Review of the family Halopteridídae (Hydrozoa, Cnidaria)

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Key words: Plumularoidea; Halopteridídae; revision; redescription; types; new species; Mediterranean; England; France; Spain; U.S.A.; Caribbean; Brazil; South Africa; Madagascar; Indonesia; Australia; New Zealand; Hawaii.
All genera and species of the hydrozoan family Halopteridídae are reviewed. Where material was available, species are described and figured and the extent of morphological variation is assessed as far as possible. The re-examined material includes samples from the Challenger, Siboga, and Galathea expeditions. Numerous types were re-examined and taxonomic revisions made where necessary. For several nominal species lectotypes are designated. Two new species are described: *Antennella kiwiana* from New Zealand and *Halopteris platygonotheca*, a wide spread species from the Indo-Pacific Ocean. *Halopteris buskii* var. *peculiaris* (Billard, 1913) is raised to species level as *Halopteris peculiaris*. Several species are sunk into synonymy: *Plumularia balei* Billard, 1911 is referred to *Antennella varians* (Billard, 1911); *Antennella variabilis* Fraser, 1936 is referred to *A. quadriaurita* Ritchie, 1909; *Plumularia nuttingi* Billard, 1911 is referred to *Halopteris polymorpha* (Billard, 1913); *Thecocaulus heterogona* Bale, 1924 is referred to *Halopteris crassa* (Billard, 1911); *Halopteris constricta* Totton, 1930 is referred to *H. minuta* (Trebilcock, 1928); *Corhiza mortenseni* Millard, 1968 is referred to *Corhiza complexa* (Nutting, 1905); *Plumularia obconica* Kirchenpauer, 1876, *Heteroplon pluma* Allman, 1883, and *Plumularia armata* Allman, 1883 are all referred to *Halopteris buskii* (Bale, 1884). *Antennella siliquosa* (Hincks, 1877), *Halopteris alternata* (Nutting, 1900), and *Halopteris tenella* (Verrill, 1874) are recognised as valid species.
The recognised genera of the Halopteridídae are: *Antennella* Allman, 1887, *Halopteris* Allman, 1887, *Monostaechas* Allman, 1877, *Schizotricha* Allman, 1883, *Antennellopsis* Jäderholm, 1896, *Corhiza* Millard, 1962, *Gattya* Allman, 1886, *Calvinia* Nutting, 1900, *Nuditheca* Nutting, 1900, *Astrolabia* Naumov, 1955, *Anarthoclada* Naumov, 1955, and *Pentatheca* Naumov, 1955. The validity of the generic division is discussed; only minor emendations are made for the genera *Halopteris* and *Schizotricha*.

Contents

Introduction

Halopteridídae are a widespread family of marine thecate hydroids occurring in all seas. Some are also frequently encountered in shallow waters and popular faunistic identification guides regularly contain some Halopteridídae. However, this study was started after an attempt to identify some Mediterranean samples made it evident that many species are not properly identifiable and that revisions are needed. The literature also is scattered widely and in publications that are difficult to access for the average institute. This study thus emphasises aspects of species recognition and identification; the taxonomy at the generic level is treated superficially only. A revision of taxa above the level of species in Halopteridídae can only be made after a thorough phylogenetic analysis has become available. Such a study will be presented in a separate publication because it must be embedded in a broader taxonomic framework including also the other plumulariids. An excellent historic review and synonymy of some of the generic names can be found in Calder (in press); Millard (1975) and Bouillon (1995) too provide many synonyms. Limitations of resources and availability of material did not allow to describe and figure all species of the family. Therefore, emphasis was placed on the more important genera *Antennella* and *Halopteris*. The distributional range of the species is also discussed briefly as re- examination of material used by other authors showed an alarmingly high number of cases in which the material was incorrectly identified. It is evident, therefore, that many records without proper descriptions and the resulting distribution patterns are rather unreliable.

Bedot (1917-1923) made a first inventory of all plumulariids known to him. The Halopteridídae, however, at that time were not recognised as a separate family. Though a thorough search has been made to list all Halopteridídae, completeness cannot be guaranteed. Many older authors did not describe stem characteristics and it is sometimes uncertain whether a species belongs to Plumulariidae or Halopteridídae (see especially *Schizotricha*, p. 133).

