

Spatial Competition among Porifera: Solution by Epizoism*

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Summary. Sponges settling on solid substrates which are separated by sediment bottoms compete for the limited space. Some species have solved this problem by occurring as epizoans, thus avoiding the risk of being expelled from the habitat. The supporting species on the other hand, are specialized in that they possess skeletogenous ectosomal structures and aquiferous processes to maintain their integrity and to escape starvation or suffocation. Although specimens are sometimes intimately interwoven no chimaerid mixing of tissues was observed.

Introduction

In sponges, as in all sedentary organisms, the dispersal of free-swimming larval stages is controlled by a number of physical and chemical parameters. Success of settlement and subsequent metamorphosis depends on the duration of favorable conditions. If these sensitive stages of the life history are completed successfully, only extreme forces will endanger the further development of the organism.

The availability of a suitable substrate is one of the critical factors for sponge colonization. In shallow water or wherever strong water movement occurs it should be solid or at least stable enough to permit development of the organism until sexual maturity is reached. Occasionally, the sponge itself contributes to the stabilization of its substrate by attaching to and thereby connecting several pieces of substrate (sand grains, shells, gravel, etc.) unless a sudden storm during establishment of the colony prevents this effort. The influence of substrate stability on the species composition of shallow-water sponges in the Adriatic Sea has been demonstrated in an earlier contribution (Rützler, 1965a). There also, some mechanisms of spatial competition were discussed. The most common situation is that fast growing and otherwise

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robust species over-grow and suffocate their less vigorous neighbors, although several observations have been made on sponges which over-grow each other to a varying degree without any harm to either specimen.

It is the purpose of this communication to discuss such species, and to present quantitative data and anatomical findings on these interspecific relationships.

Materials and Methods

Spatial competition among sponges was studied in three Adriatic localities (Istria, Yugoslavia) in May 1962, September 1964 and March 1968. The moderately wind-exposed bays of Korrente Cape and Andrija Island (Rützler, 1965 b, Fig. 25) contain stable rocks of 15—200 liters volume in 1—10 m depth. They could be turned over by two divers in order to reach the sponge-covered lower surfaces.

At the exposed Cape of Cuvi blocks of 5—15 liters were collected from 1 m depth where they were securely anchored in rock channels (Rützler, 1965 b, Figs. 25, 30).

In Polari Bay several large boulders (1—3 m³) protrude from the sandy bay bottom in about 1.5-2 m of depth (Rützler, 1965 b, Figs. 25, 32). Numerous miniature caves measuring 15—40 cm across were eroded at the bases of the boulders. The sponges clustered on the upper surface of the cavities.

The sponge crusts and clusters were measured (covered surface area in cm², to nearest 0.5 cm), removed with a knife or scalpel, fixed in 4% formalin in sea-water and, after a week, transferred to 80% ethylene alcohol. The specimen complexes were photographed or drawn in the laboratory and then roughly dissected with razor blades for gross anatomy. Representative samples were embedded in paraffin, or 12% gelatin with subsequent freezing (cryostat) and cut at 7 μ m. Mallory's stain and haemotoxylin-eosin were used for staining.

Results

Species Composition and Quantitative Data. The species composition on blocks from Korrente, Andrija and Cuvi was quite uniform. Only encrusting and low-growing (pillow-shaped) specimens were present, due to the limited vertical spaces between lower rock surface and sediment of the sea-floor. Tidal and wind-generated currents provide abundant nutrients and keep the crevices clear of sediments. The substrate itself provides protection from solar radiation and therefore inhibits growth of competing algae. The spatial limitations of these habitats exclude most scraping predators (e.g. echinoids, fishes). In summary, we are dealing with miniature cave habitats which provide all favorable conditions for abundant sponge growth but only restricted substrate areas which are separated by dynamic sediment bottoms.

