

# Symbiotic relationships between hydroids and bryozoans

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## Abstract

Hydroids have established several symbiotic relationships with bryozoans. The association with Bryozoa probably evolved independently within the Hydrozoa. In fact, three unrelated hydroid families, Lovenellidae, Cytaeidae and Pandeidae, have only one species each that is symbiotic with bryozoans, whereas the Zancleidae probably went through a wide radiation leading to specialized associations with the Bryozoa. The symbiosis with Hydrozoa is recorded in few bryozoan families: almost all zancleids are associated with species of the families Schizoporellidae, Phidoloporidae and Lepraliellidae. Other families, extremely common both in tropical and temperate waters were never recorded in association with hydroids. The association between hydroids and bryozoans seems to require a high degree of specialization resulting in peculiar trophic strategies ranging from commensalism to parasitism and in morphological modifications as tentacle reduction and hydrorhiza covering by the bryozoan skeleton.

**Keywords:** Symbiosis, hydroids, bryozoans, mutualism, parasitism, trophic strategies

## 1. Introduction

Many hydroids are symbiotic with other benthic organisms like algae, seagrasses, sponges, cnidarians, molluscs, polychaetes, bryozoans, echinoderms, tunicates, and vertebrates (Boero and Bouillon, 2005). Some of these epibionts live on the external skeletal structures of the host (e.g. several hydractiniids on the shells of gastropod molluscs, or *Probosciodactyla flavicirrata* (Brandt, 1835) on the rim of polychaete tubes), but others, like those symbiotic with bryozoans or sponges, directly settle on the living epithelium or inside the tissues of the host.

The symbiosis between hydroids and bryozoans involves several genera, namely *Zanclaea* Gegenbaur, 1857 (Fig. 1), *Halocoryne* Hadzi, 1917, *Zanclella* Boero and Hewitt, 1992, *Cytaeis* Eschscholtz, 1829, *Octotiar*a Kramp, 1953, and *Hydranthea* Hincks, 1868 (Boero and Sarà, 1987; Boero and Hewitt, 1992; Piraino et al., 1992; Gravili et al., 1996; Bavestrello et al., 2000; Boero et al., 2000). Generally, these relationships are described as mutualistic:

the bryozoan receives protection from predators such as turbellarians and molluscs by the nematocysts of the polyps, while the hydroid may exploit the water circulation generated by the feeding activity of bryozoan zooids, sometimes obtaining protection by the overgrowth of the calcareous bryozoan skeleton on the hydrorhiza. Osman and Haugsness (1981) experimentally demonstrated that the colonies of the bryozoans *Schizoporella errata* (Waters, 1878) and *Celleporaria brunnea* (Hincks, 1884) associated with *Zanclaea* hydroids are more successful competitors for space and less prone to predation than colonies of the same species without associated hydroids. Ristedt and Schuhmacher (1985) obtained similar results in a field study on the competitive ability of the coral reef bryozoan *Rhynchozoon larreyi* (Audouin, 1826) associated with an unidentified species of *Zanclaea*. Nevertheless, behavioural studies on *Halocoryne epizoica* Hadzi, 1917 and *Cytaeis schneideri* (Mutz-Kossowska, 1905) demonstrated that the relationship between hydroids and bryozoans can shift towards a form of parasitism (Piraino et al., 1992; Bavestrello et al., 2000): both hydroids, in fact, have been shown to feed directly on the bryozoan host.

