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Differential morphological features of two *Dendronephthya* soft coral species suggest differences in feeding niches

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Abstract Octocorals are characterized by pinnate tentacles and internal sclerites. Their feeding ability is determined by the morphological features of the polyps. Capture of their food by these corals is also affected by the flexibility of the colony, which in turn is determined by the features of the sclerites. We studied the morphological features of two azooxanthellate octocorals, *Dendronephthya hemprichi* and *D. sinaiensis*, whose depth distribution partially overlaps at Eilat (northern Red Sea). Following Gause's Law, such coexistence is considered to be possible if each species is adapted to utilize different food items. In order to examine this Law, the features of the polyps of the two species and their sclerites were studied. Each side of their tentacles displays 11–13 pinnules, which are longer at the tentacles' distal end compared to its median section and proximal end, with the distal pinnules of *D. sinaiensis* being longer than those of *D. hemprichi*. At the proximal end of the tentacles of *D. sinaiensis*, the pinnules emerge perpendicularly, unlike in *D. hemprichi*, where they emerge from the lateral sides; the distance between the rows of pinnules is, therefore, shorter for the former. These findings imply that the filtered phytoplankton by the two species may differ in size. Their sclerites also differ in size and shape, and therefore the expansion and contraction abilities of their polyps also differ, and may thus affect their respective feeding abilities. The findings indicate that *D. hemprichi* and *D. sinaiensis* are adapted to utilize different food items, and therefore support Gause's Law and explain the coexistence of the two species.

Keywords Octocorallia · Polyp morphology · Gause's Law · Sclerites · Niche overlap · Feeding · Red Sea

Introduction

The sub-class Octocorallia (Cnidaria: Anthozoa) comprises more than 2,000 species, with a worldwide distribution and found in a variety of habitats (Bayer 1973; Fabricius and Alderslade 2001). Octocorals are characterized by polyps with eight pinnate tentacles and internal calcareous skeletal elements, termed sclerites. The octocoral order Alcyonacea is the largest and the member species may or may not contain symbiotic algae in their tissue (they are zooxanthellate vs. azooxanthellate species, respectively). Alcyonacean species constitute the second most important benthic component on many coral reefs, including those of the Gulf of Aqaba (northern Red Sea) (Benayahu and Loya 1977, 1981).

Goldberg (1973) and Kinzie (1973) reported that various gorgonian octocoral species are adapted to specific depths that are related to the prevailing current regime. Depth partitioning between congeneric octocorals was described for *Plexaura homomalla* and *P. nina* in the US Virgin Islands, with a 20 m limit of occurrence for the former and >20 m for the latter (Lasker et al. 1983). The size of the polyps of these two species was found to be related to their feeding rates, i.e., the larger polyps of *P. nina* exhibit a higher feeding rate than the smaller ones of *P. homomalla*. Heterotrophy and photoautotrophy, however, were not the only factors that explained the depth partitioning of these species.

The feeding rate of an octocoral colony is determined by the morphological features of its tentacles, including the length of the pinnules, their shape and density, as well as by the ambient flow speed (Sebens and Johnson 1991).

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Among octocorals, the narrowly-spaced pinnules are arranged in a typical comb-like structure along each of the tentacle margins, making them suitable for filter feeding on small particles (Fabricius and Alderslade 2001). The polyps feed most effectively under an optimum ambient velocity, which determines their feeding performance and food niche, which are also related to the morphological features of the polyps (Dai and Lin 1993). Capture of food particle by the polyps is also determined by their sclerites composition and arrangement (Vogel 1981). While some types of sclerites may limit the expansion of the octocoral colonies, including their polyps, others may limit their contraction (Lewis and von Wallis 1991). Notably, there is an intraspecific variation in the morphological features of octocoral polyps that is related to their feeding capabilities and exploitation of the available food items (Kinzie 1973; Sponaugle and LaBarbera 1991; Lin and Dai 1996).

