Pseudostenotele, a new type of nematocyst, and its phylogenetic meaning within the Haleciidae (Cnidaria, Hydrozoa)*

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ABSTRACT: A new type of nematocyst, pseudostenotele, is described from hydrooids of the family Haleciidae. Its similarity with stenotele nematocyst is discussed. The phylogeny of Haleciidae is briefly outlined.

RESUME: Un nouveau type de nématocyste, les pseudosténotèles est décrit chez des hydroïdes appartenant à la famille des Haleciidae. Ses relations avec les sténotèles sont discutées. La phylogénie des Haleciidae est esquissée.

1. INTRODUCTION

The knowledge of nematocysts of thecate polyps is rather incomplete (see Bouillon 1984 for a review); the cnidome of many genera, and even families, has never been examined. The nematocysts of Haleciidae are known to be conspicuous in some genera, such as Campolecium and Hydranthea (Huvé 1954, Boero 1981), these nematocysts have been referred to as micro- and macrobasic mastigophores. The genus Halecium, the richest in species of the whole family, has mainly small nematocysts, except Halecium beauii which also possesses large macrobasic mastigophores (Bouillon 1984). Large nematocysts have often been reported from the nematophores of Ophiodissa, but have never been fully described.

2. OBSERVATIONS

The nematocysts of three species of Ophiodessa from the Mediterranean, Central California and Indian Ocean, and those present on the peculiar nematophores

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Figure 1. Pseudostenotele of Nematecium lighti.
of the only known species of Nemalectum, *N. lighti* (Hargitt 1924) are very similar. They are not assignable to any described nematoecyst type.

2.1. Description of pseudostenotes (Fig. 1, Table 1, Pls 1, 2)

Length of the capsule more than twice its width, a stout shaft is visible in the undischarged nematoecyst, occupying from half to the whole length of the capsule, according to the species. A long filament is coiled within the capsule. Two spines are generally visible near the insertion point of the shaft with the operculum. The shaft, in the discharged nematoecyst, has 1.0 to 1.3 times the size of the capsule (see Table 1). It has a short, unarmed base, which is separated by a constriction from the armed part of the shaft, which is much longer and gradually tapers distally. One to three spirally arranged rows of short spines are present along the distal part of the shaft. Two to four big spines are present at the level of the constriction. Other big spines may be present along the rows of short spines.

The position of the basal spines of the shaft in the undischarged pseudostenotes probably indicates that they have a function similar to that observed by Tardent et al. (1980) for the big spines of the stenotes. In stenotes the armed, distal part of the shaft is usually shorter than the basal part. Besides the basal ones, few other spines are present in stenotes, pseudostenotes are much richer in spines. The shape of the capsule is rounded or egg-shaped in stenotes, it is oblong in pseudostenotes. Stenotes are present in Capitata hydroids and medusae, and in the majority of the Actinulidae and Trachymedusae, but are unknown in thecate hydroids. The morphological and supposed resemblance of stenotes and pseudostenotes is probably due to parallelism.

3. DISCUSSION

3.1. The phylogenetic position of Nemalectum within the Haleciidae

Recent Barco & Tier (1997) have proposed the supraspecific classification of *N. lighti* into the family Haleciidae. However, this classification is based on some features that are currently under discussion among biologists.
phylogeny, on the basis of the reduction and disappearance of medusae stage and the appearance and specialization of nematophores and nematothecae. The redescriptions of *Nemateleum lighti* (see Bouillon 1986) provides further information about the evolutionary processes which could have led to the formation of nematophores in the family.

Nematophores are probably reduced polyps which have lost all their functions besides the defensive one. If this interpretation is correct then *Nemateleum* should be the most primitive known halecide possessing nematophores. In fact, polyp reduction is not appreciable at all, its nematophores are interpretable as specialized tentacles. The position of the nematocysts on the nematophore of *Nemateleum* and the way the nematophore is held by the polyp indicate that this structure has a defensive function, rather than an offensive one. Indeed, the nematophores are nearly permanently contracted towards the mouth and their nematocysts are disposed so that they are effective only when the nematophores are in this position.

The defensive function of microbasic mastigophores according to their position in contracted polyps, has been proposed by Boero & Sarà (in prep.) for *Hydranthea*. The presence of nematophores on the hydranth, here considered as primitive, puts *Nemateleum* in an intermediate position between *Halecium* (deprived of nematophores) and *Hyrodendron* (with nematophores, but with no nematothecae).

In *Hyrodendron* the nematophores are borne on the stem, so that they provide defence for the colony and not for the single hydranth as in *Nemateleum*.

The Haleciidae seem to have acquired their nematophores at the evolutionary level of *Nemateleum*. The presence of pseudostenotes on the tentacle-like nematophores of *Nemateleum* indicates that this genus is already well distinct from the primitive Haleciidae (*Campalecium* and *Hydranthea*, having micro- and macrobasic mastigophores) and that the formation of its nematophores does probably not derive from concentration in specialized structures (i.e. the nematophores) of the micro- or macrobasic mastigophores present on the web of *Campalecium* and *Hydranthea*. The possession of pseudostenotes in *Nemateleum* and *Ophiodissa* indicates that the species of the two genera are closely related.

The unique features of pseudostenotes suggest that the nematocysts present in halecide nematophores have undergone a separate evolution from the nematocysts of other families. Nematophores are structures analogous to the dactylozooids of athecate polyps; they are fairly widespread in Hydroid families and, in some cases, they have probably been acquired independently.

Pseudostenotes have also been found in *Zygophyllax* (Lafiocidae) (Gravier-Bonnet 1986), and recently in *Kirchenpaueria echinulata*, this last finding is a good indication that the Haleciidae could be the ancestors of the Plumularidae as suggested by Boero & Sarà (in prep.).

Further studies on Thecate and Leptomedusae nematocyst will probably lead to the discovery of new nematocyst types.
Figure 3. Phylogeny of the Haleciidae (redrawn and modified after Boero & Sarà).

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