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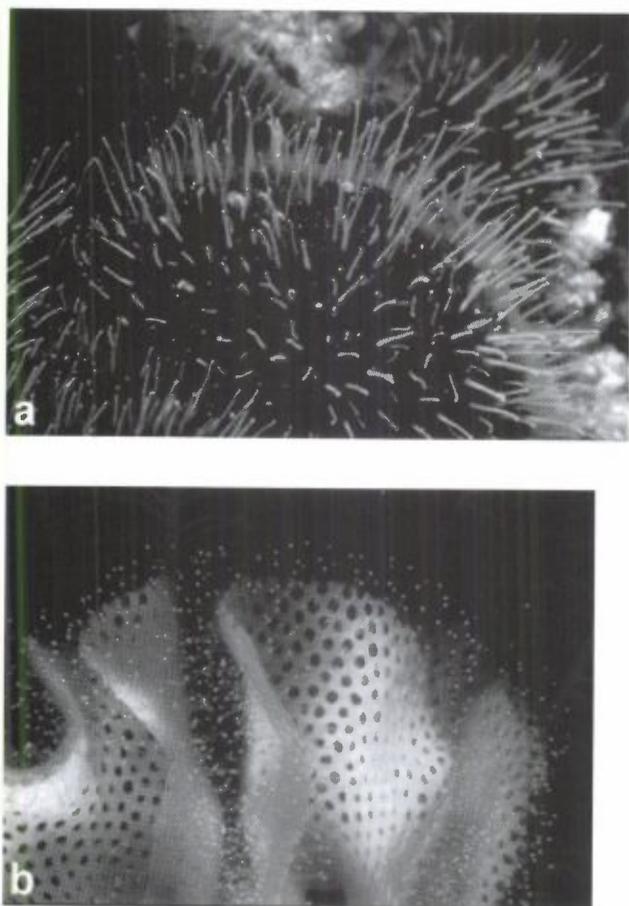


Figure 1. Field photograph of *Zanclaea divergens* symbiotic with the dark encrusting bryozoan *Celleporaria sibogae* (a) and *Zanclaea tipis* on *Triphyllozoon* cf. *inornatum* from North Sulawesi (Indonesia) coral reef (b).

## 2. Results

### *Hydroid species associated with bryozoans*

#### *Fam. Lovenellidae*

In the Mediterranean, *Hydranthea margarica* (Hincks, 1863) can live on different substrata, mainly algae, but show a constant association with the bryozoan *Chartella tenella* (Hincks, 1887). The hydrorhiza is not adherent to the surface of the bryozoan but it is anchored by perisarc projections of the hydrorhiza penetrating among the zoeciae at regular intervals (Boero and Sarà, 1987) (Fig. 2a).

#### *Fam. Cytaeidae*

The Mediterranean *Cytaeis schneideri* occurs in association with the orange encrusting bryozoan *Schizoporella longirostris* Hincks, 1886 (Bavestrello et al., 2000). The hydroid colony shows two types of gastrozooids different in size and in the ability to extend. The hydrorhiza,