The azooxanthellate alcyonaceans of the genus *Dendronephthya* (family Nephtheidae) are common in the northern Red Sea where they inhabit steep reef slopes (Benayahu 1985; Dahan and Benayahu 1997b). *D. hemprichi* has a wide Indo-Pacific distribution (Verseveldt 1965) while *D. sinaiensis* has been found so far only in the northern Red Sea (Verseveldt 1970). The taxonomy of the genus *Dendronephthya* is quite problematic and there are no efficient tools to determine species adequately, nor is there any known phylogenetic molecular signal (McFadden et al. 2010). When alive, however, *D. hemprichi* and *D. sinaiensis* are distinguishable from one another on Eilat reefs, and taxonomic identification of preserved colonies can be properly conducted by comparing them to their respective types (see below). Both species successfully flourish on various underwater artificial structures (Perkol-Finkel and Benayahu 2004, 2005). In Eilat (northern tip of the Gulf of Aqaba, Red Sea), they colonize the vertical steel pillars of Eilat's oil jetties (Eilat-Ashqelon Pipe Line Company; EAPC), which are characterized by a high-flow regime (Perkol-Finkel and Benayahu 2004). *D. hemprichi* and *D. sinaiensis* display a partially overlapping depth distribution along the pillars. The former is found at 1–32 m and the latter at 11–32 m (Grossowicz 2008). The two species are passive phytoplankton filter feeders, and were the first ever recorded feeding on these food items among members of the class Anthozoa (Fabricius et al. 1995a, b). Their life history traits exhibit similarity: both are gonochoric broadcasters (Barki 1992; Dahan and Benayahu 1997a, 1998) and feature asexual propagation by means of numerous small autonomous fragments (Barki 1992; Dahan and Benayahu 1997b). The above-noted traits of *D. hemprichi* and *D. sinaiensis* thus reveal a remarkable degree of biological and ecological similarity.

Intrigued by the distributional pattern along depth of *D. hemprichi* and *D. sinaiensis* (see above), this study examined whether the two species possess polyps with different morphological features. Such differences may in turn lead to differential feeding capabilities that reduce competition for food, following Gause's (1934) Law that two similar species dwelling in the same habitat displace each other in such a manner that each takes position of certain peculiar kind of food. Food, such as phytoplankton, is a limited resource in the oligotrophic and phytoplankton low value Red Sea (Lindell and Post 1995), especially during the summer period, when the water is nutrient-depleted (Reiss and Hottinger 1984).

Materials and methods

The study was conducted at the EAPC oil jetties, located 4 km south of the city of Eilat (Fig. 1), constructed in the late 1960s and considered as an unplanned artificial reef (Dahan and Benayahu 1997a, b; Perkol-Finkel and Benayahu 2004). Identification of colonies of *D. hemprichi* Klunzinger, 1877 and *D. sinaiensis* Verseveldt, 1970 was facilitated by comparison with their respective type material kept at the Berlin Museum für Naturkunde and the Zoological Museum of Tel Aviv University. In order to compare between the morphological features of the polyps of the two species, branches, ca 10 cm in length (n=8–10 for each species), were removed from different colonies growing on the jetty-pillars at depths of 10 and 22 m, respectively (April–May 2007). These two depths represent the highest colony density of the two species (Grossowicz 2008). The branches were brought to the Interuniversity Institute of Marine Sciences at Eilat (IUI) and placed in flow-through seawater tanks. A day later, the branches were transferred into 500 ml plastic containers filled with aerated seawater and, when fully inflated, they

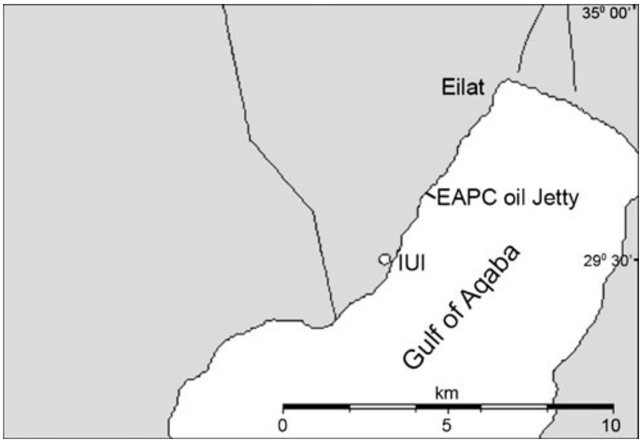

Fig. 1 Study site at Eilat, northern tip of the Gulf of Aqaba (Red Sea) (*EAPC* Eilat-Ashqelon Pipe Line Company, *IUI* The Interuniversity Institute for Marine Sciences)

