

Some consideration concerning the genus *Cladocarpus* (Cnidaria: Hydrozoa)*

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SUMMARY: In the aglaopheniid genus *Cladocarpus* Allman, 1874, there are two different types of phylactocarps. In the first type the rachis (axis) of the phylactocarp is homologous with the axis (hydrocaulus) of the Aglaopheniidae, being either unbranched or dichotomously branched with the axis composed of segments each bearing an apophysis supporting a nematophorous branch. The apophyses, and consequently also the branches, alternately point left or right. The type of the genus, *Cladocarpus formosus* Allman, 1874, has this morphology. In the second type the rachis is structurally similar to that of the hydrocladia; the composing segments bear pairs (or a pair) of nematothecae, arranged in opposite pairs. Species with this type of phylactocarp have so far been placed in *Cladocarpus* or in one of the later described genera *Dinotheca* Stechow, 1911, or *Cladocarpella* Bale, 1915. These genera have been synonymized with *Cladocarpus* by some authors. The place of *Aglaophenopsis* Fewkes, 1881, and *Nematocarpus* Broch 1918, is not clear; the genera evidently are closely related and have occasionally been synonymized or brought to *Cladocarpus*. The structure of aberrant phylactocarps in an undescribed species of *Cladocarpus* has affinities with the gonosome of *Aglaophenopsis*; but it is too early to make a decision now on the taxonomic importance of this aberrant gonosome. The structure of the gonosome of *Streptocaulus pulcherrimus* Allman, 1883, described by Quelech (1885), approaches that of the second type in *Cladocarpus* closely, though the spirally arrangement of the hydrocladia is only observed in *Streptocaulus*. The peculiarity develops from an initially pinnate arrangement of the hydrocladia. It appears that *Streptocaulus* is the oldest available genus name to accommodate the species with the second type of gonosome so far placed in *Cladocarpus*.

Keywords: Cnidaria; Hydrozoa; systematics; gonosome; *Cladocarpus*.

INTRODUCTION

In the course of a detailed study of some of the species of the hydroid genus *Cladocarpus* Allman, 1874, differences were observed in the structure of the gonosome (phylactocarp). This study has made it clear that two different types of phylactocarp can be distinguished in *Cladocarpus*. In the course of our study we also compared descriptions of the gonosome of allied genera.

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MATERIAL AND METHODS

Material has been studied from hydroid collections in the National Museum of Natural History (Rijksmuseum van Natuurlijke Historie), Leiden; the Institute for Taxonomic Zoology (Zoologisch Museum), University of Amsterdam; the Muséum National d'Histoire Naturelle, Paris; the Musée Océanographique, Institut Océanographique, Monaco; The Natural History Museum (British Museum, Natural History), London, and the Museum of Comparative Zoology, Cambridge, Massachusetts.

RESULTS AND DISCUSSION

The genus *Cladocarpus* was described by ALLMAN (1874) with the following diagnosis: "Trophosome. — Hydrocaulus with pinnate ramification. Hydrothecae with an intrathecal ridge. Nematophores fixed; lateral nematophores, one on each side of the orifice of the hydrotheca; mesial nematophores usually adnate for a greater or less extent to the front of the hydrotheca, occasionally free.

Gonosome. — Gonangia not included in corbulae, but borne on the sides or at the base of special protective branches, which are appendages of the pinnae."

The type of the genus, by monotypy, is *Cladocarpus formosus* Allman, 1874.

The type of open gonosome, in which the protection of the gonothecae is afforded by appendages of the hydrocladia was termed "phylactocarp" by ALLMAN (1883).

