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Sponge-inhabiting barnacles on Red Sea coral reefs

Abstract In this study eight different species of barnacles were found within nine species of sponges from the Red Sea. This brings to 11 the number of sponge-symbiotic barnacles reported from the Red Sea, two of these are new *Acasta* species (not described herein) and one (*A. tzetlini* Kolbasov) is a new record for this sea. This number is much higher than that of symbiotic barnacles found within sponges from either the N. Atlantic (2) or the Mediterranean (4). Two possible explanations for this are the presence of numerous predators in coral reefs and scarcity of available substrate for settlement. These factors can lead to high incidence of symbiotic relationships. Of the nine sponge species, only one (*Suberites* cf. *clavatus*) had previously been known to contain barnacles. Even at the family level, this is the first record of symbiotic barnacles in two out of the seven sponge families (Latrunculiidae, Theonellidae). Our present findings strengthen the apparent rule that the wider the openings in a barnacle shell, the fewer the host taxa with which it will associate, usually from one or two closely related families, and the more frequent it will associate with elastic sponges. Most *Neoacasta laevigata* found on *Carteriospongia foliascens* were located on the same side as the sponge's ostia, i.e. facing the incoming water. This adaptation allows the barnacles to catch more suspended particles from the water, provides them with more oxygen and prevents their exposure to discharged sponge waste. The highest density of barnacles observed on one face of a "leaf" (with ostia) was 0.389 barnacles cm^{-2} (one barnacle per 2.57 cm^2) and on average 0.181 ± 0.68, while the average on the other side was only 0.068 ± 0.52 barnacles cm^{-2}. As indicated by the Morisita index, these barnacles most frequently (58%, $n = 12$) had a clumped spatial distribution (while the rest were randomly distributed), as is to be expected from such sessile organisms with internal fertilization via copulation. The presence of *N. laevigata* induced the growth of secondary perpendicular projections of its host *C. foliascens*. Of the *N. laevigata* examined, 17% brooded 324 ± 41 embryos each, of 286 ± 17 µm total length; only 5.7% ($n = 123$) were found to be dead. Size distribution analysis of skeletal elements from dead barnacles showed them to be significantly larger than the skeletal elements of the population of live barnacles ($p < 0.05$).

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Introduction

Free-living barnacles, which are a common component of the intertidal and shallow subtidal zones, have been the subject of numerous ecological studies since Darwin published his monographs in 1851 and 1854 (and even earlier). Symbiotic barnacles, however, although known to associate with many organisms (Anderson 1994), have received far less attention and usually were only dealt with in taxonomical literature (e.g. Newman and Ross 1976; Galkin 1989). Symbiotic balanomorph barnacles appear either on motile organisms (i.e. whales, sirenians, sea turtles, crocodiles, sea snakes, crustaceans and molluscs) or on (and inside the external surface layer of) sessile organisms like sponges, cnidarians and bryozoans.

One of the difficulties faced by a barnacle inhabiting a sessile organism is how to avoid obstruction of its orifice from the overgrowing tissue of its host. It has been

suggested that selection forces drove barnacles to inhabit hosts that have a laminar or branching growth form, which does not outpace the barnacle's growth (Anderson 1994). This should limit the types of potential hosts for epizoic barnacles. Studies of coral-inhabiting barnacles led a number of researchers to the conclusion that as the barnacles became morphologically more specialized, the number of potential hosts was reduced and more species specific (Foster 1980).

To date eight barnacle species have been reported in association with sponges from the Red Sea (Kolbasov 1993). This is a relatively high level of incidence compared with the number of species from larger, well-documented areas (e.g. two and four from the N. Atlantic and Mediterranean, respectively). Our aim in the present study was to illuminate the interactions between symbiotic barnacles and their sponge hosts for a better understanding of the degree of specificity and reciprocal influence. The research goals were, therefore, to survey Red Sea sponge fauna and (i) to determine the species richness of barnacles associated with them, with good identification of host and symbiont; (ii) to evaluate barnacle host species–specificity; and (iii) to assess sponge–barnacle and barnacle–barnacle interactions.

Materials and methods

Sponges were collected in the Red Sea between 1984 and 1996 by SCUBA diving (up to 30 m depth), from its southern (Dahalak Archipelago) to its northern part (Gulf of Eilat). They were then fixed upon collection in 4% formaldehyde, and preserved in 70% ethanol. The sponges were screened for the presence of barnacles. Detected barnacles were released from the sponge tissue either surgically or by application of mild nitric acid.