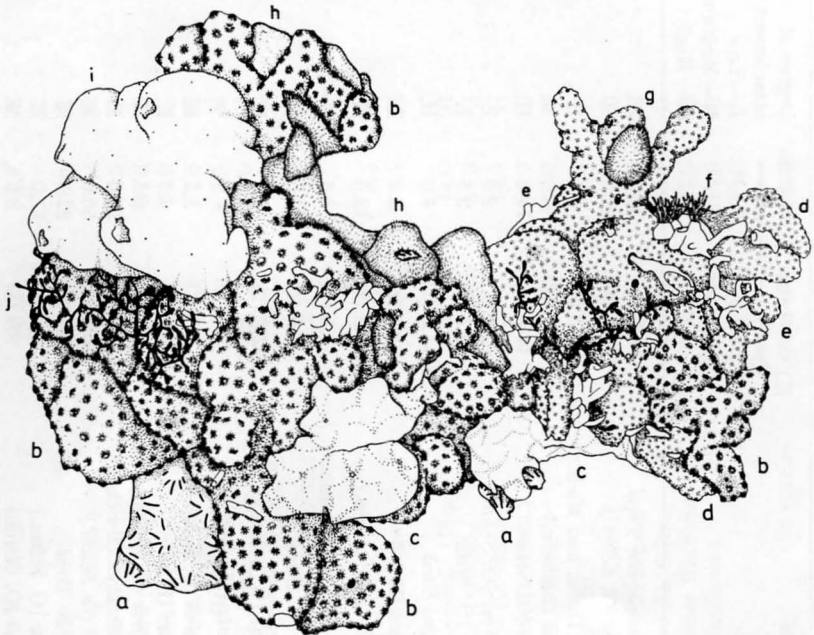


Fig. 1. Sponge assemblage from miniature cave in Polari Bay (drawing after photograph and preserved specimens before dissecting). The main supporter of most of the assemblage is *Fasciospongia cavernosa* (a). Epizoic species which in parts are also supporters are: *Ircinia spinosula* (b), *Crambe crambe* (c), *Ircinia oros* (d), *Clathrina falcata* (e), *Buskia* sp. (Bryozoa, f), *Sycon* sp. (g), *Antho involvens* (h), *Leuconia solida* (i), *Cornularia cornucopiae* (Anthozoa, j) ($1/2\times$)

The following six of a total of 34 sponge species are dominant in this environment (values in % of the area covered by the total sponge population):

<i>Ircinia oros</i>	24.7%
<i>Fasciospongia cavernosa</i>	14.2%
<i>Crambe crambe</i>	12.3%
<i>Antho involvens</i>	6.8%
<i>Ircinia spinosula</i>	6.6%
<i>Spongia virgultosa</i>	6.6%

One hundred and thirty four incidences in 54 species combinations were noted where specimens of the same or of different species were growing upon each other (Fig. 1). Where necessary, the healthy state of the overgrown sponge could be confirmed by histological sections.

Table 1. Qualitative and quantitative data on sponge epizoism

Supporting species	Total size (cm ²) (No. of specimens)	Over- grown area (cm ²)	Epizoic species	Total size (cm ²) (No. of specimens)	Epizoic area (cm ²)	Degree of attachment L = Low M = Medium H = High
<i>Penares helleri</i> (O. Schm.)	92.0 (2)	86.0	<i>Prosuberites longispina</i> Tops.	4.0 (1)	4.0	H
			<i>Antho involvens</i> (O. Schm.)	109.0 (1)	82.0	H
<i>Pachastrella monolifera</i> O. Schm.	28.5 (3)	24.0	<i>Terpios fugax</i> Duch. and Mich.	4.5 (1)	4.5	H
			<i>Myxilla rosacea</i> (Lieberk.)	12.0 (1)	5.0	M
			<i>Crambe crambe</i> (O. Schm.)	14.5 (1)	14.5	H
<i>Placospongia decorticans</i> (Hanitsch)	34.0 (1)	5.5	<i>Clathrina clathrus</i> (O. Schm.)	2.0 (1)	2.0	L
			<i>Dysidea avara</i> (O. Schm.)	3.5 (1)	3.5	L
<i>Mycale massa</i> (O. Schm.)	18.0 (1)	4.0	<i>Haliclona viscosa</i> Sarà	11.5 (1)	4.0	H
<i>Antho involvens</i> (O. Schm.)	7.5 (1)	2.5	<i>Clathrina falcata</i> (H.)	2.5 (1)	2.5	L
<i>Agelas oroides</i> (O. Schm.)	53.0 (1)	18.5	<i>Oscarella lobularis</i> (O. Schm.)	18.5 (1)	18.5	M
<i>Gellius fibulatus</i> (O. Schm.)	72.0 (1)	4.5	<i>Aplysilla sulfurea</i> F. E. Schulze	4.5 (4)	4.5	H
<i>Haliclona viscosa</i> Sarà	37.0 (2)	7.0	<i>Mycale massa</i> (O. Schm.)	8.5 (1)	7.0	H
<i>Aplysilla sulfurea</i> F. E. Schulze	3.5 (6)	3.5	<i>Gellius fibulatus</i> (O. Schm.)	122.0 (2)	3.5	H
<i>Dysidea avara</i> f. <i>pallescens</i>	9.0 (1)	2.0	<i>Clathrina falcata</i> (H.)	2.0 (1)	2.0	L
<i>Spongia virgultosa</i> (O. Schm.)	189.0 (7)	172.0	<i>Clathrina clathrus</i> (O. Schm.)	2.5 (1)	2.5	L
			<i>Clathrina falcata</i> (H.)	6.5 (3)	6.5	L
			<i>Oscarella lobularis</i> (O. Schm.)	6.5 (1)	6.5	M
			<i>Spirastrella cunctatrix</i> O. Schm.	15.0 (1)	15.0	M
			<i>Crambe crambe</i> (O. Schm.)	56.0 (2)	56.0	M
			<i>Anchinoe tenacior</i> Tops.	23.5 (1)	23.5	M
			<i>Antho involvens</i> (O. Schm.)	24.0 (1)	17.0	M
			<i>Gellius fibulatus</i> (O. Schm.)	8.0 (1)	8.0	M
			<i>Dysidea avara</i> f. <i>pallescens</i> (O. Schm.)	7.0 (1)	7.0	L
			<i>Ircinia fasciculata</i> (Pallas)	16.5 (1)	9.5	M
			<i>Ircinia oros</i> (O. Schm.)	16.5 (1)	16.5	L
			<i>Ircinia</i> (S.) <i>spinosula</i> (O. Schm.)	4.0 (1)	4.0	L