Halopteridídae were first defined by Millard (1962) as the subfamily Halopterinae of Plumulariidae. It was later raised to family level (e.g. Bouillon, 1985; Calder, in press). The family level is also accepted in this study, largely following Cornelius (1995) and Calder (in press).

The most important diagnostic character of Halopteridídae is the presence of hydrothecae on the hydrocaulus (for explanation of techincal terms see below). Cauline hydrothecae are absent in the three remaining families of Plumularoidea: Plumulariidae, Kirchenpaueriidae, and Aglaopheniidae (Aglaopheniidae sensu stricto, without the genera *Nuditheca*, *Anarthoclada*, *Astrolabia*, and *Pentatheca*). The Plumularoidea certainly are a monophyletic group: the characteristic positions of the nematothecae and the hydrothecae on one side of the hydrocladia are fairly convincing synapomorphies. Compared to outgroups as Sertulariidae, Haleciidae, and Syntheciidae (see e.g. Millard, 1975), the absence of hydrothecae on the caulus must be seen as a synapomorphy that unites a clade comprising Plumulariidae, Kirchenpaueriidae, and Aglaopheniidae. In this clade, the cauline hydrothecae are either absent or reduced to a so called 'mamelon'[1]. The homology of the 'mamelon' with cauline

[1] The original spelling (cf. Billard, 1913) has been retained.

hydrothecae is best demonstrated in the genus *Pseudoplumaria* Ramil & Vervoort, 1992b where a continuous reduction of hydrothecae to 'mamelons' can be observed. Contrary to the opinion of Calder (in press), *Pseudoplumaria* and *Polyplumaria* are therefore here included in Plumulariidae due to their reduction of the hydrothecae. The presence of hydrothecae in Halopteridídae is thus most probably a plesiomorphy and the group seems to lack a convincing synapomorphy. The occasionally cited character of "gonothecae with nematothecae" (Ramil & Vervoort, 1992b) is also not useful as some species of *Plumularia* also have nematothecae on their gonothecae (e.g. *Plumularia wasini* Jarvis, 1922; see Millard, 1975: 405). Halopteridídae, therefore, possibly are a paraphyletic group and as noted above, only a comprehensive phylogenetic analysis can possibly reveal some synapomorphies. Pending such an analysis, the group as defined here comprises the following genera: *Antennella, Halopteris, Monostaechas, Corhiza, Calvinia, Schizotricha, Antennellopsis, Nuditheca, Anarthoclada, Astrolabia,* and *Pentatheca* (order arbitrary). The last four genera contain species that are less well known and they were so far usually associated with Aglaopheniidae (see Bouillon, 1985). Due to the presence of cauline hydrothecae and following Calder (in press) these genera are here also included in Halopteridídae.

The generic limits in Halopteridídae are predominantly dependant on the shape of the colony (fig. 2). The validity of this generic divivsion is undermined by species like e.g. *Antennella varians* and *Halopteris campanula,* which can also develop colonies that fit the diagnosis for either *Corhiza* or *Antennella.* In such problematic cases, the predominant colony form was used to allocate a species to a particular genus. For some species somewhat arbitrary decisions had to be made (see *Antennella varians, Antennellopsis integerrima,* and *Halopteris campanula*).

The study of the various samples used here distinctly indicates that hydroid systematics based solely on morphological characters has reached its limits (see also remarks in Cornelius, 1995, vol. 1: 10) and many nominal species described here might actually be an assemblage of species while some could also belong to the same biological species. It is evident that methods of population genetics should be applied to obtain a better understanding of species limits and population structures, as well as to understand how much morphological variation can be expected within a biologically defined hydroid species. Unfortunately, there is so far only one such study available (Thorpe et al., 1992), but it convincingly demonstrates the potential of allozyme data for hydrozoan systematics.

