Note on *Aglaophenopsis cartieri* (Bedot, 1921) (Cnidaria: Leptolida: Aglaopheniidae) and discussion of its taxonomic position

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A fertile specimen of '*Cladocarpus*' *cartieri* Bedot, 1921, from the mid-Atlantic ridge is redescribed. The species is referred to the genus *Aglaophenopsis* of the tribe Cladocarpini of family Aglaopheniidae where it should stand as *Aglaophenopsis cartieri* (Bedot, 1921).

Introduction

Material recently received for identification from Dr Michel Segonzac, CENTOB, IFREMER, Brest, France, originating from French-Portuguese deep-water research of the mid-Atlantic ridge, yielded some colonies of the rare deepwater leptolid '*Cladocarpus*' *cartieri* Bedot, 1921, amongst which one fertile specimen. The inclusion of this species in the genus *Cladocarpus* Allman, 1874, has so far been provisional as no fertile specimens had previously been described. The gonosome of the present fertile specimen was therefore studied in detail and the relationship of the species with the various genera of Aglaopheniidae was critically reviewed.

Material

Seahma-1, DR 02, 05.08.2002, 36º36.606'N 33º25.401'W, 2400-2650 m, next to Rainbow vent field: four colonies, 7-27 mm high, sterile; one colony, 32 mm high, fertile, with two mature gonothecae, one immature gonotheca and two modified secondary hydrocladia (phylactocarps, comparable to those found in *Aglaophenopsis hirsuta* Fewkes, 1881 (MNHN Hy 1292; RMNH-Coel. 30927, four slides 5279).

Description and remarks

In this material, the morphology of trophosome agrees with the descriptions of *Cladocarpus cartieri* given by Bedot (1921, original description), Ramil & Vervoort (1992a, redescription of type material) and Calder & Vervoort (1998, second record of the species). The only difference is in the asymmetrical disposition of the paired lateral nematothecae of the first hydrotheca in some hydrocladia of the fertile colony. In these cases, one nematotheca is placed at level of hydrothecal rim (normal position), but the other is displaced downwards (fig. 1a).