<i>Hippospongia communis</i> (Lam.)	16.5 (1)	8.5	<i>Anchinoe tenacior</i> Tops.	8.5 (1)	8.5	M
<i>Cacospongia scalaris</i> O. Schm.	6.5 (1)	4.5	<i>Ircinia oros</i> (O. Schm.)	4.5 (1)	4.5	L
<i>Ircinia oros</i> (O. Schm.)	476.0 (17)	287.0	<i>Clathrina falcata</i> (H.)	3.0 (1)	3.0	L
			<i>Leuconia solida</i> (O. Schm.)	15 (1)	1.5	M
			<i>Sycon</i> sp.	0.5 (1)	0.5	L
			<i>Geodia cydonium</i> (Jam.)	16.0 (1)	16.0	L
			<i>Crambe crambe</i> (O. Schm.)	56.0 (1)	56.0	H
			<i>Antho involvens</i> (O. Schm.)	22.5 (1)	12.5	H
			<i>Haliclona cratera</i> (O. Schm.)	43.0 (1)	33.0	M
			<i>Petrosia ficiformis</i> (Poirer)	178.0 (1)	26.0	L
			<i>Aplysilla sulfurea</i> F. E. Schulze	1.0 (2)	1.0	M
			<i>Dysidea avara</i> (O. Schm.)	7.5 (1)	7.5	M
			<i>Ircinia oros</i> (O. Schm.)	163.0 (3)	123.0	M
			<i>Ircinia</i> (S.) <i>spinosula</i> (O. Schm.)	7.0 (1)	7.0	M
<i>Ircinia</i> (S.) <i>muscarum</i> (O. Schm.)	17.5 (1)	1.5	<i>Aplysilla sulfurea</i> F. E. Schulze	1.5 (1)	1.5	M
<i>Ircinia</i> (S.) <i>spinosula</i> (O. Schm.)	211.5 (9)	89.5	<i>Clathrina falcata</i> (H.)	6.5 (1)	6.5	L
			<i>Leuconia solida</i> (O. Schm.)	1.5 (1)	1.5	M
			<i>Hemimycale columella</i> (Bow.)	14.0 (1)	14.0	H
			<i>Crambe crambe</i> (O. Schm.)	41.0 (1)	41.0	H
			<i>Antho involvens</i> (O. Schm.)	14.5 (1)	14.5	H
			<i>Gellius fibulatus</i> (O. Schm.)	5.0 (1)	5.0	M
			<i>Ircinia oros</i> (O. Schm.)	7.0 (1)	7.0	M
<i>Fasciospongia cavernosa</i> (O. Schm.)	480.0 (10)	452.0	<i>Clathrina falcata</i> (H.)	2.0 (1)	2.0	L
			<i>Leuconia solida</i> (O. Schm.)	9.0 (2)	9.0	M
			<i>Crambe crambe</i> (O. Schm.)	246.0 (5)	246.0	H
			<i>Antho involvens</i> (O. Schm.)	50.0 (2)	50.0	H
			<i>Spongia virgultosa</i> (O. Schm.)	31.0 (1)	31.0	M
			<i>Ircinia oros</i> (O. Schm.)	162.5 (4)	114.0	H