Technical terms and definitions

Some of the more important terms are also depicted in fig. 1. For further terms used in hydrozoan systematics see also Millard (1975), Cornelius (1995), and Schuchert (1996).

abaxial: facing away in a direction perpendicular to the axis of reference.
abcauline: outer side of a hydrotheca or nematotheca; term is also used for hydrocladial hydrothecae or nematothecae.
adaxial: facing towards the axis of reference.
adcauline: side of hydrotheca or nematotheca facing the caulus; term is also used for

hydrocladial hydrothecae or nematothecae.

alternate: hydrocladia arise alternately on the left and on the right side of the stem.

angle of opening: refers to the inner angle formed by the plane of the hydrothecal opening and the direction of the hydrocladium or caulus.

apophysis: short process of the hydrocaulus that bears the hydrocladium.

blastostyle: strongly reduced polyp that produces gonophores.

coenosarc: living tissue that connects all polyps.

colony: assemblage of polyps that have a common gastric system, mostly connected by a system of stolons. The term colony is frequently used incorrectly by referring to an upright stem (cormoid), which may be a part of a colony only (e.g. in colonies that form feather-like upright stems).

cormoid: erect, polyp bearing elements of a colony that arise from a common hydrorhiza or hydrorhiza-like stem, e.g. one single feather-like structure of a *Halopteris* colony, or a simple stem of an *Antennella* species. In terms of comparative anatomy, a cormoid is a hydrocaulus or its homologue and all accessory structures.

gonophores: either developing medusae or sessile sporosacs (medusa homologue, see Schuchert, 1996). In this study only sessile sporosacs are encountered.

gonotheca: container in which a blastostyle produces gonophores.

gonosome: male and female gonothecae.

heteromerous segmentation: segmentation of hydrocaulus or hydrocladia by alternating hydrothecate (main segment) and non-hydrothecate segments (intersegments), oblique and transverse nodes thus alternating.

heteroneme: nematocyst which everts a thicker shaft that is continued by a thinner thread.

homomerous segmentation: segmentation of hydrocaulus or hydrocladia through uniform segments, usually separated by oblique nodes.

hydrocaulus: erect main axis in pinnate cormoids. Note that this term is also used in another meaning relating to the stalk of athecate hydroids.

hydrocladia: appendages in pinnate cormoids; sidebranches.

hydropore: hole in the bottom of the hydrotheca through which polyp is connected to coenosarc.

hydrotheca: beaker-like structure that surrounds individual polyps.

internode: part between two nodes. The term internode is here not promoted. Although widely used in English texts, this botanical term is unlogic and often misunderstood by non-specialists. It is here replaced by segment.

intersegment: a term proposed by Schenk (1965) and adopted here, corresponds to the older terms: athecate internode, ahydrothecate internode, intermediate internode, etc. (see fig. 1). This element has been named differently by various authors; the name also differs in various languages. In order to obtain a uniform nomenclature and also to avoid awkward circumscriptions the self-explanatory term "intersegment" is here used. The intersegment is a segment without hydrotheca that follows the main segment distally. The intersegment is always delimited from the main segment by a transverse node. Frequently the intersegment is fused to the main segment without a trace of a node. In such cases the distal part of the main segment is seen as a homologue of the intersegment.

main segment: a term introduced in this paper, corresponds to the older term hydro-

thecate internode (see fig. 1 and intersegment). It is a segment that bears a hydrotheca.

node: externally visible constriction in the hydrocaulus or hydrocladium, see also septum.

opposite: two hydrocladia that arise on the same level of the stem, one pointing to the right, the other to the left.

pinnate: structure of feather-like cormoids with main axis and hydrocladia on both sides, used here synonymously with plumose. Cornelius (1995) distinguished plumose from pinnate by its closer spacing of the hydrocladia. Such a distinction seems rather ill defined and arbitrary and is not accepted here.

plumose: feather-like, see pinnate which is used synonymously here.

polysiphonic: stem or hydrocladia composed of several independent tubes. The term fascicled can be used with the same meaning.

repeat: tandem-like repeated element, either composed of a main segment and intersegment, or both segments fused.

s-value: proportion of shaft length to capsule length in heteronemes.

scutum: plate or shield-like process.

segment: part of hydrocladium or caulus delimited by externally visible constrictions (nodes), see also main segment, intersegment, internode.

septum: internal transverse wall in hydrocladium or hydrocaulus, delimiting compartments, septa are not accompanied by an externally visible constriction (see node).

stem: any upright element that can bear plumes or hydrocladia. This term is a general one and it does not include any notion of homology as e.g. hydrocaulus. A hydrocaulus is one kind of stem only.

trophosome: all structures of a colony except the gonothecae.