One of the sponges in which the presence of barnacles was detected already underwater was *Carteriospongia foliascens*. Therefore, we collected several complete specimens for analysis of barnacle population density and distribution. *C. foliascens* is a very flat sponge with leaf-like processes. The side of the leaf facing the external environment is covered with ostia (inlet openings; Fig. 1b), while the inward-facing side is covered with oscula (outlet openings; Fig. 1c). Thus to examine differences in

Fig. 1 *Neoacasta laevigata* within the sponge *Carteriospongia foliascens*. **a** A general view showing a cluster of barnacles close to the "leaf" tip. Most barnacles have their openings on the same side as those of the sponge leaf. Scale bar = 20 mm. **b** Close-up of the barnacles and their openings. Note the sponge's numerous small inlet openings (ostia). Scale bar = 1.5 mm. **c** Close-up of the barnacles from their base. Note several outlet openings (oscula) of the sponge, marked with arrows. Scale bar = 2.5 mm. **d** New secondary processes of the sponge originating at the location of barnacles (marked by arrows). Scale bar = 7 mm
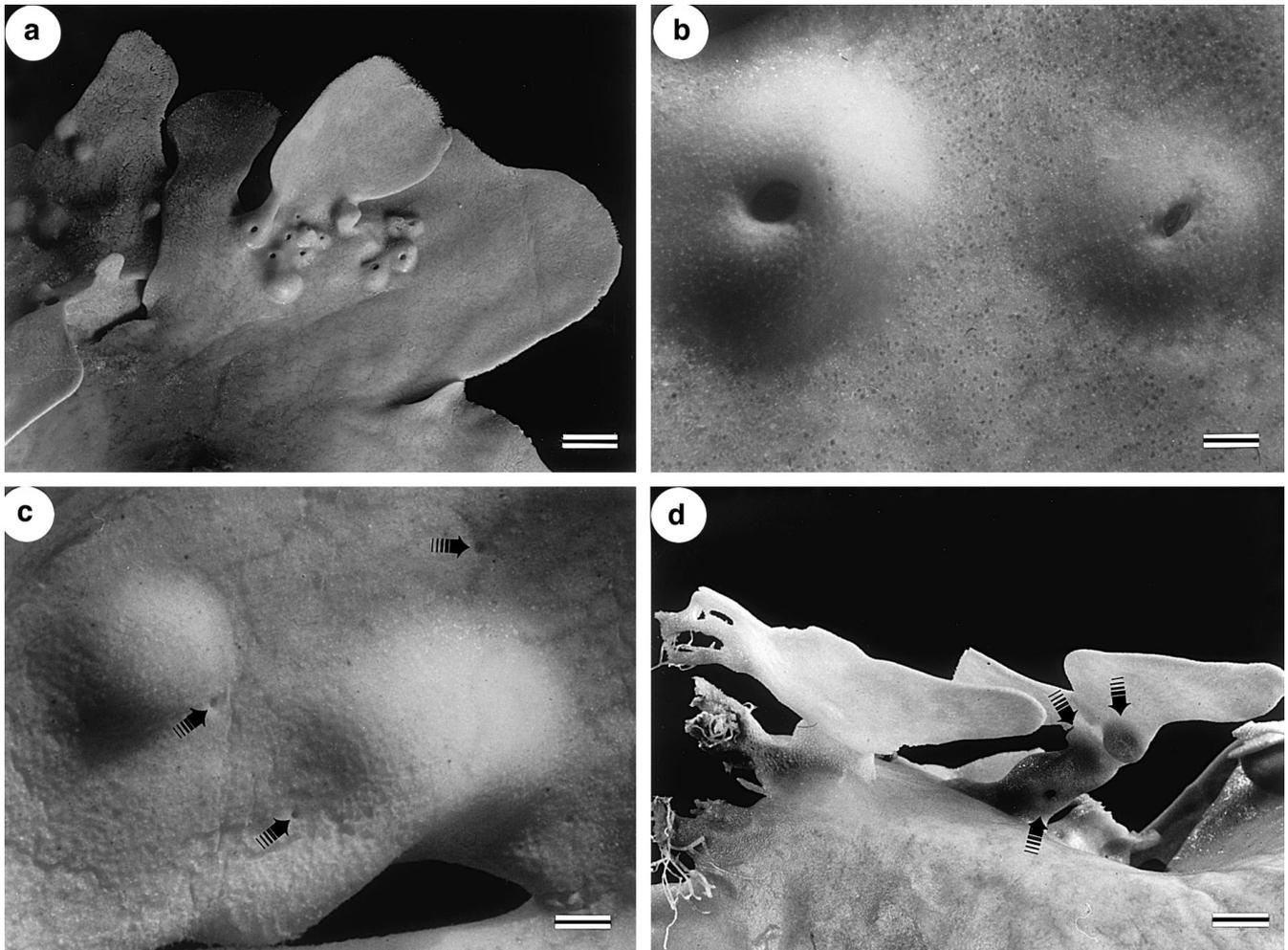
barnacle density between the two sides of the sponge, all barnacles were counted and a statistical analysis was performed based on analysis of variance (ANOVA) by permutation (Manly 1994). To determine barnacle density, the area of each leaf-like process of the sponge was measured using a computerized image analyzer (Olympus, CUE-3). The pattern of barnacle distribution on each side of the sponge leaf was examined by placing a grid containing three rows of equal-sized squares (500 mm^2 each) on the sponge; counts were taken of all barnacles in each respective square. Age distribution and reproductive state of the barnacles were examined to determine whether they were alive and whether they were brooding embryos. Each barnacle was measured for base length, base width and scutum length. Counts and measurements were repeated for both sides of the leaf-like sponge. Based on these samplings, the Morisita index was applied to determine the type of barnacle distribution on each side of the sponge's leaf (Krebs 1989).