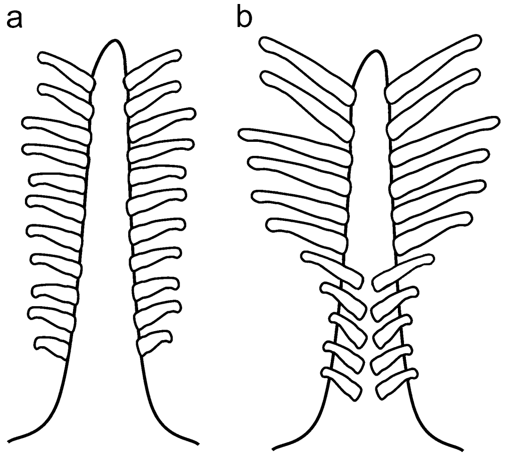

Fig. 2 Tentacles: **a** *Dendronephthya hemprichi*, **b** *D. sinaiensis*

were relaxed by the introduction of magnesium sulfate (10%) (see Vasconcelos et al. 2006). After relaxation took place, 12–16 polyps from each branch were clipped off by scissors and preserved in 2.5% seawater glutaraldehyde. These polyps were used for determination of their morphological features following decalcification. The polyps were decalcified in a mixture of equal volumes of formic acid (50%) in sodium citrate (15%) for 30 min and then replaced in 2.5% glutaraldehyde (Yacobovitch et al. 2003). The polyps underwent dehydration through a graded series of ethanol (from 30 to 99%), critically point-dried with liquid CO_2 and then gold-coated. Sclerites were isolated from several other polyps (ca 10) using 10% sodium hypochloride, air-dried and gold-coated. The polyps and the sclerites were examined under a JEOL JSM 840a scanning electron microscope (SEM). The SEM micrographs were used to determine the following morphometric features of the polyps of each species: length of tentacles, number of pinnules along a tentacle margin, length of pinnules, and distance between rows of pinnules on a given tentacle. For each of the species, the first 1–4 pinnules along each margin of the tentacle were classed as proximal, the following 5–8 pinnules as median, and the remainder (up to 12–13) as distal. The length and width of the different types of sclerites found in the polyps were measured using an Olympus Soft Imaging System (SIS) Scandium to the nearest 0.01 mm (51 sclerites of each species). The length-to-width ratio of the spindles was calculated for each species. Additionally, in order to characterize the arrangement of the sclerites in the polyp, polyps from three different colonies of both species were removed, subjected to dehydration in xylene overnight, and examined under a light microscope (Nikon DS-Fi1).

All statistical analyses were performed by Statistica 7.1. Average values were compared by Student's *t* test for independent samples. Variance was tested by *F* test and homogeneity of data was tested by Cochran C. one-way ANOVA followed by Bonferroni post-hoc. Normality of the dependant variables was assessed by the Kolmogorov–Smirnov test (KS). All values are presented at a confidence interval of 95%.