Material and Methods

Except for the figures with magnifications below 20 times, all other figures were made with the help of a camera lucida (drawing tube) fitted to an Olympus BH-2 compound microscope. Comparable parts of a cormoid generally have identical magnifications throughout all figures. Measurements indicated that the figures are rather distortion free and thus dimensions can be measured directly in the figures. Measurements given in tables were also taken with the camera lucida. At least three measurements were made per character and the range found is tabulated. In cases where it was obvious that a character varied in size depending on its position within the plume, care was taken to obtain the complete range. Segment length (fig. 1) was always measured as maximal length, from proximal to distal tip.

Nematocysts were only rarely available for study. They were studied as given in Schuchert (1996), but mostly without chemical treatment. The s-value given for some heteronemes is defined above (Technical terms and definitions).

The descriptions provided in this study have been made quite uniform; the structure was adopted from the exemplary good descriptions of Millard (1975). Her uniform text structure greatly facilitates species comparisons. In this study, redundant information is also given occasionally; this is done for the sake of uniformity as it will facilitate transformations into tables used in a cladistic analysis.

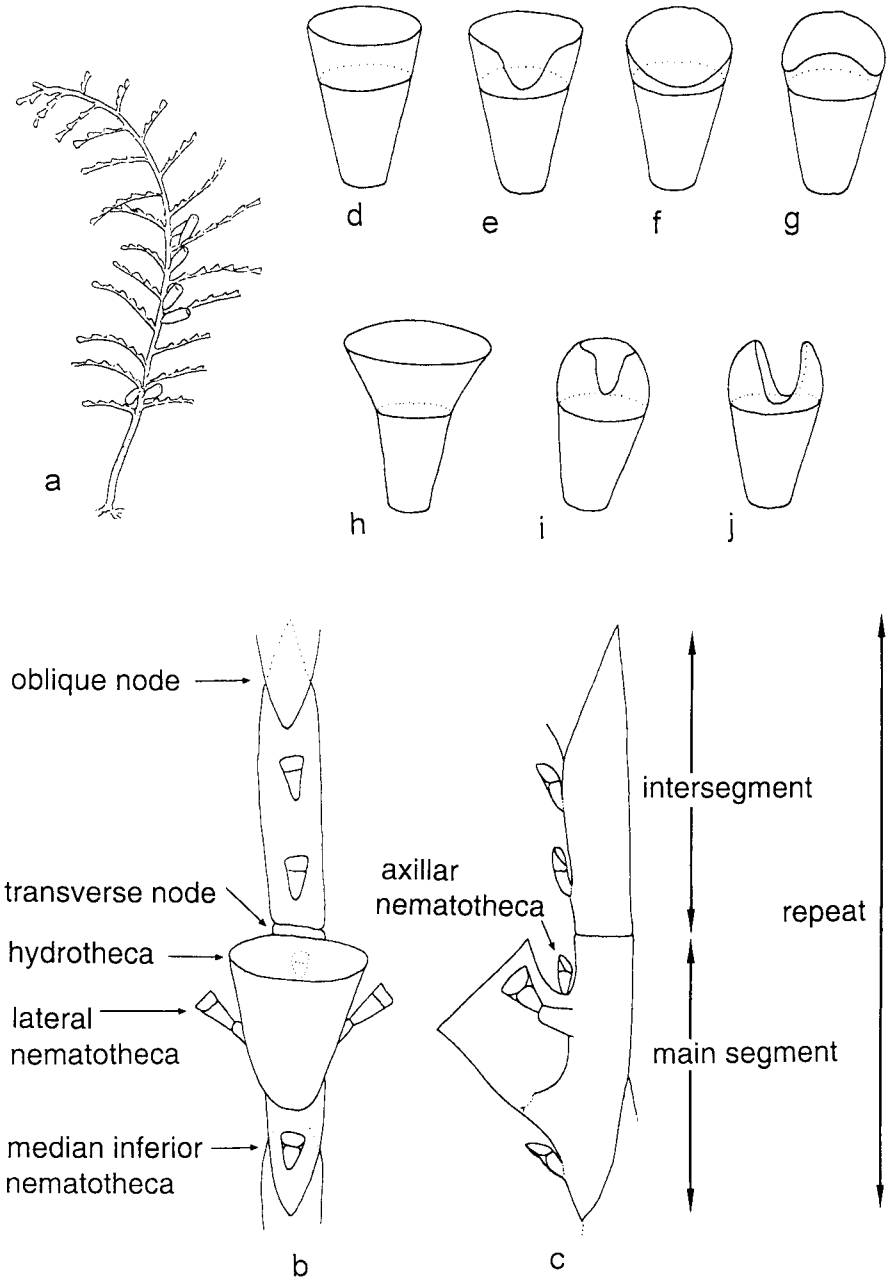

Fig. 1. Important anatomical terms used in this study; a, cormoid with hydrocaulus and hydrocladia; b, part of hydrocladium in frontal view; c, hydrocladium in lateral view; d-j, various shapes of lateral nematothecae, all seen from inner side; d, conical without emargination; e, conical with emargination; f, conical with inner side lowered; g, conical bivalved; h, funnel-shaped; i, inwardly rolled wall of upper chamber, with emargination; j, inwardly rolled wall with emargination on inner- and outer side, spanner- type.

The references given for each species do not represent a complete bibliography; only important studies and studies available to the author are included. Occasionally some important works that were not available to the author are also included; these are indicated in the reference section.

Abbreviations of institutions

Material for examination was obtained from the following institutions:

MACT = Musée de l'Afrique Centrale, Tervuren, Belgium.
MCZH = Museum of Comparative Zoology, Harvard, Massachusetts, U.S.A.
MHNG = Museum d'Histoire Naturelle de Genève, Switzerland.