Results

Species identification and distribution

Eight different species of barnacles were found in this survey within nine species of sponges in the Red Sea (Table 1). Only a single barnacle species was found within each particular sponge species, except *Euacasta dofleini* which was found inhabiting two sponge species.

Neoacasta laevigata (Gray). The morphology of the described specimen is typical of the species. The barnacle base may vary from cup-shaped to slightly flattened. A basal margin with six ribs, six main teeth and several

Table 1 Distribution of sponge-inhabiting barnacles from the Red Sea and their world distribution (? unidentified species)

Barnacle	Red Sea distribution (present study)		World distribution		Location (depth distribution)
	Sponge family	Sponge species	Sponge family	Sponge species	
Neoacasta laevigata (Gray)	Spongiidae	*Carteriospongia foliascens*[b]	Spongiidae	*Phyllospongia* sp.	Zanzibar, Madagascar, New Guinea, Islands, Philippines, South China Sea, Andaman, Palau, Red Sea (1–2.5 m)
			Dysideidae	*Dysidea* sp.	
Euacasta dofleini (Krüger)	Theonellidae	*Theonella conica*[b]	Chalinidae	*Gellius* sp.	South Japan, South China Sea, Indonesia, New Guinea, southeastern Africa, Red Sea (3–280 m)
	Callyspongiidae	*Callyspongia* sp.[b]	Chalinidae	*Haliclona* sp.	
			Callyspongiidae	*Callyspongia diffusa*	
			Myxillidae	*Iotrochota* sp.	
			Crellidae	*Crella* sp.	
			Pachastrellidae	*Pachastrella* sp.	
			Stellettidae	?	
			Axinellidae	*Pseudaxynassa* sp.	
			Desmacidonidae	?	
			Thorectidae	*Cacospongia* sp.	
			Leucettidae	*Leucetta* sp.	
Acasta cyathus Darwin	Thorectidae	*Hyrtios erecta*[b]	Spongiidae	*Ircinia campana*	Florida, N. Carolina, Caribbean Sea, Morocco, eastern Africa, Manaar Bay, Singapore, Indonesia, Philippines, western Australia, Red Sea (2–180 m)
			Spongiidae	*Ircinia felix*	
			Spongiidae	*Spongia tubulifera*	
			Dysideidae	*Dysidea* sp.	
			Aplysinidae	*Verongula ardis*	
			Callyspongiidae	*Callyspongia (Spinosella) vaginalis*	
			Haliclonidae	?	
			Geodiidae	*Erylus ministrongulus*	
			Tetillidae	*Cinchyra keukenthali*	
			Stellettidae	?	
			Mycalidae	?	
			Coppatiidae	?	
Acasta tzetlini Kolbasov[a]	Axinellidae	*Acanthella carteri*[b]	Axinellidae	?	Madagascar, Red Sea[a] (2–12 m)
Acasta pertusa Kolbasov	Latrunculiidae	*Diacarnus erythraenus*[b]	Haliclonidae	*Haliclona* sp.	Red Sea (3–39 m)
Acasta sp. nov. 1[a]	Latrunculiidae	*Negombata magnifica*[b]			Red Sea[a] (3–40 m)
Acasta sp. nov. 2[a]	Myxillidae	*Acarnus* sp.[b]			Red Sea[a] (8–12 m)
Membranobalanus longirostrum (Hoek)	Suberitidae	*Suberites* cf. *clavatus*	Suberitidae	*Suberites inconstans*	Western Pacific and Indo-Pacific: Indonesia, Sunda Strait, Manaar Bay, Bay of Bengal, Pamban, Red Sea (2–20 m)
			Spirastrellidae	*Spirastrella purpurea*	