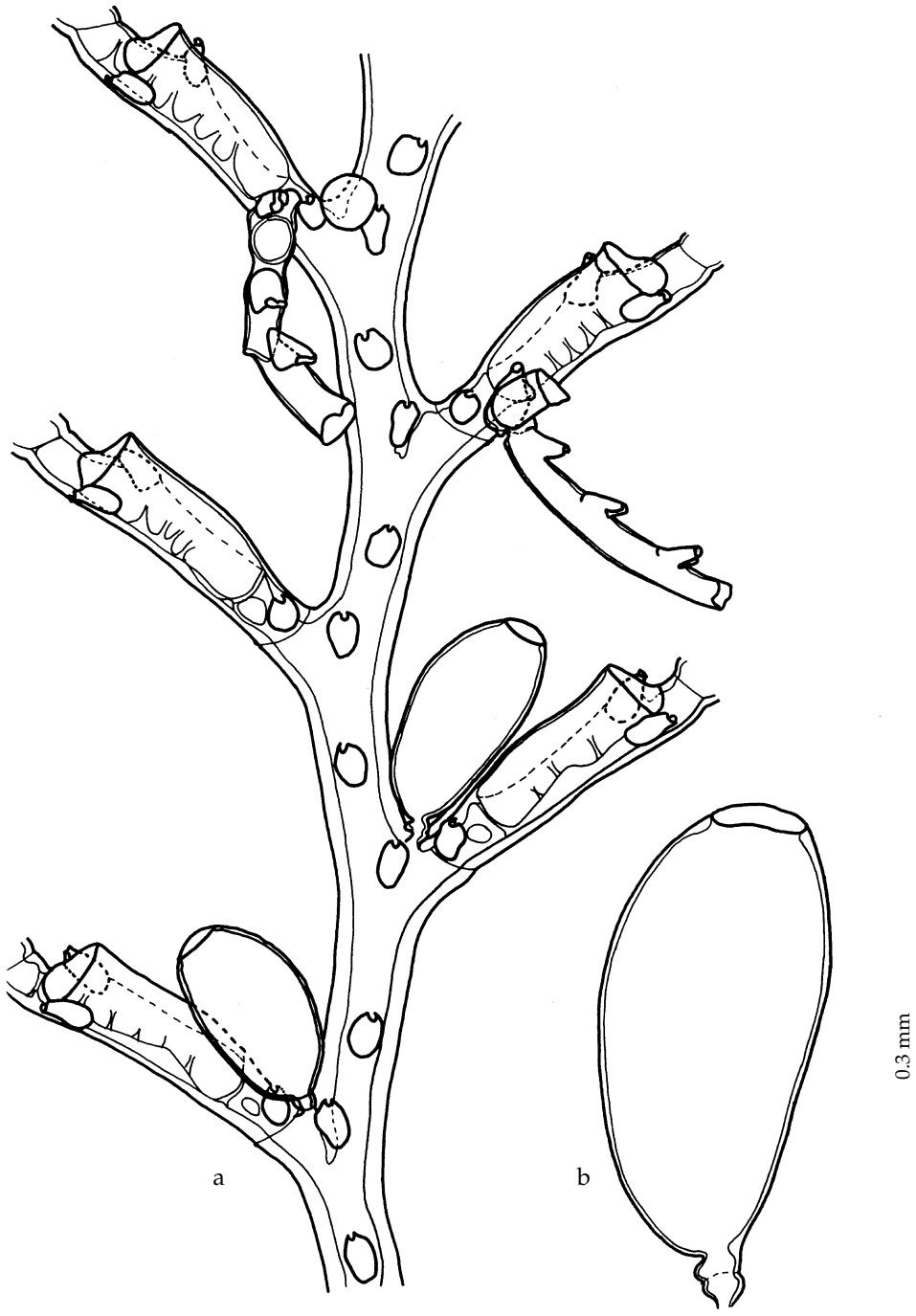


Fig. 1. *Aglaophenopsis cartieri* (Bedot, 1921), Seahma-1, DR 02. a, part of colony with first hydrocladial internodes, two gonothecae and two phylactocarps in frontal view; b, gonotheca, lateral view.

The gonosome, so far unknown, lacks the characteristic phylactocarps as observed in *Cladocarpus* Allman, 1874, or in *Streptocaulus* Allman, 1883, with the gonothecae inserting on the rachis of the phylactocarp. Here, the gonotheca arises directly from the hydrocladial apophysis, between the two axillary nematothecae (fig. 1a, b).

The gonothecae are ovoid, with smooth walls, narrowing basally into a short pedicel (fig. 1b). The aperture is apical and circular, closed by a lid. The gonothecae are 520-590 μm long and have a maximum diameter of 280-290 μm; they bear no nematothecae.

Two hydrocladia produce protective ramuli, phylactogonia, phylactocarps or "modified secondary hydrocladia", very similar to the phylactogonia described for the genera *Aglaophenopsis* Fewkes, 1881 and *Nematocarpus* Broch, 1918. These phylactocarps arise from the first hydrocladial internode on unmodified hydrocladia, inserting laterally between the hydrothecal base and the mesial infracalycine nematotheca. Their structure is, basically, that of an unbranched axis with a linear series of unpaired nematothecae (figs 1a, 3), but there are some differences between the two phylactocarps present.

The first, most basal phylactocarp, proximally has a small tubular structure, open and damaged distally. In addition there is a basal, unpaired nematotheca below the tubular structure, and there are three distal, unpaired nematothecae (fig. 3a). The tubular structure may represent an abortive or degenerated hydrotheca (damaged in this case) or the basal part of a branch (implicating a branched phylactocarp). The first possibility seems unlikely as its morphology is quite different from that of hydrothecae found on the hydrocladial internodes (fig. 2).