MVM = Natural History Museum of Victoria, Melbourne, Australia.
NHMV = Natural History Museum Vienna, Austria.
NMNH = National Museum of Natural History, Smithsonian Institution, Washington DC, U.S.A.
MNHN = Muséum National d'Histoire Naturelle, Paris, France.
NZOI = New Zealand Oceanographic Institute, Wellington, New Zealand, now renamed to NIWA Oceanographic.
RMNH = National Museum of Natural History (Nationaal Natuurhistorisch Museum), Leiden, The Netherlands.
ROMIZ = Royal Ontario Museum, Department of Invertebrate Zoology, Toronto, Canada.
SAM = South African Museum, Capetown, South Africa.
ZMA = Institute for Systematics and Population Biology (Zoological Museum), University of Amsterdam, The Netherlands.
ZMC = Zoological Museum, Copenhagen, Denmark.

Systematic part

Family Halopteriididae Millard, 1962

Diagnosis.— Plumularoidea forming colonies with erect cormoids arising either from creeping stolons, or from any strand of a polysiphonic stem formed by stolon-like tubes. Cormoid main axis bears hydrothecae, either simple or bearing hydrocladia in alternate or opposite positions. Cormoid main axis may be accompanied by stolon-like tubes. Hydrocladia either unbranched or branched. Hydrothecae with toothed or untoothed rim. Nematothecae of variable structure, one- or two chambered, movable or immovable, at least three associated with every hydrotheca, one or two inferior and one pair of laterals. Nematothecae not fused to the hydrotheca, with the exception of the genus *Antennellopsis* in which the lateral nematothecae are partly fused to the hydrotheca. Gonophores as fixed sporosacs contained in a gonotheca. Gonothecae arising from caulus or hydrocladia, never protected by hydrocladia or modified hydrocladia, not aggregated, usually dimorphic and with at least the female normally bearing nematothecae.

Remarks.— This family contains the following genera: *Antennella, Halopteris,*

Monostaechas, Schizotricha, Antennellopsis, Corhiza, Gattya, Calvinia, Nuditheca, Anarthoclada, Astrolabia, and *Pentatheca.* The order given is arbitrary, the better known and more important genera coming first.

The gereric limits of Halopteridídae depend largely on the colony form. Schematic drawings of the colony forms found in Halopteridídae are shown in fig. 2.

Some genera are here subdivided into artificial groups. This subdivision usually neither implies a phylogenetic cohesion nor a taxonomic one. It is solely done for the purpose of bringing together species that resemble each other so that they are easier to compare and identify.