[a] New record to the Red Sea
[b] New host for barnacles

minor teeth was the rule, but sometimes only the six ribs and six main teeth were found.

Euacasta dofleini (Krüger) is possibly the most variable species morphologically among the acastines. It inhabits a wide range of different sponges and has a wide geographic and bathymetric distribution (3 to 280 m).

Acasta cyathus Darwin is also a morphologically very variable species. The typical form has a very wide radius, a flat base and the opercular plates have a characteristic form. The examined specimens were similar to the typical form. Variations found included a typical scutum with strong radial striae; an articular ridge about one-half the width of the tergal margin, usually truncated, but occasionally long. The tergum spur was from one-third to one-half the width of the basal margin, with a rounded or truncated end. The internal surface of the tergum was usually without depressor crests, but sometimes with two depressor crests.

Acasta tzetlini Kolbasov specimens from the present study and from other localities, do not exhibit any distinct differences, except in the development of radial striae in the scutum and forms of the tergal spur.

Acasta pertusa Kolbasov specimens from the present study did not differ morphologically from the type specimen. Barnacles taken from *Diacarnus erythraenus* were found to contain embryos all year round (data not shown).

Acasta sp. nov. 1. The cirri were found to be reduced (third to sixth pairs bear only five to six segments), possibly after molting. Only one of the examined specimens was found alive, so no conclusion can be drawn concerning the armament and setation. This species (Fig. 2A) differs from other *Acasta* which possess large slits or windows: from *A. fenestrata* Darwin in having internal ribs of lateral plates; from *A. foraminifera* Broch in its carinolateral which reaches the base; from *A. alba* Barnard in its scutum having feebly developed internal sculpture (the pits of adductor and depressor muscles); from *A. tzetlini* Kolbasov in the width of the tergum spur being smaller (about one-third of the width of the basal margin) and the fact that its scutum does not bear radial striae; from *A. armata* Gravier in the absence of a chitinous process on its scutum; and finally from *A. pertusa* Kolbasov in the forms of its lateral plates. *Acasta* sp. nov. 1 is similar to *A. rimiformis* Kolbasov from New Guinea, but differs from it in having the well-developed internal ribs of lateral plates and an absence of radial striae or ribs on the outer surface of the scutum. A complete description of this species awaits the finding of additional live specimens.

Acasta sp. nov. 2. Although all the examined specimens were already dead upon collection in the field, they represent an unusual species (Fig. 2B). It differs from other acastines in having special lateral processes of parietes below the radii (the so-called pseudoradii). A complete description of this species also awaits the discovery of further live specimens.

Membranobalanus longirostrum (Hoek) which in other studies was found within two other sponges (one of them also a *Suberites* species) did not show substantial morphological differences among the various hosts.

Ecological notes regarding *Neoacasta laevigata*

The discovery of numerous specimens of *Neoacasta laevigata* in nearly all *Carteriospongia foliascens* individuals examined enabled a more quantitative study. This sponge has two distinctive sides to each leaf-like process. On one side the sponge ostia (water inlet openings) are concentrated while its oscula (water outlet openings) are located on the other side (Fig. 1). Examination of barnacle distribution between the two sides of these leaf-like processes revealed that significantly more barnacles were found on the ostia side, which faced the external environment and thus the incoming water ($p < 0.05$; ANOVA by permutation). The highest density of barnacles observed on one face of a leaf (with ostia) was 0.389 barnacles cm^{-2} (one barnacle per 2.57 cm^2) and on average 0.181 $\pm$ 0.68, while the average on the other side was only 0.068 $\pm$ 0.52 barnacles cm^{-2}. Barnacle density did not depend on size of the leaf as seen by the absence of statistically significant differences in density of barnacles on leaves of various sizes. Similarly, the linear regression of barnacle density dependence on leaf size was not significant, and the R^2 values were low for both ostia and oscula sides (0.17 and 0.31, respectively).