The first type of phylactocarp is composed of a simple or dichotomously branched axis supporting a series of lateral ramifications bearing nematothecae. The axis is formed by a regular succession of segments each with a lateral apophysis, supporting the nematothecae-bearing branch and 2 or 3 nematothecae: 1 inferior nematotheca, under the apophysis, and 1 or 2 axillary nematothecae. This type of phylactocarp resembles the characteristic structure of the axis (hydrocaulus) in the family Aglaopheniidae. A clear example of this type of phylactocarp is seen in *Cladocarpus sigma* (ALLMAN, 1877) var. *elongata* Bedot, 1921 (Fig. 1). Here the axis of the phylactocarp is divided into segments by transverse septa (nodes), each with a lateral apophysis alternately directed left or right and in the same plane as the axis, supporting the nematothecae-bearing branches in regular, pinnate disposition. Each segment has 3 nematotheca, one under the apophysis and two axillary nematothecae. The lateral branches are not divided into internodes and have numerous nematothecae either unpaired or opposite and subopposite. The phylactocarps of *Cladocarpus formosus*, the type of the genus, are similar, though in this species the axis of the phylactocarp is dichotomously ramified and also, judging from ALLMAN's figure (1874, pl. 68 Fig. 1a), divided into segments on some of which an inferior nematotheca can be seen and at least one axillar nematotheca occurs on the ramifications. However, we

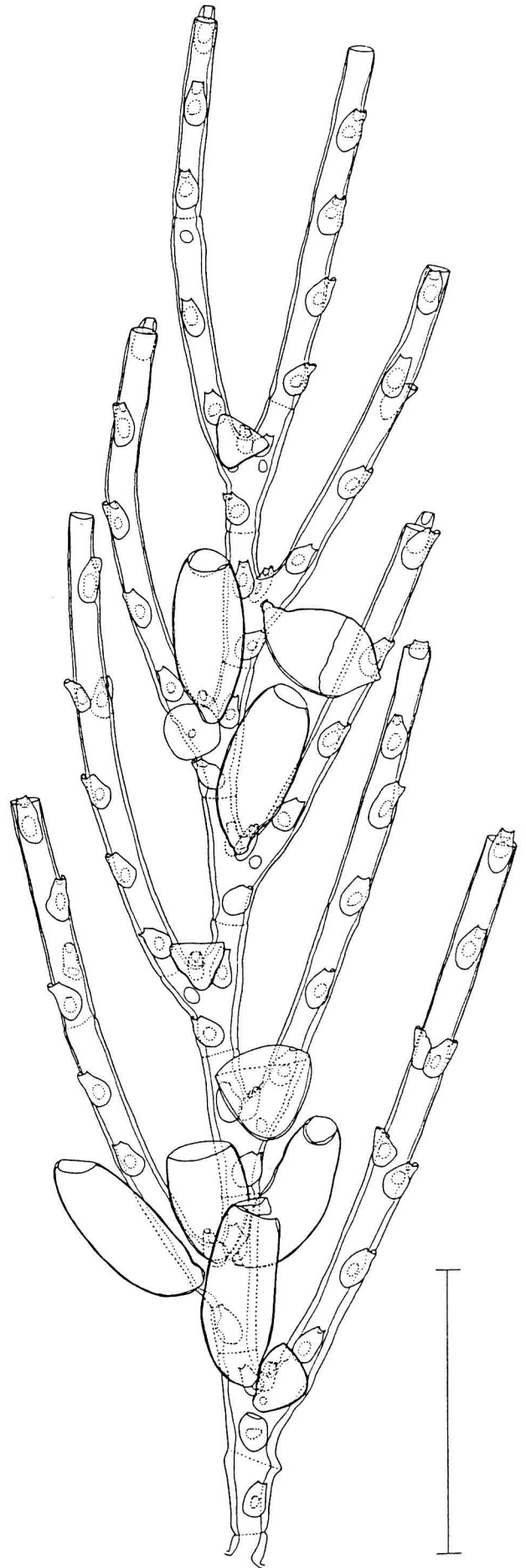


FIG. 1. — Phylactocarp of *Cladocarpus sigma* (Allman, 1877) var. *elongata* Bedot, 1921, from Seamount 1 Stn CP 12, Gorrington Bank, 36°24.2' N-11°43.2' W, 1005-1040 m, 23.09.1987. Scale bar = 0.5 mm.

have been unable to find a more detailed description of the phylactocarp of this species in the literature; NAUMOV (1969) described it as unsegmented while in BROCH's (1918) figure no segmentation of the axis can be observed.