Key to the genera of the Halopteridídae as defined here:

1. Lateral nematothecae fused to hydrotheca ..... ***Antennellopsis***
- Lateral nematothecae not fused to hydrotheca, either movable or fused to its pedicel 2
2. Unbranched, erect stems arise directly from creeping hydrorhiza ..... ***Antennella***
- Erect structures branched, either as cormoids, branched hydrocladia, or polysiphonic stems 3
3. Stem polysiphonic, tubes all of equal importance and all giving rise to hydrocladia or cormoids ..... ***Corhiza***
- Stem monosiphonic, or polysiphonic with main axial tube that bears hydrocladia 4
4. Hydrothecae with more than one marginal tooth ..... ***Gattya***
- Hydrotheca with even rim or one tooth only 5
5. Hydrocladia branched basally, arising successively on ahydrothecate basal segment of previous hydrocladium ..... ***Monostaechas***
- Hydrocladia unbranched, or if branched, second order branches arise from side of hydrothecae bearing part of other hydrocladium 6
6. Cauline and cladial hydrothecae differ in morphology and two widely separated pairs of immovable lateral nematothecae present ..... ***Astrolabia***
- Not both condition as stated above found together 7
7. Stem normally monosiphonic, cormoids pinnate ..... ***Halopteris***
- Stem polysiphonic and with one main axial tube bearing hydrocladia 8
8. Lateral nematothecae not fused to their pedicels, hydrocladia branched, part adcauline hydrothecal wall free ..... ***Schizotricha***
- Lateral nematothecae immovable, fixed to their pedicels, hydrotheca completely adnate 9
9. Median inferior nematotheca absent, two widely separated pairs of immovable lateral nematothecae ..... ***Pentatheca***
- Median inferior nematotheca present 10
10 Hydrocladia not branched, lateral nematotheca scale-shaped ..... ***Anarthroclada***
- Hydrocladia branched, lateral nematotheca one-chambered, cup-shaped ..... ***Nuditheca***

Genus *Antennella* Allman, 1877

Diagnosis.— Halopteridídae with stems arising directly from creeping stolons, stems normally unbranched, not polysiphonic. Hydrotheca cup-shaped, with untoothed rim. Lateral nematothecae not fused to hydrotheca.

Type species.— *Antennella gracilis* Allman, 1877.

Remarks.— Although Allman (1877) used both spellings, *Antennella* and *Antenella*, the former is here used in accordance with most other authors and also Bedot (1912), acting as First Reviser (Calder, in press). However, no distinction is made here in the synonymy.

Most recent authors interpreted the stems of the species of *Antennella* as hydrocladia. However, earlier authors (e.g. Bale, 1884: 121) noted that they can also be seen as homologues of the caulus of pinnate forms. Such an interpretation is also more logical if *Antennella* should stay in Halopteridídae. The proximal structure of the stem of species *Antennella* with its several transverse nodes and often also with a marked oblique hinge-joint clearly resembles a hydrocaulus. Additionally, in some species of *Halopteris* that also produce simple stems, the number of nematothecae sometimes shows that these *Antennella*-like stems are homologous with hydrocauli of the pinnate form (see *H. diaphana*). However, in some cases a homology with the hydrocladia is also possible. Colonies of *Plumularia filicaulis* Kirchenpauer, 1876 also