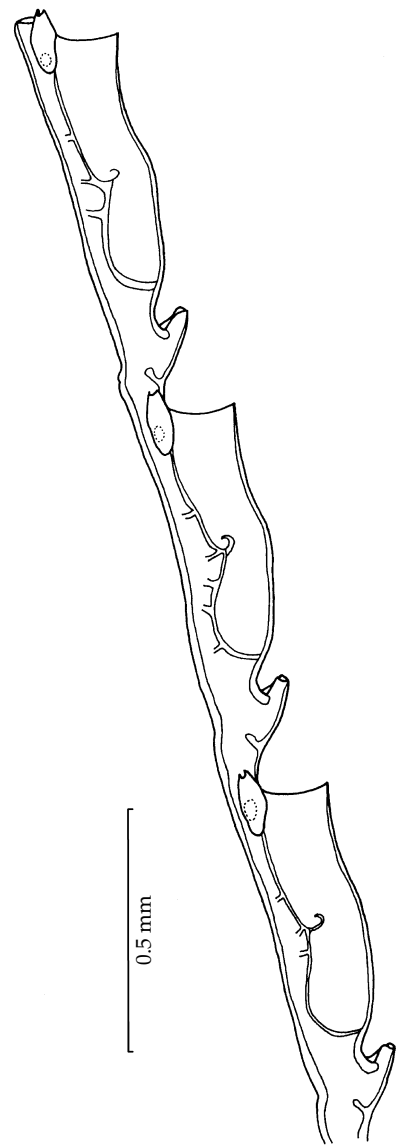
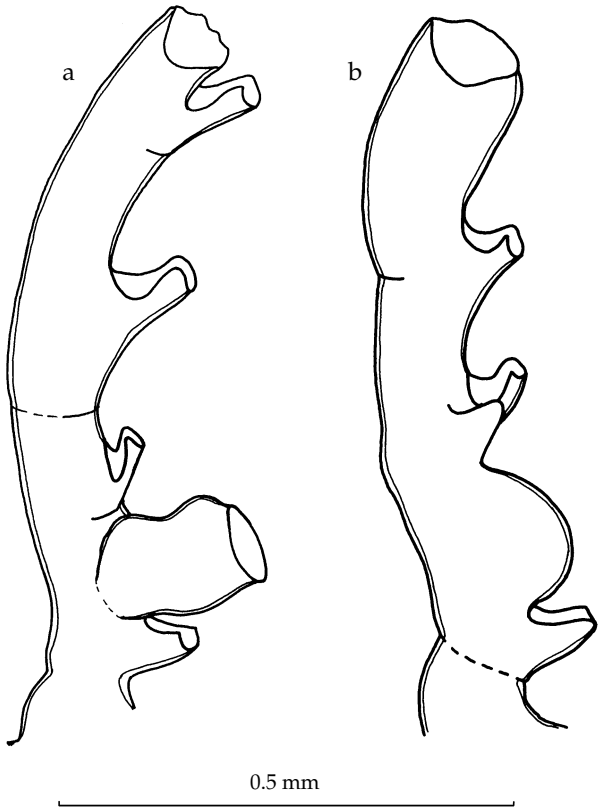


Fig. 2. *Aglaophenopsis cartieri* (Bedot, 1921), Seahma-1, DR 02, part of hydrocladium in lateral view.

The second phylactocarp, the most distal in the colony, has in its basal part a cupuliform (semispherical) structure, covered by perisarc (like a developing bud), that might develop into a hydrotheca or a branch (comparable to damaged structure of the first phylactocarp). Below the cupula is an unpaired nematotheca and above it two distal, unpaired nematothecae (fig. 3b). The first distal nematotheca (just above the



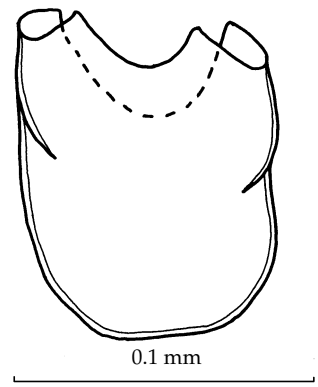


Fig. 4. *Aglaophenopsis cartieri* (Bedot, 1921), Seahma-1, DR 02, second unpaired nematotheca with a pair of apical funnels from distal phylactocarp, frontal view.

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Fig. 3. *Aglaophenopsis cartieri* (Bedot, 1921), Seahma-1, DR 02. a, proximal and b, distal phylactocarp from fertile colony, lateral view.

cupula) is a modified (aberrant?) nematotheca, partially bifurcated. It has a pair of apical funnels directed left and right, each one with a gutter-shaped aperture (fig. 4). The second distal nematotheca is a normal nematotheca with only one aperture. In the hydrocladial apophysis from which this phylactocarp originates there is a developing (immature) gonotheca with the shape of a flattened disk (fig. 1a).