17 species $\Sigma 1,751.5$ (65) $\Sigma 1,172.5$

26 species $\Sigma 1,608.5$ (73) $\Sigma 1,172.5$

All data relevant to the observed epizoism of Adriatic sponges are listed in Table 1. The degree of attachment was classified as "low" when the specimens separated during handling or fixation; as "medium", if they had to be peeled from each other forcibly; as "high", if mechanical separation resulted in injuring either of the specimens. For the systematic description of the species see Rützler (1965 b).

Table 2. *Summary of data on sponge epizoism*

Position of sponges within association	Number of species	Total size of specimens in % of total population	Over-grown area in % of total specimen size	Epizoic area in % of total specimen size	Degree of attachment (%)		
					H	M	L
Supporting only	8	21.7	82.5		57.6	27.0	15.4
Epizoic only	17	24.5		78.5	27.5	37.5	35.0
Supporting or epizoic	9						
Supporting		30.5		56.0	27.7	42.5	29.8
Epizoic		23.3		67.0	51.5	36.5	12.0

Total number of specimens: 34. Total size of population: 3,360.0 cm².

Total number of species combinations: 54. Total contact area: 1,172.5 cm².

Total number of incidences: 134.

A summary of the listed data (Table 1) is given in Table 2. From this it appears that "supporting only" species are quite specialized in their function; they share a much higher percentage of coverage and stronger attachment than the facultative supporters. Of the epizoic species it can merely be said that either they arrive too late to occupy the primary substrate or they were expelled thence by their competitors. However, by means of epizoism they still are able to survive in the habitat. Whether they again expelled other species commonly occurring in the area (Rützler, 1965 b) but not found in the studied samples cannot be decided without experimental evidence. Successions of different species did not occur during the 6 years' duration of the observations.

Anatomy of Attachment. Electron microscopy studies by Brønsted and Carlsen (1950) and Borojevic and Lévi (1967), revealed that sponges are attached to their substrate by a layer of interwoven collagen fibrils secreted on contact with the substrate by basopinacocytes or basopinacoblats. At least among the species investigated, it is likely that this "horny" layer corresponds to spongin "A" as understood by Gross *et al.* (1956).

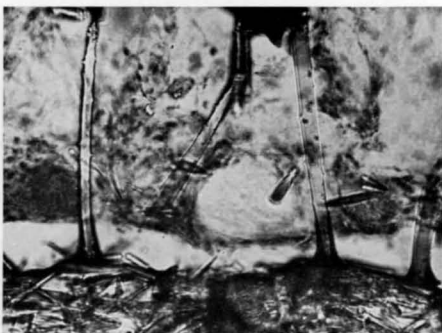


Fig. 2. *Antho involvens* growing on *Penares helleri*. The crevice between the two specimens and an ostium of *Penares* can be noted (paraffin section, $7\ \mu\text{m}$, Mallory stain) ($50\times$)

Fig. 3. Acanthostyles of *Antho involvens* glued onto the cortex of *Penares helleri* (paraffin section, $7\ \mu\text{m}$, Mallory stain) ($240\times$)

Fig. 4. Same preparation as in Fig. 2. Oxeon of *Penares* partly protruding into *Antho* ($50\times$)

From Table 1 it becomes apparent that all supporting species which are frequently or heavily overgrown either have a cortex of siliceous spicules (*Penares*, *Pachastrella*) or belong to keratose genera (e.g. *Spongia*, *Ircinia*, *Fasciospongia*). The latter possess a well-developed ectosomal membrane of parallel bundles of spongin "A" fibrils. How important is a skeletogenous ectosomal structure for successful overgrowth? Is the integrity of the two specimens involved unimpaired or do incidences of chimaerid specimens occur, as described by Little (1966)?