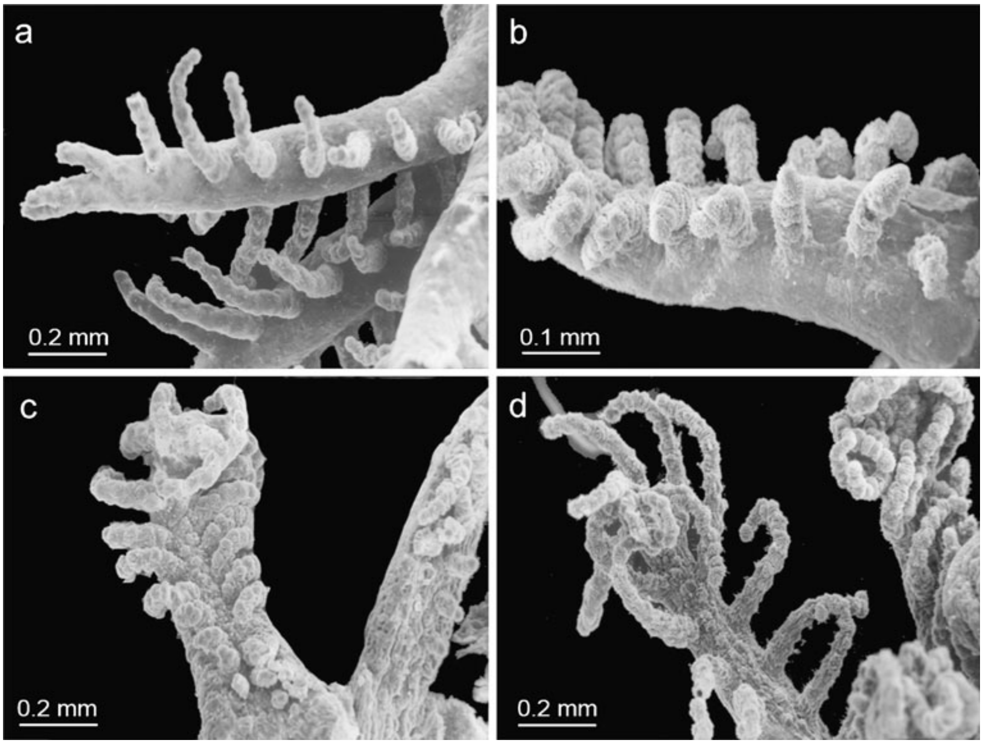

Fig. 3 Scanning electron micrographs: **a**, **b** tentacles of *Dendronephthya hemprichi*, **c**, **d** tentacles of *D. sinaiensis*

Table 1 *Dendronephthya hemprichi* and *D. sinaiensis*: comparison between average length of proximal, median and distal pinnules along the tentacle, and average distance between rows of adjacent pinnules (mm ± SD)

Morphological features	Proximal pinnules (1–4)	Median pinnules (5–8)	Distal pinnules (9-12/13)	Statistics
D. hemprichi				
Average length of pinnules	0.080±0.030 (*n*=67)*	0.160±0.38 (*n*=72)	0.149±0.49 (*n*=46)	One-way ANOVA *p*=0
Average distance between rows of pinnules	0.050±0.008 (*n*=19)	–	0.056±0.007 (*n*=19)	*t* test *p*=0.02*
D. sinaiensis				
Average length of pinnules	0.091±0.038 (*n*=40)*	0.174±0.049 (*n*=52)	0.192±0.043 (*n*=35)	One-way ANOVA *p*=0
Average distance between rows of pinnules	0.028±0.005 (*n*=10)	–	0.052±0.005 (*n*=11)	*t* test *p*=0*

– No data, *n* sample size, *significant difference

Results

Each side of the eight tentacles of *D. hemprichi* and of *D. sinaiensis* features one row of 11–13 pinnules (*n*=20 tentacles examined for *D. hemprichi* and *n*=17 for *D. sinaiensis*). In *D. hemprichi*, the pinnules emerge from the lateral sides along the entire length of the tentacle and are mostly directed outwards (Figs. 2a and 3a, b). In *D. sinaiensis,* at the proximal end of the tentacle the pinnules emerge perpendicularly from its upper (oral) surface (Figs. 2b and 3c, d).

Comparisons between the length of the proximal and distal pinnules (Fig. 2) and the distance between their rows in *D. hemprichi* and *D. sinaiensis* are presented in Table 1 (data were normally distributed, KS, $p>0.1$). In both species, the proximal pinnules (1–4) were significantly shorter than the median and distal ones (5–8 and 9-12/13). In both *D. hemprichi* and *D. sinaiensis* the distance between the rows of the proximal pinnules was significantly shorter than that between the distal ones (*t* test, $p=0.02$, $p=0$, respectively). Table 2 presents a comparison between the morphological features of the two species, revealing that *D. hemprichi* has longer tentacles than *D. sinaiensis*. In *D. sinaienis*, the distal pinnules are significantly longer than those of *D. hemprichi*, and the distance between the two rows at the proximal end is shorter than in *D. hemprichi* ($p<0.01$ for both, data were normally distributed, KS, $p>0.1$). All other comparisons between the morphological features of the two species did not reveal significant differences (Table 2). In addition, the distance between two adjacent pinnules was measured for both species as an indication of pinnules density: *D. hemprichi*: 0.024±0.018 mm, $n=6$ vs. *D. sinaiensis*: 0.0184±0.007 mm, $n=9$, and did not significantly differ ($p=0.11$).