Analysis of the spatial distribution of barnacles on each side of the sponge's leaf, using the Morisita index, revealed that on most of the leaves (58%, $n = 12$) the barnacles had a clumped distribution, whereas the rest were randomly distributed.

Since marine invertebrate size frequently relates to age, we measured sizes of several barnacle skeletal elements. These barnacles usually had an elongated base which varied in size (Table 2). Whereas the ratio between the largest and smallest scutum found was 3.15, the ratio in base length was 3.44. Indeed, examination of the distribution of three group sizes for each of the two factors (base and scutum length) revealed normal distribution (Fig. 3).
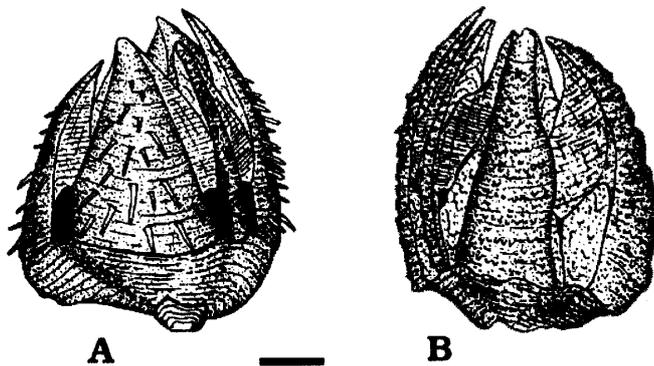

Fig. 2 Two new undescribed species of *Acasta* from Red Sea sponges. **A** *Acasta* sp. nov. 1 from *Negombata magnifica*. Scale bar = 1.4 mm. **B** *Acasta* sp. nov. 2 from *Acarnus* sp. Scale bar = 0.8 mm

Table 2 Size dimensions of *Neoacasta laevigata* within the sponge *Carteriospongia foliascens*

	Base length (mm)	Base width (mm)	Scutum (mm)
Min.	2.00	1.67	1.25
Max.	6.88	5.69	3.94
Mean	4.79	3.93	2.57
SD	1.08	0.89	0.60
n	116	113	113
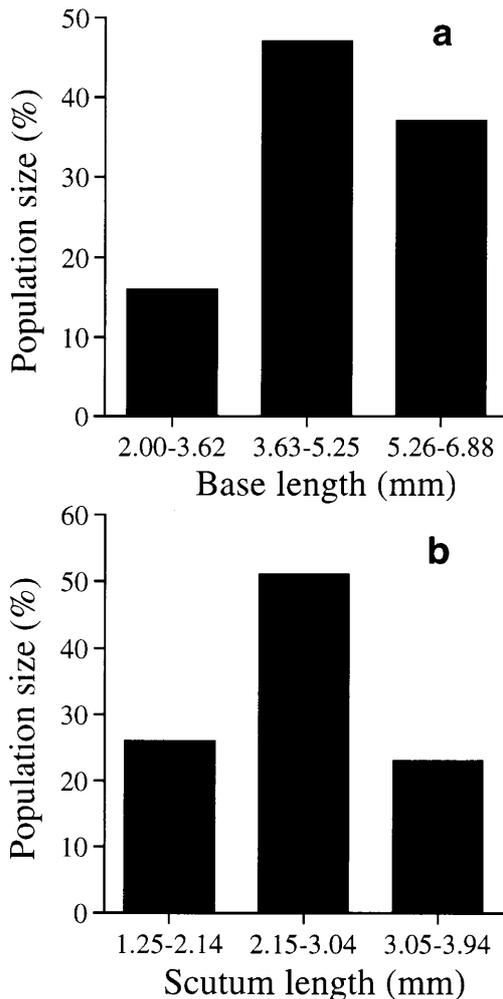
Fig. 3 *Neoacasta laevigata.* Size distribution of skeletal elements. **a** Base length; **b** scutum length

Only 5.7% (*n* = 123) of the barnacles examined were found to be dead. Size distribution analysis of skeletal elements from dead barnacles was established primarily through measurements of base length, since the scutum was only found on two occasions. The base length measurements averaged 5.73 ± 0.81 mm, and were significantly greater than the average for the entire population of live barnacles (4.72 ± 1.07; *p* < 0.05).