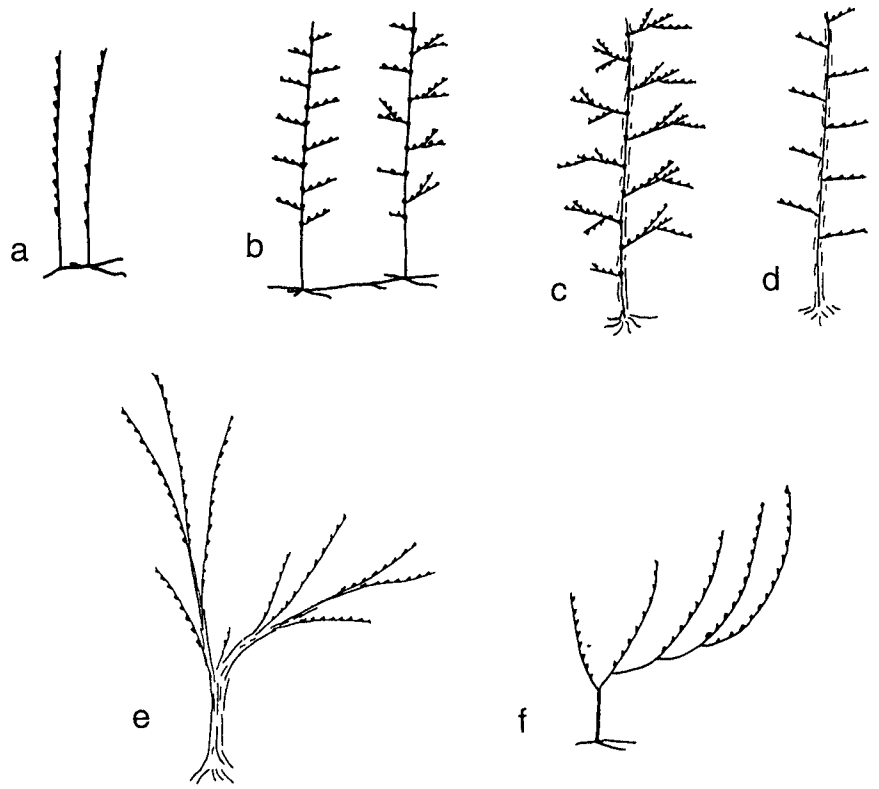

Fig. 2. Colony forms of the Halopteridídae (simplified); a, *Antenella*; b, *Halopteris*; *Gattya*; *Astrolabia*; c, *Schizotricha*, *Nuditheca*; d, *Anarthroclada*, *Pentatheca*; e, *Corhiza*; f, *Monostaechas*.

form simple, *Antennella*-like stems, which must be homologised with hydrocladia as the hydrocauli of *Plumularia* are devoid of hydrothecae (see Millard, 1975: 390). Some authors therefore incorrectly refer to *Plumularia filicaulis* (= *Plumularia lucerna* Mulder & Trebilcock, 1911) as *Antennella filicaulis* (cf. Bedot, 1917: 124; Bedot, 1921b: 4).

Antennella was often considered the most primitive member of Halopteridídae (fig. 2) from which all other genera evolved (e.g. Millard, 1962). Outgroup comparisons with other thecate families outside the superfamily Plumularoidea, however, indicate that the branched form is more probably the ancestral form and *Antennella* is a simplified form derived from pinnate ancestors. The simple form is thus apomorphic. Because several species of *Halopteris* easily form simple stems, a multiple origin of *Antennella* is plausible.

All known species of *Antennella* are here clustered into artificial groups to allow easier comparison (see page 12).

Antennella secundaria group

Remarks.— This group contains *A. secundaria* and *A. avalonia*. For their distinction see remarks under *A. avalonia*.

Antennella secundaria (Gmelin, 1791)
(figs 3-4, table 1)

Sertularia secundaria Gmelin, 1791: 3856.

Plumularia secundaria; Kirchenpauer, 1876: 28, pl. 1 fig. 18, pl. 6 fig. 7; Marktanner-Turneretscher, 1890: 252, pl. 6 fig. 1; Pictet, 1893: 53, pl. 2 fig. 26; Pictet & Bedot, 1900: 27, pl. 6 fig. 7.

Antennella gracilis Allman, 1877: 38, pl. 22 figs 6-7; Nutting, 1900: 77, pl. 13 fig. 5; Stechow, 1909: 85; Fraser, 1938a: 58.

Antennella secundaria; Ritchie, 1910b: 822; Stechow, 1909: 84; Billard, 1912: 467; 1913: 8, fig. 1, pl. 1 figs 1-3; Bedot, 1914: 82, pl. 5 figs 1, 7, 8; Jäderholm, 1919: 20; Jarvis, 1922: 349; Stechow, 1925b: 493; Broch, 1933: 19; Leloup, 1938: 18, fig. 13; Millard, 1958: 199; Pennycuik, 1959: 176, pl. 3 figs 4-5; Riedl, 1959: 653; Millard, 1962: 274; Mammen, 1965: 296, fig. 93; Rees & Thursfield, 1965: 158; Van Gemerden-Hoogeveen, 1965: 54, figs 29-31; Millard, 1968: 273; Millard & Bouillon, 1973: 77-78, fig. 10E; Rho & Chang, 1974: 135, 146; Millard, 1975: 332, fig. 107F-L; Rho, 1977: 275, 423, pl. 90 fig 89; Vervoort & Vasseur, 1977: 64, fig. 28; Millard, 1978: 188; Boero, 1981: 182; Boero & Fresi, 1986: 145; Rees & Vervoort, 1987: 113, fig. 23a-b; Gili et al., 1989: 83, fig. 11A; Cornelius & Ryland, 1990: 152, fig. 4.21; Park, 1990: 84; Ryland & Gibbons, 1991: 525, fig. 1; Ramil & Vervoort, 1992a: 143, fig. 37a-d; Cornelius, 1995: 121, fig. 28A-C, E-G (not fig. 28D).