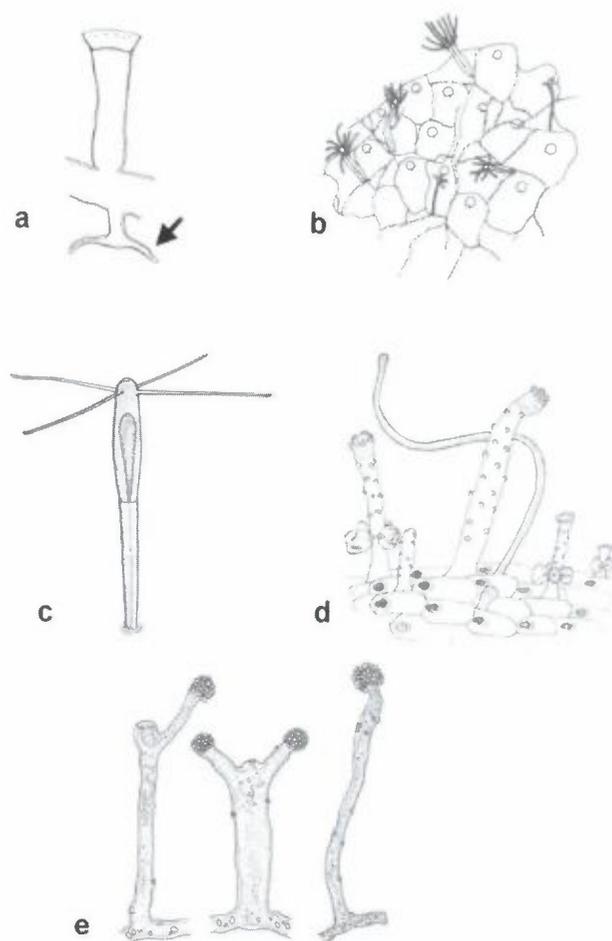


Figure 2. Examples of hydroid species symbiotic with bryozoans. *Hydranthea margarica* showing specialized hydrorhiza with perisarc projections (arrow) (redrawn from Boero and Sarà, 1987) (a). Polymorphic colony of *Cytaeis schneideri* (redrawn from Bavestrello et al., 2000) (b). Polyp of *Octotiarca russelli* (redrawn from Boero and Bouillon, 1989) (c). Polymorphic colony of *Zanclaea tipis* (redrawn from Puce et al., 2002) (d) and *Zanclella bryozoophila* (redrawn from Boero and Hewitt, 1992) (e).

covered by perisarc, grows on the bryozoan surface, in the grooves between adjacent zoeciae (Bavestrello et al., 2000) (Fig. 2b).

#### *Fam. Pandeidae*

The tropical *Octotiarca russelli* Kramp, 1953 is symbiotic with the bryozoan *Steginoporella mandibulata* Harmer, 1926. The hydrorhiza grows under the bryozoan skeleton; the hydranths, characterized by four tentacles, arise among zoeciae (Boero and Bouillon, 1989) (Fig. 2c).

#### *Fam. Zanclaeidae*

Three zancleid genera are involved in the association with bryozoans: *Halocoryne*, *Zanclaea*, *Zanclella*.

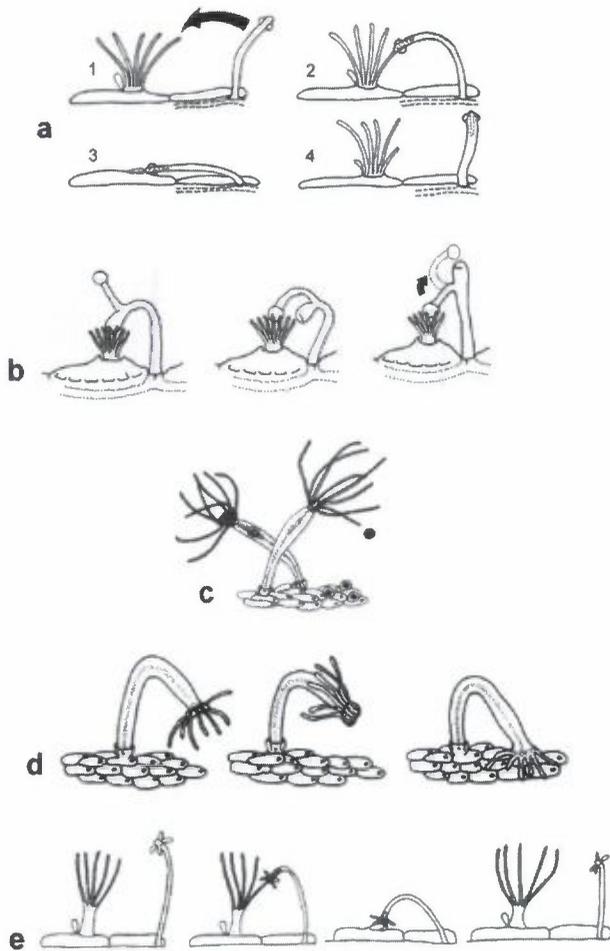


Figure 3. Feeding strategies of some hydroid species symbiotic with bryozoans. *Halocoryne epizoica* "biting" the lophophoral tentacle (redrawn from Piraino et al., 1992) (a). *Zanclella bryozoophila* exploiting the water current produced by the bryozoan (redrawn from Boero and Hewitt, 1992) (b). Large gastrozooids of *Cytaeis schneideri* feeding on newly released bryozoan larvae (c) and protruding the gastrovascular wall that adheres to the bryozoan surface (d). Filiform gastrozooids of *C. schneideri* engulfing the tip of a single lophophoral tentacle (e). (c–e, redrawn from Bavestrello et al., 2000).