The remarkable case of 100% coverage occurred in one of the species with cortical siliceous skeleton, *Penares helleri*. The epizoic *Antho involvens* covered and extended beyond it so that the true situation was only discovered in the micro-anatomical preparation (Fig. 2). The

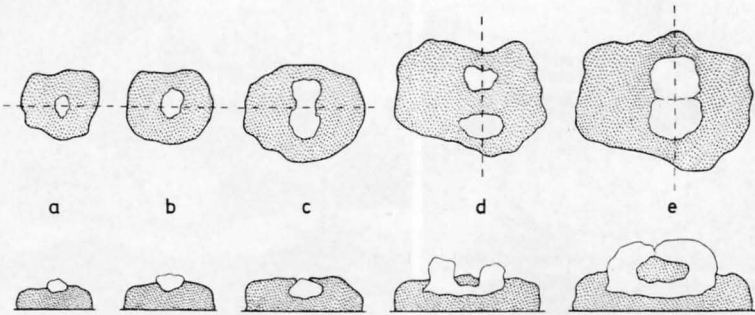


Fig. 5a—e. *Ircinia spinosula* (stippled) and *Ircinia oros* in different states of overgrowing each other (schematic reconstruction; upper row in top view, lower row in cross section): *Ircinia oros* is settled (a), expands (b), is being partly overgrown (c, d), continues to grow at the free ends (d) which fuse together enclosing part of *Ircinia spinosula* (e) ($1/3\times$)

question arises as to how *Penares* is able to sustain its water currents and hence obtain food and dispose of waste products. Fig. 3 shows how the spicules (acanthostyles) of *Antho* are glued onto the cortex of *Penares* by means of small patches of spongin. The tissue in between these points of attachment is elevated leaving a crevice of 30—50 μm . Assuming that this crevice is not an artifact its presence would make the necessary water circulation possible. In favor of this view is also the fact that ostia are developed and apparently functional in *Penares*. The supporting species suffered complete loss of pigments as the only sign of its unusual situation. On the other hand, several of the large *Penares* oxeas were noted projecting partially into the choanosome of *Antho* (Fig. 4). This can be explained as a reaction to too close a contact and consequent obstruction of water circulation. Similar reactions have been observed in *Tethya* (?) (unpublished) which expels its large diactines under unfavorable conditions.

In most other instances the contact is more intimate, parts of the supporting specimen, however, still being exposed to water. Usually, the basal membrane of the epizoic specimen is firmly fused with the ectosomal membrane of the supporter which in such places has no openings to the aquiferous system developed.

The history of a case of competition could be reconstructed from dissection of a mass consisting of two *Ircinias* (*Ircinia oros* and *Ircinia spinosula*) (Fig. 5). By alternative overgrowing the two specimens were finally completely interwoven. At the areas of contact the overgrown specimens had lost all pigments and even the conuli, which are otherwise typical surface structures.

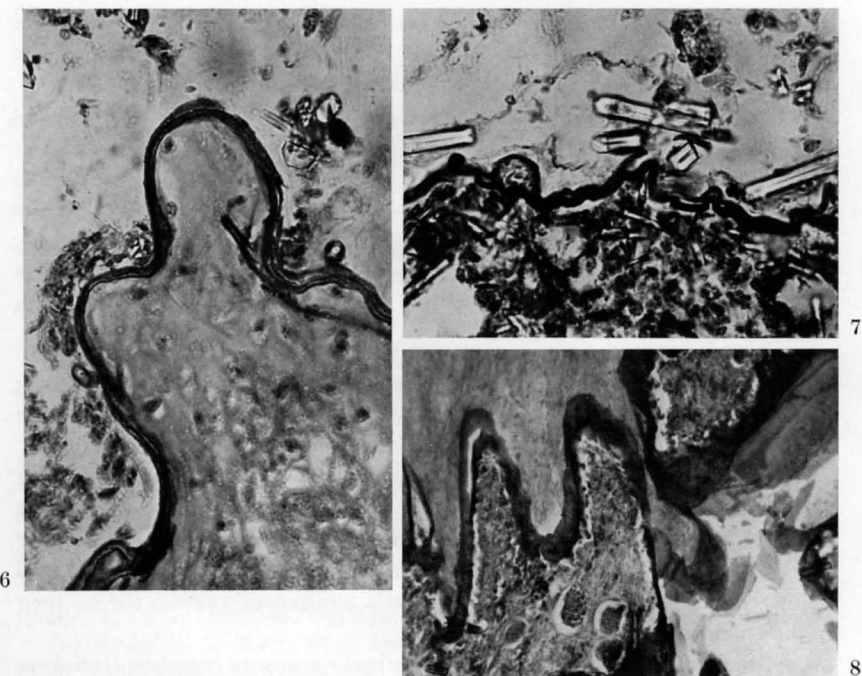


Fig. 6. Close attachment of *Crambe crambe* on *Ircinia spinosula*; surface and basal membranes fused together (paraffin section, 7 μ m, Mallory stain) (240 \times)

Fig. 7. Preparation as in Fig. 6; *Haliclona viscosa* on *Mycale massa* (240 \times)

Fig. 8. Preparation as in Fig. 6; *Crambe crambe* on *Fasciospongia cavernosa* (240 \times)

Conuli and similar surface processes are not always lost but often closely duplicated by the epizoic specimen, e.g. *Haliclona viscosa* on *Mycale massa*, *Crambe crambe* on *Ircinia spinosula*, *Ircinia oros* on *Fasciospongia cavernosa*, *Crambe crambe* on *Fasciospongia cavernosa* (Figs. 6—8).