Polyps of both *D. hemprichi* and *D. sinaiensis* contain spindles up to 3 and 2.5 mm respectively (Fig. 4a, b), which comprise the supporting bundle (see Fabricius and Alderslade 2001). The polyp head features shorter spindles up to 0.5 mm (Fig. 4c, d, respectively). Both types of sclerites are covered with rather evenly scattered warts. The tentacle sclerites are from 0.02 to 0.1 mm long (Fig. 4e, f, respectively). In addition, the stalk of *D. sinaiensis* features short and thick antler-shaped sclerites (Bayer et al. 1983), up to 0.1 mm (Fig. 5), which are not found in *D. hemprichi.* The average length-to-width ratio of the spindles of *D. hemprichi* is 11.71±3.04, and *D. sinaiensis* is 17.53±5.73 (n=51 sclerites examined for each species), with a significantly lower ratio for the former compared to the latter [all ratios normally distributed (KS, $p>0.02$) with a non-similar variance (F-test, $p<0.05$), t-test $p<0.001$], making the *D. sinaiensis* spindle-shaped sclerites much narrower. In both species, the spindles are arranged in the characteristic polyp armature known for the genus *Dendronephthya* (Fabricius and Alderslade 2001). Light microscopy examination did not reveal any striking difference in sclerite arrangement in the two species.

Table 2 *Dendronephthya hemprichi* and *D. sinaiensis*: comparison between average morphological features of polyps (mm ± SD)

Morphological features	*D. hemprichi*	*D. sinaiensis*	*t* test
Average length of tentacle	0.667±0.108 (*n*=19)	0.560±0.109 (*n*=13)	*p*=0.01*
Number of pinnules along margin of tentacle	11–13 (*n*=20)	11–13 (*n*=17)	
Average length of proximal pinnules (1–4)	0.080±0.030 (*n*=67)	0.091±0.038 (*n*=40)	*p*=0.09
Average length of median pinnules (5–8)	0.160±0.38 (*n*=72)	0.174±0.049 (*n*=52)	*p*=0.08
Average length of distal pinnules (9–12/13)	0.149±0.49 (*n*=46)	0.192±0.043 (*n*=35)	*p*=0*
Average distance between adjacent rows of proximal pinnules	0.050±0.008 (*n*=19)	0.028±0.005 (*n*=10)	*p*<<0.05*
Average distance between adjacent rows of distal pinnules	0.056±0.007 (*n*=19)	0.052±0.005 (*n*=11)	*p*=0.15