#### Genus *Halocoryne*

In the Mediterranean Sea, *Halocoryne epizoica* presents polymorphic colonies occurring on the bryozoan *Schizobrachiella sanguinea* (Norman, 1868) (Piraino et al., 1992). The reticular hydrorhiza is normally covered by the bryozoan skeleton. Gastrozooids and dactylo-gonozooids are very contractile and lack tentacles (Boero et al., 2000) (Fig. 3a).

Two tropical species *H. frasca* Boero et al. 2000 and *H. pirainoid* Boero et al., 2000 show polymorphic colonies

living in association with unidentified bryozoans. Also their hydrorhizae grow under the bryozoan skeleton (Boero et al., 2000).

#### Genus *Zanclea*

In the Eastern Pacific (Central California), *Zanclea bomala* Boero et al., 2000 is associated with an unidentified bryozoan (Boero et al., 2000) and in Indonesian waters lives on the reteporiform bryozoan *Triphyllozoon* cf. *inornatum* Harmer, 1934 (unpublished). Boero et al., 2000 observed the hydrorhiza hidden under the bryozoan skeleton, while the colony associated with *Triphyllozoon* cf. *inornatum* shows the hydrorhiza clearly visible on host skeleton.

*Zanclea divergens* Boero et al., 2000 was described from Papua New Guinea (Boero et al., 2000) and is also widely recorded from North Sulawesi in association with the encrusting dark bryozoan *Celleporaria sibogae* Winston & Heimberg, 1986 (Puce et al., 2002) (Fig. 1a) and with an unidentified white-yellow spotted bryozoan (unpublished). The colonies growing on *C. sibogae* show the hydrorhiza covered by the bryozoan skeleton (Boero et al., 2000; Puce et al., 2002) while on the unidentified white-yellow spotted bryozoan the hydrorhiza runs in the grooves among zoecie (unpublished).

The tropical species *Zanclea retractilis* Boero et al., 2000 and the New Zealand species *Zanclea polymorpha* Schuchert, 1996 were recorded living in association with the encrusting bryozoan *Rhynchozoon larreyi* (Schuchert, 1996; Boero et al., 2000). In both species the hydrorhiza grows under the bryozoan skeleton. *Z. retractilis* is not polymorphic, whereas *Z. polymorpha* shows gastrozooids, dactylozooids and rare gonozooids (Schuchert, 1996).

The Indonesian *Zanclea tipis* Puce et al., 2002 lives in association with the reteporiform bryozoan *Triphyllozoon* cf. *inornatum* (Fig. 1b). The hydrorhiza, covered by perisarc, grows under the bryozoan skeleton and the polymorphic colony is composed of gastro-gonozooids and dactylozooid (Puce et al., 2002) (Fig. 2d).

*Zanclea exposita* Puce et al., 2002 was recorded from Indonesian waters associated with the encrusting bryozoan *Rhynchozoon* sp.. The colony is not polymorphic and the naked hydrorhiza grows on the bryozoan surface (Puce et al., 2002).

The Mediterranean *Zanclea sessilis* (Gosse, 1853) was observed in association with the bryozoan *Beania* sp. and the tropical *Zanclea protecta* Hastings, 1930, *Zanclea giancarloii* Boero et al., 2000 and *Zanclea hirohitoi* Boero et al., 2000 were observed in association with unidentified bryozoans. The colonies of *Z. sessilis*, *Z. protecta*, *Z. giancarloii* are not polymorphic, while *Z. hirohitoi* is characterized by gastrozooids, dactylozooids and tentaculozooids. The hydrorhiza of all these four species grows under the bryozoan skeleton (Gravili et al., 1996; Boero et al., 2000).