Another surface structure — membrane incorporated sand grains in *Ircinias* — can either be lost or solidified during contact. For example, where *Crambe crambe* is attached to *Ircinia oros* the usual netlike sand structure on the *Ircinia* surface has turned into a solid sand layer. Likewise, *Leuconia solida* is anchored on a thick sand layer on the *Ircinia oros* surface. On the other hand, where *Haliclona cratera* touches *Ircinia oros* all conuli, pigment and sandgrains are lacking, the *Ircinia* is slightly depressed at the contact area; exceptionally, a concentration of ostia was developed there. This *Haliclona-Ircinia* relation is the only one which can be suspected to be of more than a facultative nature. *Haliclona*

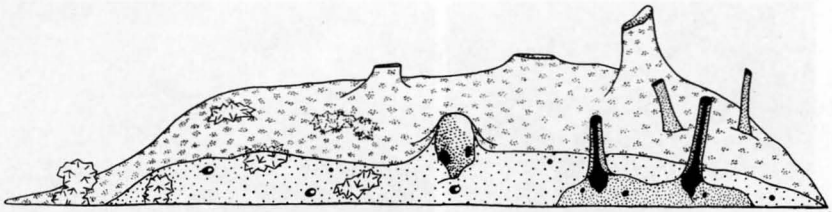


Fig. 9. *Gellius fibulatus* supporting and overgrowing *Aplysilla sulfurea* (left), which thus also occurs endozoic. *Spongia virgultosa* (right) overgrown by *Gellius*, only the oscular tubes are showing on the surface (1×)

cratera has usually been found attached to *Ircinia oros* (Topsent, 1925; Rützler, 1966), but also on *Ircinia fasciculata* (Sarà, 1958; 1961) *Ircinia spinosula* and *Petrosia ficiformis* (Rützler, 1966).

An unusual relation was observed between *Gellius fibulatus* and *Aplysilla sulfurea* (Fig. 9). The small growing species of *Aplysilla* not only settles on *Gellius* but is enclosed in the tissue as the supporting specimen grows. Thus it lives in unchanged condition several millimeters below the *Gellius* surface using its host's aquiferous system for its own requirements.

A very close attachment and intermingling occurs between *Haliclona viscosa* and *Mycale massa*. The histological sections, however, reveal that although both specimens grow into each other in a very complex way they remain clearly separated by basal and ectosomal membranes (Fig. 7).

Spongia virgultosa and *Fasciospongia cavernosa* seem to be specialized "supporters". In fact, in the course of this work they have never been observed other than completely overgrown, with the exception of the oscular tubes or processes which remain uncovered for water exchange (Fig. 9).

Epizoic organisms other than sponges were rarely seen. The tunicate *Didemnum maculosum* (Milne-Edwards) was the only one which was sometimes closely attached to sponges. Anthozoans, like *Cornularia cornucopiae* Pallas and bryozoans, like *Buskia* sp. use stolons when settling (Fig. 1). The scyphozoan *Stephanoscyphus* is a well known endobiont of sponges. Neither type can be considered as a significant epizoan of sponges.

To summarize, one might say that skeletogenous surface and basal structures are always present where epizoism occurs, and they may even be strengthened by incorporated sand. No chimaerid mixing of specimens from different species was found. Firm cortical structures and tubular aquiferous processes facilitate a high degree of epizoism. With

the possible exception of *Haliclona cratera* all observed incidences are cases of facultative epizoism.

Further study of more and different isolated substrate types will be needed to obtain a complete picture of the occurrence and mechanism of epizoism among sponges. For this purpose the suitability of mangrove (*Rhizophora*) roots in certain parts of the tropical Atlantic has already been pointed out (Rützler, 1970). A more experimental approach to the subject might reveal chemical attractions or immunological reactions influencing the interspecific relations among supporting and epizoic species.

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