Barnacle presence was frequently noted to influence sponge morphology. In such cases, the sponges started to grow, from the point of barnacle location, a secondary leaf-life process perpendicular to the primary one. The existence of leaf divergence could thus indicate barnacle presence. Indeed, in 87% (*n* = 127) of all cases of secondary perpendicular projections, there was at least one barnacle at the origin of these projections. Alternatively, it can be argued that barnacles settle preferentially in places where the sponge is thicker. However, since most barnacles exist on the sponge in locations without such projections, and some projections are devoid of barnacles, the second alternative seems to be less likely.

Of all barnacles opened, 17% brooded embryos. The size of these reproductive barnacles, although slightly larger, was not significantly different from the size of nonbreeding ones. The studied barnacles contained 324 ± 41 embryos (*n* = 2), of total length 286 ± 17 μm (*n* = 18). The reproductive period, however, is unknown, since samples were taken only during a single month (October).

Discussion

Sponges are known to contain an array of secondary metabolites (i.e. natural products) with potent biotoxic and cytotoxic properties (Bakus et al. 1986; Faulkner 1996). These compounds are considered to act in a variety of ways, mostly as defensive mechanisms against predators (Pawlik et al. 1995), against pathogens (Becerro et al. 1994), and to assist in competition with neighboring benthic organisms (Porter and Targett 1988; Sears et al. 1990; Butler et al. 1996). This raises the question of whether barnacles are able to settle on such chemically active substrates, and maintain close contact between the sponge and their own tissues. The present study verified the ability of several barnacle genera to maintain a high degree of coexistence with sponges, which results in a non-free-living state in species of these barnacle genera. Moreover, these symbiotic barnacles occupy different sponges from various families (Table 1), many of which are considered toxic. Residence in sponges may thus provide the barnacle with protection from predators, which avoid the sponges' chemical defense mechanisms. In addition, such barnacles may reduce their own investment in physical armor (i.e. skeleton), and thus may allocate the energy conserved to other activities (e.g. growth or reproduction).

Of the nine sponge species found in the present study to harbor barnacles, only one (*Suberites* cf. *clavatus*) had previously been known to contain barnacles (Table 1). Even at the family level, this is a first record of barnacle symbionts in two out of the seven sponge families (Latrunculiidae, Theonellidae). The latter is of special interest, since lithistid sponges (like the Theonellidae) are well documented in fossil records (Enay 1990). Examination of such fossils may, therefore, enable scientists to trace back the initial appearance of symbiotic barnacles in that group of sponges.

Two of the symbiotic barnacles are apparently new species of *Acasta* (Fig. 2), while the rest are known. With

the exception of *A. tzetlini*, all these barnacles were previously recorded in the Red Sea (Table 1). Our finding elevates the number of known sponge-associated barnacles in the Red Sea to 11. This high number of species compared with other locations (see Table 2 in Kolbasov 1993) deserves explanation. It appears (with the possible exception of Australia) that sponge-associated barnacles are frequent in tropical coral reefs, whereas in cooler environments the number of species drops significantly. It was suggested that the observed difference is phylogenetically driven, since the acastine center of origin is in the South China Sea to Indonesia (Kolbasov 1993). The Red Sea, however, is quite far from this region. Therefore an alternative ecological factor may explain the observed high species abundance. Coral reefs are considered to have a high number of predators, while having a low amount of available substrate for settlement. This can lead to a high incidence of symbiotic relationships (Levinton 1995). Indeed in the Red Sea free-living barnacles are rare in coral reefs, whereas barnacles symbiotic with stony corals, gorgonians and sponges are much more common (Brickner 1994). In addition, the number of studies carried out in the Red Sea specifically examining the presence of these barnacles is higher than in other places including most other Indo-Pacific sites.