### Genus *Zanclella*

*Zanclella bryozoophila* Boero and Hewitt, 1992 was recorded from Central California associated with *Schizoporella* sp. The hydrorhiza is embedded in the bryozoan host and the polymorphic colony is composed of gastrozooids and gonozooids with a reduced number of tentacles (Boero and Hewitt, 1992; Boero et al., 2000) (Fig. 2e).

The tropical *Zanclella diabolica* Boero et al., 2000 and *Zanclella glomboides* Boero et al., 2000 were observed living in association with unidentified bryozoans. Both species shows polymorphic colonies with gastrozoid and dactylozooids characterized by a reduced tentacle number and their hydrorhizae grow under the bryozoan skeleton (Boero et al., 2000).

### Behavioural adaptations

Hydroids are generally considered as carnivorous, capturing their prey by means of nematocysts (Gili and Hughes, 1995). However, when symbiotic with other organisms, hydroids evolved unusual trophic strategies (Cerrano et al., 1998; Cerrano et al., 2000). Hydroid species living in association with bryozoans are able to exploit their host both directly and indirectly (Boero and Hewitt, 1992; Piraino et al., 1992; Bavestrello et al., 2000; Puce et al., 2002). Several species of bryozoan-inhabiting hydroids, in fact, show trophic strategies so to exploit lophophoral water currents to collect particulate matter.

The dactylozooids of *Zancllea tipis* usually bend over lophophores and insert their apex among the lophophoral tentacles. The enlarged apex of the dactylozoid may collect the microparticles that stick on its surface (Puce et al., 2002). Similarly, the gastrozooids of *Zanclella bryozoophila* bend over until the hypostome is inside the tentacular crown of the lophophore. They also extend the tentacle inside the lophophore while the mouth is placed near the tip of lophophoral tentacles or is held upright. This action is immediately followed by the tentacle bending up toward the hypostome then touching the mouth suggesting the ingestion of particles collected inside the lophophore (Boero and Hewitt, 1992) (Fig. 3b).

*Halocoryne epizoica* is a micropredator of the bryozoan host, biting off the distal portions of its lophophoral tentacles. When the lophophores are everted, the polyps elongate so to come in contact with the tentacles of the lophophore. After few minutes of "touching", the polyps engulf the tip of a single lophophoral tentacle. The lophophore retracts and pulls the tip of the hypostome under the bryozoan operculum, to be released after few minutes. When the "bitten" lophophores evert again, the base of the broken tentacle is still visible and the piece of tentacle is in the coelenteron (Piraino et al., 1992) (Fig. 3a).

*Cytaeis schneideri* performs a parasitic behaviour on its bryozoan host (Bavestrello et al., 2000). Large gastrozooids

feed on newly released bryozoan larvae (Fig. 3c) and, furthermore, protrude the gastrovascular wall from the hypostome so to make it adhere to the bryozoan surface (Fig. 3d); after this behaviour, the pigment granules present in the bryozoan cuticle are found in the polyp coelenteron. Moreover, filiform gastrozooids are specialized in engulfing the tip of a single lophophoral tentacle, but, in contrast to *H. epizoica*, the tentacle tip is never broken (Fig. 3e). Probably, *C. schneideri* engulfs the particles stuck on the tentacle by this way.

On the contrary, in the association between *Zancllea divergens* and *Celleporaria sibogae*, the bryozoan exploits the hydroid by touching polyps with lophophoral tentacles until they regurgitate a mucous aggregate of particles. By means of rapid contraction, lophophores fragment the mucous into small portions on which they feed (Puce et al., 2002).