The second type of phylactocarp has an unbranched axis, distinctly and regularly divided into segments that bear two series of nematothecae placed in the same plane with the axis and composed of opposite pairs. In this case the basal structure of the phylactocarp is comparable, in our opinion, with the structure of the hydrocladia. This type of phylactocarp was first mentioned by ALLMAN (1883: 50-51, pl. 17) in his description of *Cladocarpus pectiniferus* (cf. Fig. 2). However, this author interpreted the two phylactocarps that come from the base of the first hydrotheca of the hydrocladium as being parts of a single phylactocarp, described in the following manner: "Phylactocarp springing from the proximal internode of the hydrothecal ramules, and consisting of a very short stem, which immediately divides into two jointed and pectinate branches which carry the gonangia on their sides". This interpretation of the structure of the phylactocarp, having an axis dividing dichotomously, evidently resembles that of the phylactocarp of *Cladocarpus formosus* and was the reason for ALLMAN to include *C. pectiniferus* in the same genus. This faulty interpretation was corrected by BILLARD (1910), who studied ALLMAN's type during his revision of the hydroid collection of the British Museum (Natural History) and pointed out that in reality two separate phylactocarps were present, one on each side of the basal hydrocladial internode slightly under the base of the proximal hydrotheca. In spite of this correction BILLARD included *C. pectiniferus* in the genus *Cladocarpus* into which genus other species with both types of phylactocarp have been included. Nevertheless various authors have described genera for species included in *Cladocarpus*, or closely allied to that genus, without using characters of the phylactocarps as distinctive characters. Thus the genus *Dinotheca* STECHOW, 1911, was primarily based by its author on the curious U-shape of the hydrotheca. When instituting the genus the gonosome was still unknown; it was later described by the same author (STECHOW, 1925) who mentioned in the diagnosis of *Dinotheca*, that its gonosome is identical with that of *Cladocarpus* ("wie bei *Cladocarpus*"). The phylactocarps of *Dinotheca dofleini* Stechow, 1911 (the type of *Dinotheca* Stechow, 1911) conform to the second type of *Cladocarpus* phylactocarp described above. *Dinotheca* was synonymized with *Cladocarpus* by