In our opinion these appendages (presumed phylactocarps) are directly related to the gonothecae because one of the two is associated with an (immature) gonotheca. Moreover, in the hydrocladia arising from apophyses with fully developed gonothecae a foramen is visible in the first internode at exactly the same position where the phylactocarps in the other hydrocladia are inserted; probably these phylactocarps were lost. In the same cormoid, other hydrocladia without gonothecae on their apophyses also bear such a foramen on the first hydrothecate segment (fig. 1a).

Discussion

The taxonomic status of the various genera of Aglaopheniidae has been discussed by various authors: Stechow, 1913; Broch, 1918; Vervoort, 1972; Bogle, 1975; Millard, 1975; Bouillon, 1985; Ramil & Vervoort, 1992a; Calder, 1997; Ramil et al., 1998, and Schuchert, 2001.

Table 1. Table listing the phylactocarpal differences in *Aglaophenopsis* Fewkes, 1881, *Streptocaulus* Allman, 1883, *Cladocarpus* Allman, 1874, and *Cladocarpoides* Bogle, 1984

	Morphology of phylactocarp	Disposition of nematothecae	Insertion of gonothecae
Aglaophenopsis	Usually unbranched and segmented axis without lateral apophysis and branches; if branched, the secondary branches arise in the same manner and have the same structure as the primary phylactocarp (secondary phylactocarps)	Unpaired	At hydrocladial apophysis or at apophysis supporting the phylactocarps
Streptocaulus	Usually unbranched axis regularly segmented and without lateral apophysis and branches; if branched, the secondary branchlets are secondary phylactocarps	Paired	At axis, between paired nematothecae
Cladocarpus	Simple or dichotomously branched axis, with a regular succession of segments, each with a lateral apophysis and branches	Unpaired, subopposite and opposite	At lateral apophysis of phylactocarpal branches
Cladocarpoides	Open "corbula-like" structure with a central axis (rachis) supporting pinnately arranged modified hydrocladia, each with a single hydrotheca with its accompanying nematothecae, and ending in a nematophorous spike; bifurcated nematophorous branchlets arising from the modified hydrocladia and arching over the front of the rachis.	Unpaired (at nematophorous branches)	At rachis of "corbula-like" structure

In order to better define the generic attribution of '*Cladocarpus' cartieri*' we will start our discussion with the recent review of the family Aglaopheniidae Marktanner Turneretscher, 1890, by Calder (1997), who arranged the genera of this family in two subfamilies: Gymnangiinae Calder, 1997, in which the gonothecae are unprotected, and Aglaopheniinae Marktanner-Turneretscher, 1890, in which the gonothecae are protected by phylactocarps. It is clear that '*Cladocarpus' cartieri* belongs in the latter. This subfamily, Aglaopheniinae, is further subdivided by Calder into two tribes: Aglaopheniini Marktanner-Turneretscher, 1890, and Cladocarpini Calder, 1997. In the first, Aglaopheniini, the gonothecae are protected by a phylactocarp formed from a highly modified hydrocladium, either in the shape of a corbula with corbula-ribs protecting the gonothecae (as for instance *Aglaophenia* Lamouroux, 1816, and *Lytocarpia* Kirchenpauer, 1872), or in the shape of modified hydrocladia forming open, gonotheca-bearing phylactogonia (*Macrorhynchia* Kirchenpauer, 1872, *Nematophorus* Clarke, 1879, and *Monoserius* Marktanner-Turneretscher, 1890). In the second tribe, Cladocarpini, the phylactocarps arise from the first internode of unmodified hydrocladia, inserting laterally from the unpaired median (infracalycine) nematotheca. The phylactocarp can