### Morphological adaptations

Decrease in tentacle size and/or number is a common feature of bryozoan-inhabiting-hydroids. The hydranths of *Octotiaru russelli* have just 4 tentacles (Fig. 2c), fewer than other pandeids (Boero and Bouillon, 1989). *Cytaeis schneideri* and many zancleids (3 of 10 *Zancllea* species known to grow on bryozoans, all *Zanclella* and *Halocoryne* species) are polymorphic (Fig. 2b, d), their polyps have few small tentacles or no tentacles at all. Moreover, in several *Zancllea* species the tentacles are reduced to sessile capitations (Boero et al., 2000; Puce et al., 2002).

The reduction in tentacle number and size is possibly due to the utilization by the hydroid of the feeding currents generated by the lophophores, with a shift from macrophagy to microphagy. Moreover, micropredator-parasitic species as *Halocoryne epizoica* and *C. schneideri*, feed directly on bryozoans, biting the lophophore or collecting particles sticking to it, and do not use tentacles even when they are present (Fig. 3a, e). Piraino et al. (1992) suggest that the ability of *Zanclella* to touch the lophophore without causing its retraction (Fig. 3b) might be a preadaptation for the direct utilization of the bryozoan as a food source by the associate hydroid, as seen in *H. epizoica*. Since the direct exploitation of the lophophore is present both in zancleids and in a cytaeidid, this ability evolved independently in the two clades.

The presence of a specialized hydrorhiza is a common feature of bryozoan-inhabiting-hydroids; in several species the hydrorhiza can grow under the skeleton of the bryozoan. The hydrorhiza of *Hydranthea margarica*, the only thecate hydroid known to be associated with bryozoans, is loose on the bryozoan surface, being anchored to the skeleton of the host by specialized perisarcular projections and not by adhesive substances (Boero and Sarà, 1987) (Fig. 2a). The hydrorhizae of zancleid hydroids typically grow under the bryozoan skeleton and polyps protrude from holes among