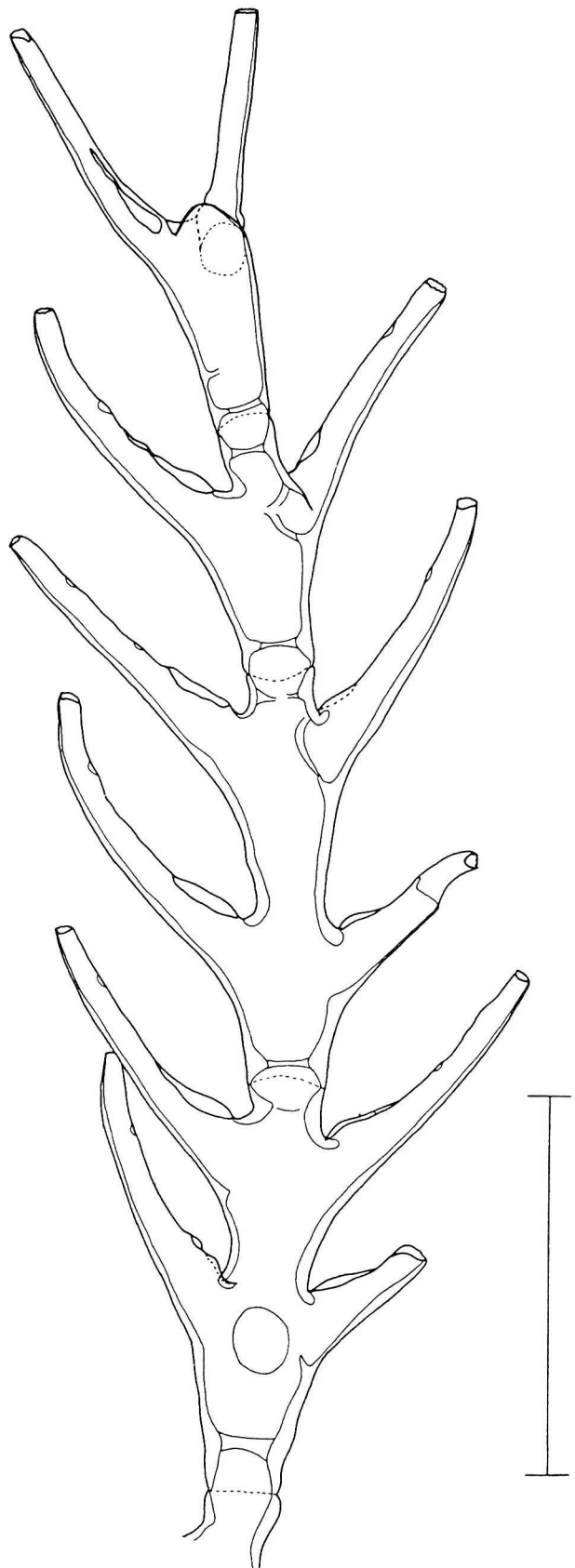


FIG. 2. — Phylactocarp (without gonothecae) of *Cladocarpus pectiniferus* (Allman, 1883) from Balgim Stn DR 22, 36°35.4' N-07°23.6' W, 466 m, 31.05.1984. Scale bar = 0.5 mm.

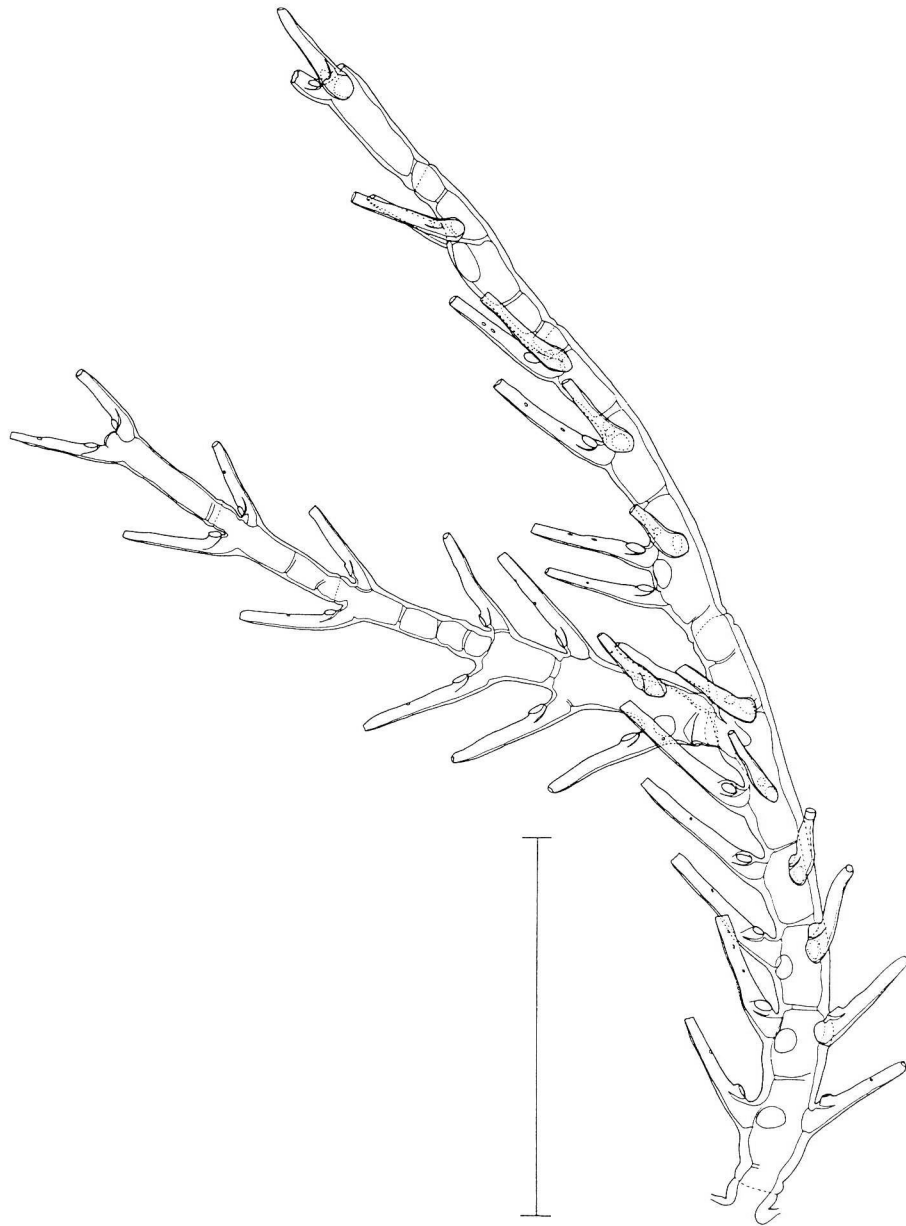


FIG. 3. — Phylactocarp (without gonothecae) of *Cladocarpus* sp. showing development of "secondary" phylactocarp, from Seamount 1 Stn DW 06, Gorringe Bank, 36°30.2' N-11°37.9' W, 250 m, 22.09.1987. Scale bar = 0.5 mm.