n Sample size, *significant difference

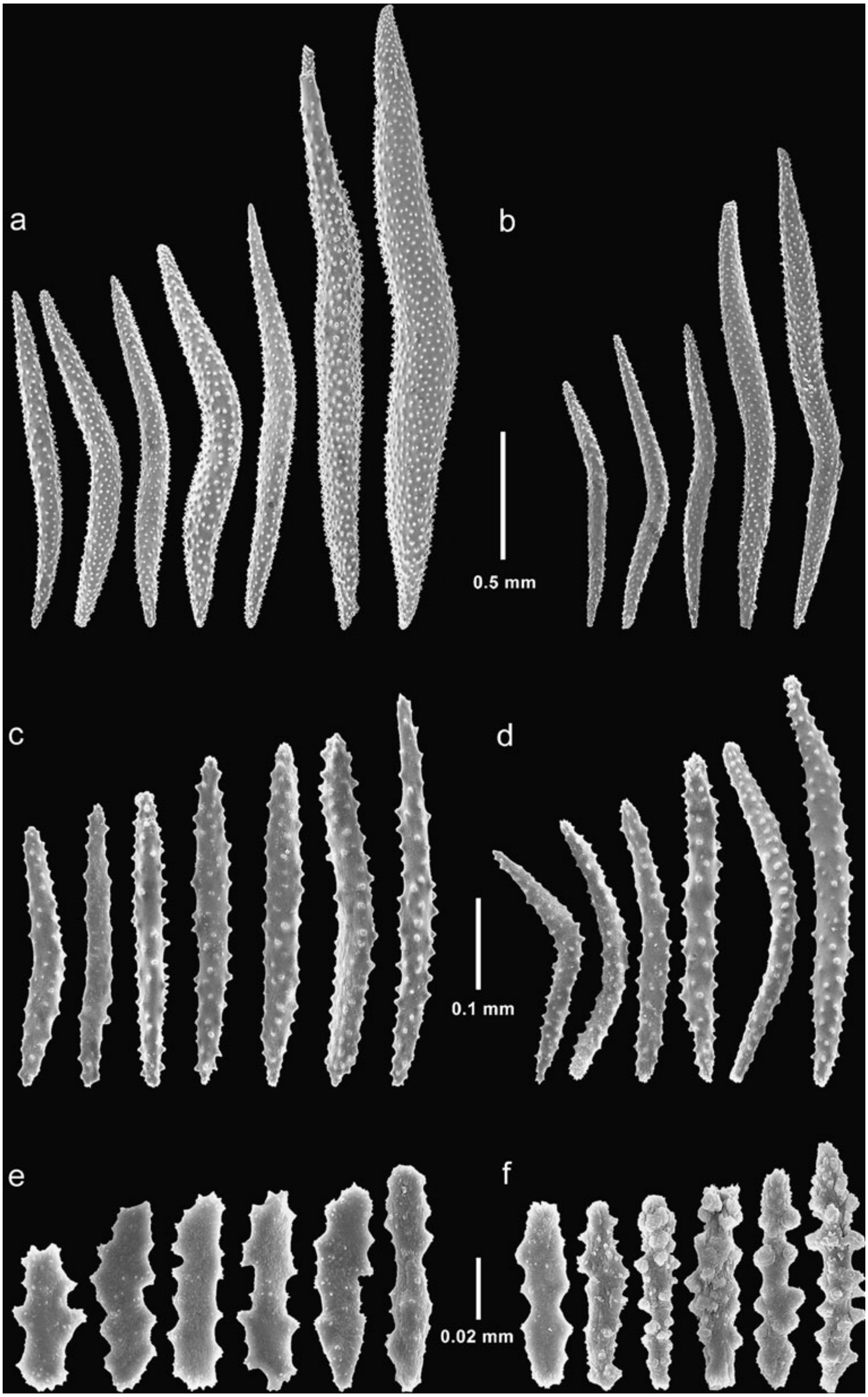

Fig. 4 Scanning electron micrographs of sclerites; spindles of supporting bundle: **a** *D. hemprichi*, **b** *D. sinaiensis*; spindles of polyp head: **c** *D. hemprichi*, **d** *D. sinaiensis*; tentacle sclerites: **e** *D. hemprichi*, **f** *D. sinaiensis*

Discussion

Filter feeding by marine organisms consists in the separation of particles from fluids by the use of porous media, such as a sieving mechanism (see Rubenstein and Koehl 1977). A filter feeder is most effective at collecting particles only within a certain range of ambient water velocity and particle sizes (Jørgensen 1955; Rubenstein and Koehl 1977;