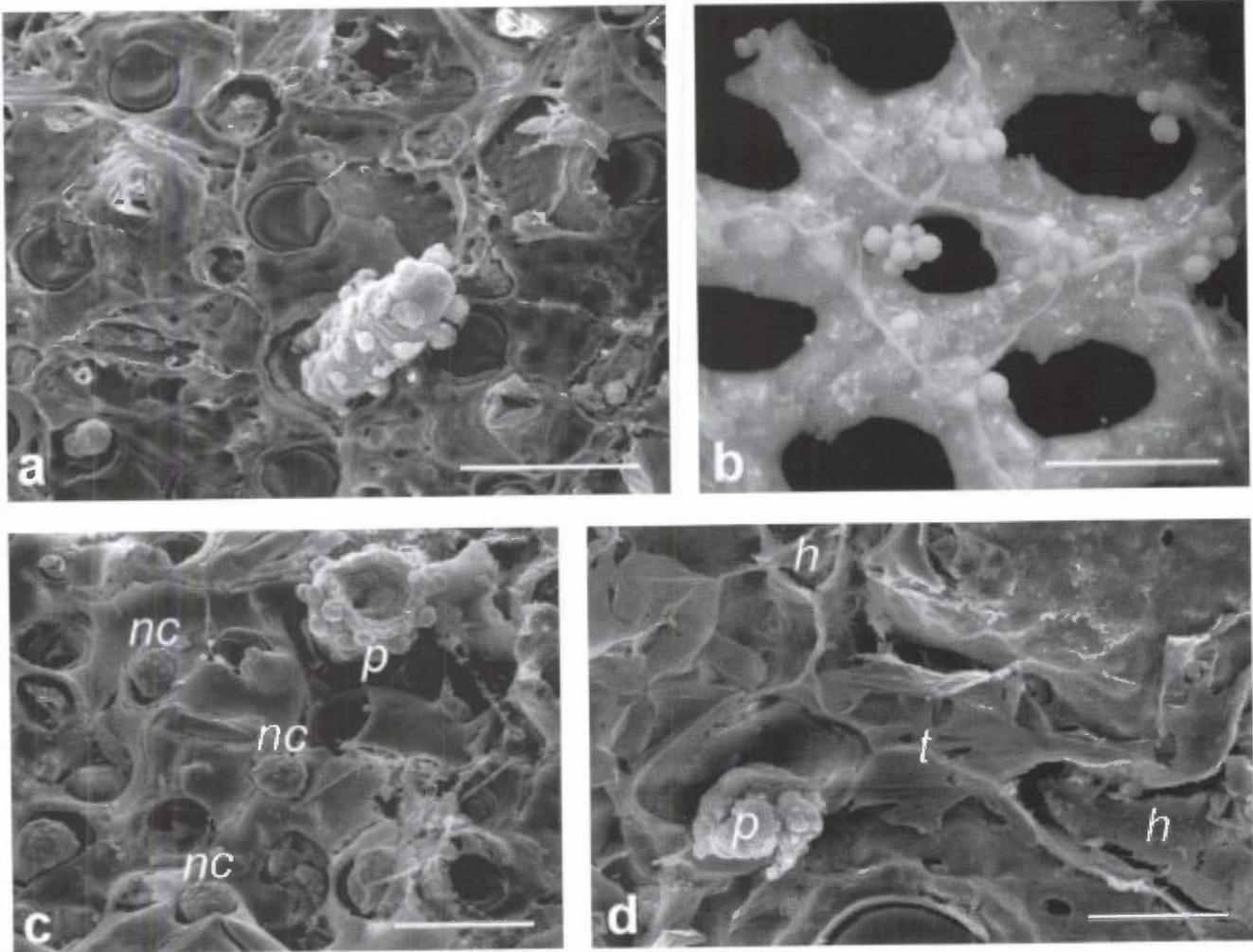


Figure 4. Scanning electron microscopy (SEM) image of a polyp of *Zanclea* sp. arising from a hidden hydrorhiza and protruding among zoeciae (a). *Zanclea bomala* associated with *Triphyllozoon* cf. *inornatum* showing the hydrorhiza covered only by a calcareous tube (b). SEM image of a polyp (p) and nematocyst clusters (nc) of *Zanclea divergens* symbiotic with *Celleporaria sibogae* arising from a hidden hydrorhiza (c). SEM image of *Z. divergens* symbiotic with the white-yellow spotted bryozoan showing the polyp (p), "holes" from which polyps will arise (h) and the calcareous tube (t) enveloping the hydrorhiza (d). Scale bars: 250  $\mu$ m (a, c); 700  $\mu$ m (b); 100  $\mu$ m (d).

zoeciae (Fig. 2d; Fig. 4a, c). Moreover, the polyps of *Zanclella* and of some *Zanclea* species, when disturbed, can completely retract under the bryozoan skeleton, becoming invisible (Boero et al., 2000).

Hydroid stolons grow on bryozoans by following the grooves that delineate adjacent walls of zooids; bryozoans react by overgrowing the hydrorhizae with their calcareous skeletons (Osman and Haugness, 1981; Ristedt and Schuhmacher, 1985). The defence by bryozoan skeletons can replace perisarcal protection: the hydrorhiza of zancleid hydroids associated with bryozoans is often naked (Puce et al., 2002).

Hydroid epibiosis induces other morphological responses in epibiotic hosts, besides the covering of the hydrorhizae: the colonies of *Rynchozoon larreyi* have a homogeneous appearance, but the skeleton changes from a

regular rhomboid structure to an irregular reticulate pattern when epibiotic hydroids are present. This alteration is due to the formation of skeletal appendages during zoid growth and to a special mode of frontal budding. The protection offered by *Zanclea* polyps against small predators is indicated by the fact that avicularia, the typical anti-predator zooids of bryozoans, are rare in symbiotic colonies of *R. larreyi* (Ristedt and Schuhmacher, 1985).