be of varied nature, being branched or unbranched, with or without hydrothecae, occurring on a restricted or on a large number of basal hydrocladial internodes, in the latter forming a very open protective structure of the gonothecae, that may either insert on the phylactocarps or on the apophysis bearing the phylactocarp. It seems quite clear that '*Cladocarpus' cartieri* belongs to one of the genera of Cladocarpini: *Cladocarpus* Allman, 1874, *Aglaophenopsis* Fewkes, 1881, *Streptocaulus* Allman, 1883, *Nematocarpus* Broch, 1918, *Cladocarpoides* Bogle, 1984, or *Carpocladus* Vervoort & Watson, 2003; all these genera being primarily distinguished by the structure of their phylactocarps. *Cladocarpus, Aglaophenopsis* and *Nematocarpus* have been lumped together by Bouillon (1985: 165), a conclusion also accepted by Schuchert (2001: 133). Ramil & Vervoort (1992b) have compared the structure of the phylactocarp in certain species of *Cladocarpus* and in *Streptocaulus pulcherrimus*; they concluded that two different types of phylocarp structure are evident and proposed to remove to *Streptocaulus* such species of *Cladocarpus* that have a phylactocarp in structure similar to that of *Streptocaulus pulcherrimus* (for instance '*Cladocarpus*' *pectiniferus* Allman, 1883), being composed of an undivided or branched rachis, originating from the basal part of the first hydrocladial internode, and composed of internodes each with a pair of long, diverging, opposite nematothecae, the gonothecae springing from the basal portion of the internodes. In the genus *Cladocarpus* they propose to accommodate provisionally such species of which the gonosome is still unknown, as well as the species with a gonosome like that of *Cladocarpus elongatus* Bedot, 1921, in which the rachis of the phylactocarp, straight or branched, is composed of a number of segments with three nematothecae and one apophysis, alternatingly arranged along the length of the rachis. Each apophysis supports an undivided nematophorous branch; the gonothecae insert on the apophyses of the rachis. Though this point of view is not shared by Schuchert (2001: 134) we prefer to maintain this division as a valuable tool to arrange the many species formerly brought to *Cladocarpus* though we bear in mind that a future phylogenetic analysis might make it necessary to make amendments. In *Streptocaulus* the occasional presence of hydrothecae on the phylactogonia has been observed (Ramil et al., 1998) and in both *Streptocaulus* and *Cladocarpus* additional phylactocarps have been observed besides those found in the first hydrocladial internode.

The taxonomic position of *Aglaophenopsis* Fewkes, 1881, and *Nematocarpus* Broch, 1918, has been the subject of controversy and still there is no uniformity of conception. We believe the two are congeneric but should be kept separate from *Cladocarpus*, *Streptocaulus* and *Cladocarpoides* because of differences in the structure of the phylactocarps. The presence, absence or development of internal ribs or rings in the internodes composing the phylactocarp in our opinion should not be included in that discussion as these characters are highly variable in one species and highly varied in Cladocarpini. In both *Aglaophenopsis* and *Nematocarpus* the phylactocarps spring from an apophysis just under the first hydrotheca of a hydrocladium. The apophysis may be associated with the infracalycine nematotheca, replacing one of its (two) funnels, may slightly press aside that hydrotheca and (or) the hydrotheca may be slightly smaller than those on non-phylactocarp bearing internodes. The phylactocarp is a curved structure composed of several internodes bearing nematothecae and occasional hydrothecae, usually restricted to the basal internodes. It may be branched, the branches invariably inserting at the base of (phylactogonial) hydrothecae and are composed of nematothe-

cae-bearing internodes. The gonothecae insert at the hydrocladial apophyses (Allman, 1874; Nutting, 1900; Bogle, 1975) or at apophyses supporting the phylactocarps (Vervoort, 1972). In *Aglaophenopsis* such phylactocarps are restricted to the first internode of (primary) hydrocladia; in *Nematocarpus* they also occur on following internodes of the hydrocladia. This difference we do not consider to be of enough importance to keep both genera separate so we are inclined to sink *Nematocarpus* Broch, 1918, into the synonymy of *Aglaophenopsis* Fewkes, 1881.

As far as *Cladocarpoides* Bogle, 1984, is concerned, the structure of the phylactocarp with its pinnately arranged, antler-like, hydrothecate phylactogonia sets it quite apart from the remaining genera of Cladocarpini though in principal the structure of that phylactocarp is morphologically comparable with that of the genus *Cladocarpus* as we have defined it above. *Carpocladus* comes close to *Cladocarpoides*, particularly in the structure of the long, elongated gonosome, inserting at the basal internode of a normal hydrocladium. The hydrocladiate branch of the phylactogonium is moderately sclerotized and carries a normal hydrotheca; it does not end in a spine. The remaining branch of the phylactogium (nematophorous branch) is not ramified. The gonothecae spring from the apophyses of the rachis and are protected by the phylactocarps that curve over the row of gonothecae, the whole forming an open corbula.

'*Cladocarpus*' *cartieri* in the structure of the gonosome, as far as known as present, best fits into the genus *Aglaophenopsis* Fewkes as defined above, where it should stand as *Aglaophenopsis cartieri* (Bedot, 1921).

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