MILLARD (1975), a point of view shared by BOUILLON (1985) and REES and VERVOORT (1987).

The genus *Cladocarpella* Bale (1915: 303), instituted for *Cladocarpella multiseptata* BALE, 1915, is characterized as follows: "Hydrosoma as in *Cladocarpus*, but with some of the internodes of the hydrocladia (other than the proximal ones) giving off secondary 'gonangial' ramules, the internodes of which consist of closed ventricose receptacles, with one or two lateral sarcothecae". The principal character distinguishing *Cladocarpella* from *Cladocarpus* s.l. is provided by the phylactocarps that do not exclusively originate from the proximal internode of each hy-

drocladium, but may also rise from following internodes, a hydrocladium consequently bearing several pairs of phylactocarps. In structure the phylactocarps of *Cladocarpella* agree with the second *Cladocarpus* type described above. *Cladocarpella* was synonymized with *Cladocarpus* by BILLARD (1918), an opinion shared by VERVOORT (1966) and BOUILLON (1985).

The genus *Aglaophenopsis* Fewkes, 1881, was considered a valid genus by VERVOORT (1972) and BOGLE (1975), but was included in *Cladocarpus* by BOUILLON (1985). The relationship between both genera is far from clear. As far as the gonosome is

concerned *Aglaophenopsis* is characterized by a phylactocarp occasionally bearing hydrothecae, and if ramified, the branches originate from the base of a phylactogonial hydrotheca in the same manner as the phylactocarps. In this connection a colony of *Cladocarpus* sp. was collected by the SEAMOUNT 1 Expedition from an eastern Atlantic sea-mount (36° 30.2' N-11° 37.9' W). This colony had phylactocarps of the second type but showing numerous variations, the distal part of some phylactocarps bear normal hydrothecae, from the base of which "secondary" phylactocarps arise. In this specimen, the development of such "secondary" phylactocarps from the normal point of insertion of the gonothecae (i.e., from the axis of the phylactocarp between the two nematothecae of one pair, Fig. 3) was observed. These observations seem to bridge the gonosomal differences between both genera, bringing *Aglaophenopsis* closer to the group of species in *Cladocarpus* with the second type of gonosome described above. Differences seem to exist, nevertheless, in the disposition of the nematothecae of the phylactocarps of *Aglaophenopsis*, or at least in some of its species (as for instance *A. hirsuta* Fewkes, 1881), where the nematothecae are unpaired (as are the nematothecae in the phylactocarps of the second type described above). A further study of the gonosome of the species of *Aglaophenopsis* will be necessary for a final decision on its taxonomic position.

Nematocarpus BROCH (1918: 74) was also included in *Cladocarpus* by BOUILLON (1985); the following diagnosis was given by BROCH (1918): "Singly or doubly pinnate colonies, the apophyses of the primary stem tubes bearing hydrocladia, which in fully developed colonies are secondarily branched. All sarcothecae immobile. The secondary hydrocladium is formed from the proximal sarcotheca branch on the primary, and stands in no relation to the gonangia. The latter are not surrounded by any protective organs". In BOGLE's (1975) opinion *Nematocarpus* is closely allied to *Aglaophenopsis*, with which it should either be synonymized or be considered as a subgenus. Furthermore she concluded, after study of the figures of the gonosome of *Nematocarpus ramuliferus* (ALLMAN, 1874, type species of the genus) in ALLMAN (1874) (as *Halicornaria ramulifera*) and BROCH (1918), that the phylactocarps in this species give better protection to the gonangia than those of *Aglaophenopsis hirsuta*. Thus the principal difference between the two genera lies in the fact that in *Aglaophenopsis* the phylactocarps rise exclusively from the proximal internode of the hydrocladia, while in *Ne-*

matocarpus they may also arise from following internodes, a distinction comparable to that observed in *Cladocarpus* and *Cladocarpella*. To this we may add that in *Nematocarpus* the nematothecae of the phylactocarps are unpaired.