Of the six previously recorded barnacles, three were found in hosts from one of the families already known to contain these barnacles (Table 1). One barnacle (*Acasta cyathus*) was found in a thorectid sponge which is very close to the already known spongiid hosts. *Euacasta dofleini* was retrieved from a theonellid sponge which is taxonomically remote from the previously known hosts. These last two findings of barnacles (*E. dofleini* and *A. cyathus*) within the Thorectidae and Theonellidae correspond well with them being the most generalist regarding host specificity, as well as geographical and depth distribution. The genus *Acasta* appeared in the fossil record in the Miocene (Kolbasov 1996), and the species *A. cyathus* has also been detected in that period (Buckeridge 1985). The antiquity of these species may explain their present circum-tropic distribution and wide range of hosts. Other geographically widely distributed barnacles like *Neoacasta laevigata* or *Membranobalanus longirostrum* are, on the other hand, more specific in their selection of hosts, and have as yet been found in only two sponge families.

Kolbasov (1993) observed that several barnacle species residing in elastic sponges have slits, which in some species are wider and have a window-like appearance. He further noted that the wider the openings, the fewer the hosts with which the barnacle is associated, usually from one family. Our present findings generally support this observation and broaden the apparent rule. We observed that the greater the barnacle's tissue connection with its host, via either its lateral opening or membranous (instead of calcareous) base, the narrower its range of hosts. These hosts were also from only one or two (usually closely related) families. This observa-

tion was reinforced when we examined barnacles with large areas of tissue contact, which also had a more extensive geographical distribution than their local host (e.g. *Membranobalanus longirostrum*). In this case the species was determined to be associated with only three species of hosts. All the specimens of *Acasta tzetlini* (a species with skeletal slits) found so far were collected from axinellid sponges, and only within a relatively limited geographic distribution. A restricted distribution and limited range of hosts was also recorded for *A. pertusa*, the species with the largest windows observed in the present study (Fig. 4). This latter species, however, occupied two species of elastic sponges from different, not closely related families. While *Neoacasta laevigata* has a wide geographical distribution and no skeletal slits, it has still been reported from only three closely related hosts over its entire distribution. If the above-mentioned rule is valid, we would expect to find more hosts harboring *N. laevigata*. Yet, since *N. laevigata* is the most adapted (apomorph) species in the genus *Neoacasta* (other species have a flattened base, latticed scutums, or scutums with radial striae), its circle of hosts might be expected to be narrower compared
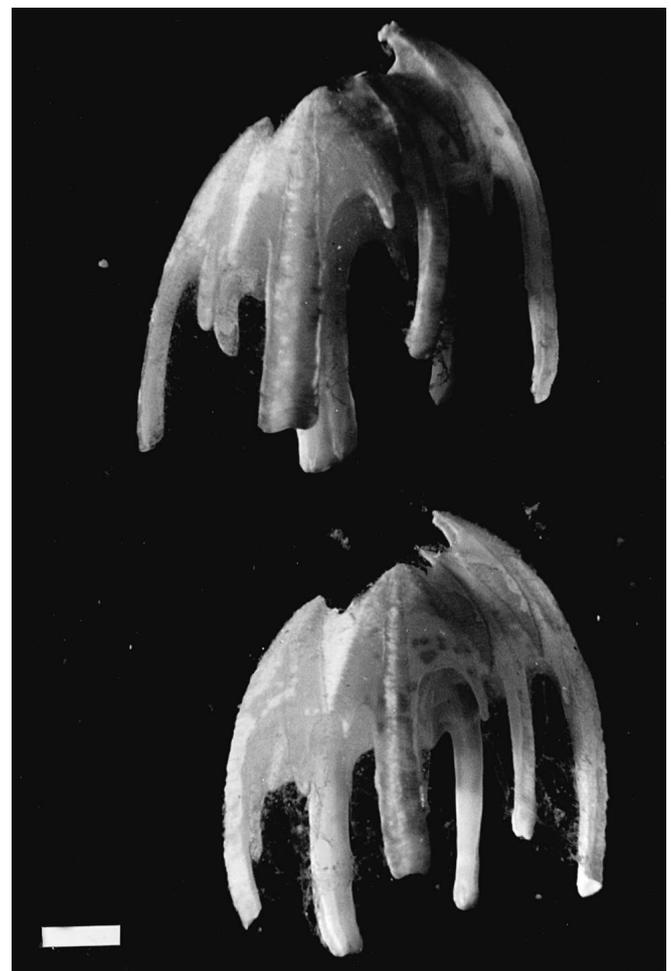

Fig. 4 *Acasta pertusa*. Skeleton with extremely large "windows". Scale bar = 1.0 mm

with other *Neoacasta* species. Finally, demonstrating the rule the two most generalist barnacles have the greatest range of hosts; both *Euacasta dofleini* and *A. cyathus* have minimal tissue contact with their hosts since they have a calcareous base and no slits in their skeleton.

