Extrusive Bacterial Ectosymbiosis of Ciliates

Giovanna Rosati

1 Introduction

The number of well-established associations between ciliates and bacteria, reported in the literature, increases steadily. The majority of these studies refer to endosymbiotic associations; yet, ectosymbiotic bacteria have been reported to occur in different ciliate species. Although these associations appear to be well established and are potentially important for both the bacteria and the ciliate host, an interaction has actually been demonstrated only for a few cases.

Ectosymbiotic sulfur-reducing bacteria occur in a number of marine anaerobic ciliates, some of which also harbour endosymbiotic methanogens. The ectosymbiotic bacteria have different morphologies even in ciliate species of the same genus (Fenchel et al. 1977; Fenchel and Finlay 1991). Ectosymbiotic bacteria have also been reported for two anaerobic freshwater ciliate species, but only for those specimens retrieved from sulphate-rich environments (Finlay et al. 1991; Esteban and Finlay 1994). The production of H_2 in hydrogenosomes of the ciliates is probably significant in maintaining the symbiotic associations. The ciliates, very likely, could exist without the symbionts but the symbionts enhance their growth rate and yield, maintaining a low level of hydrogen tension (Fenchel 1991).

The association with chemolithoautotrophic sulfide-oxidizing bacteria has proven to be vital for some ciliates that inhabit marine sulfidic environments. The case of the genus *Kentrophoros*, originally described by Raikov (1971), is now a classic: these ciliates are known to carry a layer of bacteria on their dorsal side. The bacteria are able to divide on the ciliate surface and the ciliate phagocytizes the bacteria through the entire dorsal side, thus depending on its ectosymbionts for food. More recently, a second association has been described, which consists of sulfur-oxidising bacteria and the peritrich ciliate *Zoothamnium niveum* (Bauer-Nebelsick et al. 1996). The latter is a sessile, colonial species, which is invariably covered by bacteria. Preliminary studies indicate that nutrition of the host occurs by utilization of low molecular weight

G. Rosati (e-mail: rosatig@deee.unipi.it)
Dipartimento Etologia, Ecologia, Evoluzione, Università di Pisa, Via A. Volta 4–6, 56126 Pisa, Italy

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organic compounds produced by the symbionts, and also by digestion of the symbionts in trophic cells of the host colony (Rinke et al. 2003). Both *Kentrophorus* and *Zoothamnium* adopted behavioural traits that are used to optimise the physiological activity of their symbionts. Chemolithotrophic sulfide-oxidising bacteria require both sulphide and oxygen that coexist at only low concentrations in the natural environment. *Kentrophoros* is a microaerophile and shows a chemosensory response toward oxygen; in the natural environment, it moves vertically in sediments, always positioned just at the interface between oxidised and anaerobic sulfide-reducing layers (Fenchel and Finlay 1995). The feather-shaped colonies of *Zoothamnium* rhythmically expand and contract, thus exposing the ectosymbiotic bacteria alternatively to oxygenated water above and sulphidic water below the boundary layer on the surface of highly sulphidic peat (Ott et al. 1998).

The present study deals with an ectosymbiotic association which does not involve chemolithoautotrophic bacteria. Based on the current knowledge, the association appears unique with respect to at least two characteristics: 1) the peculiarity of the bacteria involved (referred to as epixenosomes) and 2) the kind of ecological advantage provided to the ciliate host.

2 The Ciliate Host

The eukaryotic partners of the consortium are marine, sand-dwelling, hypotrich ciliates. They have been assigned to the *Euplotidium* genus. Since Noland (1937) erected this genus, six species have been described. *Euplotidium itoi* and *E. arenarium* are the only two species characterised at the electron microscopical level.

A lateral view of *E. itoi* at SEM is shown in Fig. 1. The organism is oval in shape, 60–90 µm long and 40–52 µm wide. The somatic ciliature on the flat ventral surface consists of 12 frontoventral cirri, 6 transversal cirri and 1 left marginal cirrus. The huge buccal cavity is bordered by a well-developed series of membranelles. A prominent oral plate is present. On the dorsal convex surface are five rows of short cilia (dorsal bristles). In a depression of the body surface lies the band in which epixenosomes (from the ancient Greek *epi* = on, *xenos* = alien, *soma* = body) are inserted. The band extends along both sides and at the anterior end of the dorsal surface. *E. itoi* and *E. arenarium* are morphologically very similar; they only differ in the shape of the macronucleus (two elongated pieces in the former species and moniliform, i.e., like a string of beads in the latter) and the absence of a peristomial plate in *E. arenarium*.