The bryozoan reaction to the presence of different hydroid species leads to different hydrorhizal covering patterns. While *C. schneideri* and *H. margarica* show a completely uncovered hydrorhiza, the hydrorhiza of *O. russelli*, *Zanclella*, *Halocoryne* and several *Zanclea* species is hidden under the bryozoan skeleton. However, in some *Zanclea*-bryozoan associations the hydrorhiza is only enveloped by a thin calcareous tube that leaves it clearly

visible on the bryozoan surface (Fig. 4b, d). Probably, the hydrorhizal covering pattern is related to a species-specific interaction between hydroid and bryozoan. In fact, the same bryozoan (*Triphyllozoon* cf. *inornatum*) shows different hydrorhizal covering patterns for two associated *Zanclaea* species (*Zanclaea tipis* and *Zanclaea* cf. *bomala*): the hydrorhiza of *Z. tipis* is completely covered by the bryozoan skeleton, while that of *Zanclaea* cf. *bomala* is only enveloped by a thin calcareous tube (Fig. 4b). *Zanclaea divergens* is associated with two bryozoans (the dark encrusting *Celleporaria sibogae* and an undetermined yellow-white spotted encrusting species) and offers a different case to that of *Triphyllozoon* cf. *inornatum*. When *Z. divergens* lives on *C. sibogae*, its hydrorhiza is completely hidden and polyps arise from holes in the bryozoan skeleton (Fig. 4c), but when it is associated with the yellow-white spotted species, the hydrorhiza is evident and covered only by a thin calcareous tube (Fig. 4d). Also the calcareous tube is provided with holes from which polyps, nematocyst clusters and medusa buds arise (or will arise) (Fig. 4d). Probably, *Zanclaea* is able to inhibit the deposition of the bryozoan skeleton in these selected portions.

### 3. Discussion

Bryozoans are strong competitors for space. Their colonies can face overgrowth by other organisms by both mechanical (avicularia and vibracularia) and chemical defences. In particular, they produce a large variety of secondary metabolites with antifouling properties (Anthoni et al., 1990; Kionya et al., 1994). These defence systems limited the evolution of symbiotic associations with other groups, with the exception of hydroids, that commonly establish symbioses with bryozoans. The relationships evolved independently in four taxonomically unrelated families. However, the Lovenellidae, Cytaeidae, and Pandeidae have only one species each that is symbiotic with bryozoans, whereas most species of the Zanclaeidae are involved in this association, with peaks of diversity in tropical waters.

Few bryozoan families have species symbiotic with hydroids: almost all bryozoan-inhabiting-zanclaeids are associated with species of Schizoporellidae, Phidoloporinidae, and Lepraliellidae. Other families, extremely common both in tropical and temperate waters, are never associated with hydroids. The bryozoans associated with hydroids share two key features: large and strongly calcified colonies; sessile avicularia able to clamp shut only in a very restricted area surrounding the zooids. Strong calcification enhances hydrorhizal protection, whereas avicularian features might be crucial in allowing planula settlement. It is intriguing that the species of bugulids, extremely common in tropical waters, are always

devoid of hydroids. This could be due to the low level of calcification, but also to the wide presence in these species of regularly spaced penduncled avicularia able to protect the entire colony. Obviously the establishment of the symbiosis is also affected by the chemical defences of the bryozoan that the hydroid must face.

Intensive research on bryozoan-inhabiting-hydroids is relatively recent. Boero et al. (2000) described a great diversity of species in all the Zanclaeidae, showing how a family formerly retained as rather uniform was, instead, speciose. The ethology of bryozoan-inhabiting-hydroids, furthermore, is probably still partly known and the described behavioural patterns have surprising features, from the biting behaviour of *Halocoryne epizoica* to the sucking activities of *Cytaeis schneideri*.

The association of hydroids and bryozoans, thus, is a promising field in biodiversity research, leading to the discovery of both new taxa and new ethological patterns, thus enhancing our understanding of the evolution of strict symbioses, ranging from mutualism to parasitism.

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