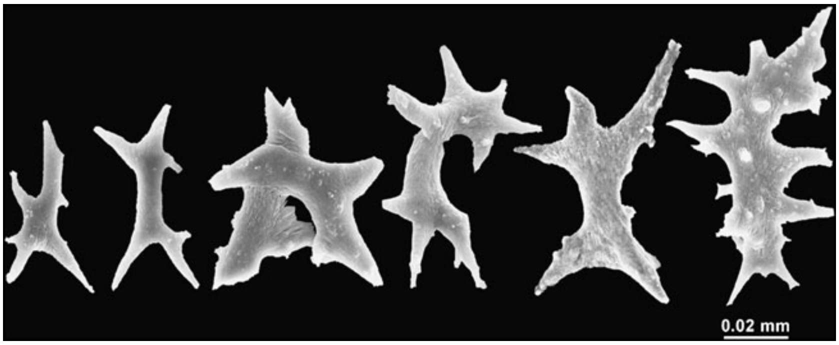

Fig. 5 Scanning electron micrographs of *D. sinaiensis* antlers

Vogel 1981). The comb-like pinnules along the margins of the tentacles of the genus *Dendronephthya* appear to be more suitable for feeding on small particles or uptake of dissolved organic matter (DOM) than for capturing zooplankton (Fabricius et al. 1995a, b). Notably, the latter studies provided the first recorded evidence for feeding on phytoplankton in *Dendronephthya* species. The density of the pinnules indicates their suitability for filtering a certain particle size (Rubenstein and Koehl 1977). The denser the pinnules, the greater their chance of capturing small particles; while the more they are elongated, the greater the surface area for such capture, and thus capture efficiency (Lasker et al. 1983). The length of the pinnules at the distal end of a *D. sinaiensis* tentacle is significantly greater than in *D. hemprichi* (Table 2). The filtering abilities and, consequently, the size of the food particles ingested by the two species are thus expected to differ. In *D. sinaiensis*, the distance between the two rows of pinnules at the proximal end of the tentacle is significantly smaller than in *D. hemprichi* (0.028±0.005 vs. 0.050±0.008 mm respectively, Table 2, $p<<0.05$). Similarly, at *D. sinaiensis*, the distance between rows at the proximal end of the tentacle is significantly smaller than between rows at its distal end (Table 1). Such a narrow space between the two rows of pinnules at the proximal end of the tentacle is suggested to assist transportation of the smaller filtered particles to the mouth-opening. For example, we assume that phytoplankton particles in a size-range of 0.025–0.050 mm, such as the Red Sea dinoflagellates *Ceratium fusus* (see Post et al. 2002) and *Ceratocorys* sp. (see Rutman and Fishelson 1969) which are 0.025 and 0.050 mm in size, respectively (Menden-Deuer et al. 2001), will be consumed by *D. hemprichi* and not by *D. sinaiensis*. However, smaller phytoplankton items, such as the green algae *Nannochloropsis* sp. and *Tetraselmis* sp. (Fabricius et al. 1995a, b) may be captured easily by *D. sinaiensis*' longer and denser pinnules (see "Results"). We also suggest that *D. sinaiensis* has a somewhat narrower feeding niche in contrast to *D. hemprichi*, which seems to be a more generalist feeder. Therefore, if such a feeding-related partitioning of food items does indeed exist in *D. hemprichi* and *D. sinaiensis*, then Gause's (1934) Law is validated. Lasker et al. (1983), who examined the feeding rates of *Plexaura homomalla* and *P. nina* (see also "Introduction"), concluded that the morphological differences between their polyps led to different feeding habits and feeding rates. It was assumed that *P. nina*, which has larger polyps, is found at greater depths with prevailing weaker currents compared to shallower depths (Lasker et al. 1983, Witman and Dayton 2001). Since in our study a significant difference was found between the length of the tentacles of the polyps of *D. hemprichi* and *D. sinaiensis*, the difference between the particle sizes that they consume can be related to both the length of the pinnules and the distance between rows of pinnules along the tentacle as well as to the tentacles length. These results supply a solid background for future experimental work aimed at verifying the above.

Both *D. hemprichi* and *D. sinaiensis* posses the spindle-shaped sclerites (Fig. 4a, b) that are characteristic of the genus (Fabricius and Alderslade 2001). The antler-shaped sclerites found in *D. sinaiensis* are smaller compared to the spindles (0.1 vs. >1 mm: see Figs. 4b, d and 5). Indeed, it has been argued that *Dendronephthya* species displaying antler-shaped sclerites should probably be assigned to another genus (van Ofwegen, personal communication), an issue that requires future studies. Since antlers are also found in the tissue that surrounds the internal canals of the colony stalk (Fabricius and Alderslade 2001), it is unlikely that they play any role in supporting the polyps or in the feeding process. The spindle-shaped sclerites of *D. sinaiensis* are narrower than those of *D. hemprichi* (length-to-width ratio 17.53±5.73 vs. 11.71±3.04, respectively; Fig. 4a, b), and the shape of the former might confer on the tentacles a certain flexibility (Lewis and von Wallis 1991), thereby differentiating the filtering ability of the two studied species. The different flexibility of the tentacles of these two species is therefore also suggested to affect their filtering ability.

Our findings have revealed significant differences in morphological features of the polyps of *D. hemprichi* and *D. sinaiensis*, which may have led to differences in the size of the phytoplankton items upon which they feed. Although a long time has elapsed since Gause's (1934) Law was proposed, it is still being cited (e.g., Wang et al. 2005; Brucet et al. 2006; Gravel et al. 2006; Roney et al. 2009), and its validity is still being tested (e.g., Mikami et al. 2004; Roney et al. 2009).

Our current morphological findings imply the likelihood of agreement with Gause's principle, which can explain the partial depth overlap of the two octocoral species, whose coexistence is possible due to their different nutritional requirements in regard to a limited resource in an oligotrophic sea (Lindell and Post 1995). Future research is still required, however, in order to determine the specific preferences in terms of captured food items and feeding behavior of the studied species.

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