Barnacles which inhabit other sessile organisms (e.g. corals and sponges) face the danger of being overgrown and completely buried by the host tissue. A barnacle settling on sessile organisms that grow along an axis perpendicular to the barnacle growth direction and location of the opening (e.g. erect branching or foliaceous forms) would thus appear to avoid overgrowth. It is evident, however, that sponge-inhabiting barnacles are not confined to host species which have branching or thinly encrusting morphology (Anderson 1994; Table 1, present study). Two species of massive hemispherical-shaped sponges were found as hosts in the present study (*Theonella conica* and *Suberites* cf. *clavatus*), but they appear to be slow growing (M. Ilan, unpublished data). This slow growth rate probably allows the symbiotic barnacles to exist without being buried by the growing sponge tissue. It should be noted, however, that in other studies (see Table 1) barnacles have been found to inhabit massive sponges which might be of a faster growing variety (e.g. *Ircinia felix* and *I. campana*). The mode (if one exists) of how barnacles cope with overgrowth in such sponges is still an open question.

Most *Neoacasta laevigata* found on *Carteriospongia foliascens* were located on the side which faces the incoming water. This is an adaptation which allows the barnacles to trap more suspended particles from the water. Moreover, in still water, the active water pumping during sponge filtering activity provides more oxygen, prevents exposure to the discharged sponge waste and provides particles for the symbiotic barnacles as well, reducing their need to filter actively. Since barnacles generally feed on particles larger than those taken in by sponges, no competition for food particles should exist between the two symbionts. Furthermore, the direction of the sponge pumping activity may facilitate settlement of *N. laevigata* cyprids on the side of the sponge bearing the ostia.

The fact that the symbiotic *Neoacasta laevigata* had a clumped distribution on most *Carteriospongia foliascens* sponges was expected, since a key factor in the pattern distribution of barnacles on a substrate is the distance from the nearest neighbor, as these are sessile organisms which copulate (Lewis 1992). The random distribution of barnacles on some sponge leaves, however, might be a result of several processes. Table 1 shows that *N. laevigata* is restricted to very few, closely related sponges. This might be the result of some chemical attraction of its larvae to the host, as was observed for several other symbionts (reviewed by Pawlik 1992). This is in contrast to other free-living barnacles, which have demonstrated the probable presence of a chemical metamorphosis inducer in conspecific tissue that causes gregarious settlement (Clare 1995). Indeed, in the case of *N. laevigata* the macro-distribution, locating a host, is probably chemi-

cally mediated; but in the event of no additional stimulus, the micro-distribution on the sponge will be random, as has occasionally been observed. Such micro-distribution, however, might be affected by an additional conspecific-derived stimulus which causes clumped distributions. Another possible explanation for the apparent pattern of barnacle distribution is that our observation recorded a dynamic situation. In early stages of sponge colonization, therefore, gregarious settlement may still be absent. With an increase in barnacle density, however, such a pattern of distribution should appear. The opposite situation may occur when a sponge outlives its inhabitants; upon barnacle death sponge tissue may cover their remains and thus obscure initial gregarious settlement. One possible factor favoring gregarious settlement, as mentioned above, is the need for close settlement which could enable the copulation that characterizes barnacles. However, if settlement occurs at random, yet on a specific but limited substrate, the distance between individuals may still allow cross fertilization.

The normal size distribution of the barnacles may indicate continuous reproduction and settlement of new recruits all year round. This conclusion substantiates observations in which cold water barnacles have a single annual brood, whereas warm water barnacles produce several broods per year (Barnes 1989; Anderson 1994). It might be argued that the small number (5.7%) of barnacles found dead was a result of a young population the members of which had not reached maximal size (and age). Indeed the size of the dead barnacles was significantly larger than the live population's individual mean size.

The profound effect induced by barnacle presence on *Carteriospongia foliascens* morphology (the growth of secondary perpendicular projections) is intriguing and raises several questions. For example, what mechanism does the barnacle use to induce the sponge tissue to grow in a plane different from the regular one? How do the new projections influence the water-filtration efficiency of the sponge (and the barnacle)? Do the new projections help the sponges to withstand the high rate of sedimentation in their habitat? These are questions that remain for future study.

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