores and their hosts is an important character for species identification and may be used to discriminate between species from the family Coeloplanidae. The degree of specificity and host identity varies between different species of Coeloplanidae. Some ctenophore species are host specific and restricted to only one host (e.g., *C. bannwarthi* on the spines of *Diadema setosum* and *C. huchonae* on the stems of *Dendronephthya hemprichi*). Some are restricted to a group of morphologically similar hosts as in *C. loyai* on the mushroom corals *H. limax* and *C. echinata*, or *Coeloplana waltoni* that lives on various species of shallow water gorgonians. Others like *V. multiformis* are generalist, living on various hosts and habitats, and can be found on hard substrate like beach rocks as well as on various hosts ranging from algae to invertebrates. *C. willeyi* is found on both algae and on the spines of sea urchins.

Conclusion and future directions

Available literature and our own data suggest that: (1) differentiation between *Coeloplana* and *Vallicula* is possible based on only one character—the shape of the tentacle sheath; and (2) differentiation between *Coeloplana* species is possible with a combination of five characters (i.e., color, pattern, oral groove, oral lappets and host identity). As we have shown, color and pattern are very important characters in the taxonomy of benthic ctenophores. Because these two characters will change post fixation, we recommend basing ctenophore species identification on live specimens, using color photos and videos as part of the identification.

Finally, there is a need to develop molecular markers for species identification that will allow a thorough revision of the known species. We are currently in the process of doing this analysis.

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