The genus *Cladocarpoides* BOGLE (1984: 135), is distinctly differentiated from *Cladocarpus* by the fact that the gonothecae emanate from the rachis (axis) of a "corbula-like" structure originating from the proximal internode of a non-modified hydrocladium. This "corbula-like" structure is composed of a central axis (rachis) from which grow pinnately arranged modified hydrocladia, each with a single hydrotheca and terminating in a "nematophorous spike". The gonotheca is protected by nematothecae-bearing branches growing from the modified hydrocladia.

In our opinion none of the genera discussed above should include the species of *Cladocarpus* s.l. having the second type of phylactocarp. However, there appear to be distinct affinities with the genus *Streptocaulus* ALLMAN (1883: 48), with type *Streptocaulus pulcherrimus* Allman, 1883¹. At the institution of this genus by ALLMAN the gonosome was unknown and the principal character given by ALLMAN was the spiral arrangement of the hydrocladia along the length of the hydrocaulus. The gonosome was described by QUELCH (1885: 11-13), who gave the following characterization of the phylactocarps: "They are unbranched and jointed, and are placed either on consecutive mesial nematophores or irregularly. The joints are similar throughout, generally three or four in number to each appendage, narrowed at the base and expanded at the top, so as to be obconical or subtriangular; the expanded upper lateral edges chiefly formed by two rather short nematophores, one on each edge, between which is placed the narrow base of the joint above, while below this joint of juncture and on the front of the joint (that is on that part which looks towards the hydrothecae below which the appendage is situated) is seated the gonotheca, which thus occupies the upper anterior portion of the joint". This definition agrees well with the morphology of the phylactocarps of the second type described above, the only clear differences being that in *S. pulcherrimus* the division of the rachis of the phylactocarp into internodes is distinct while these internodes are slightly different in shape. In addition

¹ A second species of *Streptocaulus* was described by FRASER (1937: 6, pl. 2 Fig. 10) as *Streptocaulus gracilis*. Of this species the gonosome is unknown. It is principally founded on the spirally arrangement of the hydrocladia and from the appearance of the nematothecae it may very well belong in the family Plumulariidae.

the phylactocarps in *S. pulcherrimus* develop singly (unpaired) while in the other species with the second type of phylactocarp they usually are paired. The principal difference between *Streptocaulus* and the species of *Cladocarpus* that have the second type of gonosome thus remains the spiral disposition of the hydrocladia in *Streptocaulus*. According to QUELCH's (1885) observations this spiral position develops gradually, the hydrocladia in the lower parts of the stem being pinnately arranged and by torsion of the axis gradually obtain a spiral arrangement: "These basal hydrocladia are confined to one side of the stem and are alternately arranged on each side of a line of more or less rounded adnate nematophores, and spread in opposite directions, thus having a strictly pinnate disposition. Above this basal part the planes of the hydrocladia gradually become closer, until the hydrocladia become placed in one and the same plane intermediate between their former positions, and are attached not on each side, but in the direct line of the nematophores of the stem. The torsion of the stem now gives the spiral arrangement which is so distinctive of this form".

Summarizing it may be concluded that, in our opinion, the genus *Cladocarpus* s.l. contains two groups of species with a different morphology of the phylactocarp. Those of the first group described above should remain in *Cladocarpus* sensu restricto, having as type *Cladocarpus formosus* Allman, 1874. The second group should be removed from *Cladocarpus* and be placed in a separate genus for which the oldest available name appears to be *Streptocaulus* Allman, 1883, type *Streptocaulus pulcherrimus* Allman, 1883. As *Cladocarpus* s.l. contains a number of species with unknown gonosome a further subdivision of both *Cladocarpus* sensu restricto and *Streptocaulus* does not appear unlikely. It might be advisable to maintain such species of which the gonosome is still unknown within the genus *Cladocarpus* sensu restricto [cf. REES's (1939) treatment of the genus *Campanulina*].

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