Plumularia dubiaformis Mulder & Trebilcock, 1911: 119, pl. 2 fig. 7; Vervoort & Vasseur, 1977: 68.

Antennella natalensis Warren, 1908: 318, fig. 14.

Antennella dubiaformis; Bedot, 1917: 124.

Antennella paucinoda Fraser, 1935: 110, pl. 2 fig. 10 [not *Plumularia paucinoda* Nutting, 1905].

Antennella secundaria dubiaformis; Watson, 1973: 183, figs 45-46; Vervoort & Vasseur, 1977: 64.

Halopteris catharina; García-Corrales et al., 1978: 47, fig. 20; Gili & Castello, 1985: 19, fig. 6D.

Material examined.

- 1) Roscoff (France, Atlantic), MHNG 293, coll. Bedot, 22.vi.1912, fertile stems up to 27 mm high.
- 2) (France, Atlantic), MHNG without number, Bay of Biscay, coll. Bedot, 63 m, no date, fertile, stem up to 20 mm high.
- 3) Amboina, Indonesia, MHNG without number, coll. Pictet & Bedot, 8.vii.1890, 25 m (see Pictet & Bedot 1900), infertile, 8 mm high.

- 4) Pico, Azores, MHNG 335, coll. Bedot, no date, depth 1160 m, up to 48 mm high, fertile.
- 5) Azores, MHNG 386, coll. Bedot, no date, depth 1250 m, fertile, up to 20 mm high.
- 6) Rovigno, Adriatic Sea, NHMV 1139, coll. Marktanner-Turneretscher (1890), slide, infertile, up to 12 mm high.
- 7) Pto. de Castillo, Ria de Arosa, NW Spain, RMNH Coel. 2155, many fertile stems on solitary ascidian, up to 2 cm high.
- 8) Seychelles, MACT 2.724 and 2.748 (2.724 from Mahé, Beau Vallon glacis; 2.748 from Praslin), coll. Millard & Bouillon (material described by Millard & Bouillon, 1973), many fertile stems, some branched, up to 8 mm high.
- 9) Holotype of *Antennnella gracilis* Allman, 1877, MCZH, no number, from Carysfort Reef (Florida, USA), 110 m, 21.iii.1869.
- 10) S. Lucie Inlet, Florida, U.S.A., ROMIZ no B1090, coll. R. Roesch, 4.x.1976, depth 87 m, infertile, up to 20 mm, could belong to another species as nematocysts differ.

Description (after European material).— Colonies forming ramified, tubular stolons from which rise upright, normally unbranched stems.

Stems composed of a basal part divided into variable number of segments by means of transverse nodes, last node oblique, segments with a variable number of nematothecae. Remainder of stem heteromerously segmented by alternating oblique and transverse nodes. Transverse nodes often indistinct or absent in more proximal parts of the stem.

Hydrotheca cup-shaped, walls in side view rather straight, converging towards base, rim even, opening forming an angle of 45 to 55° with the main axis, adcauline side adnate for half of its length or less. Each hydrotheca surrounded by four nematothecae: one median inferior not reaching the hydrothecal base, one pair of laterals situated on well formed pedicels, and an axillar one. Intersegments or their homologues if fused to main segment normally with two median nematothecae, rarely three.

Nematothecae all two-chambered. Median inferior nematothecae with adcauline wall of upper chamber much lowered. Lateral nematothecae conical, inner side of wall of upper chamber lowered almost to bottom. Axillar nematotheca rather variably developed.

Gonothecae of both sexes on the same stems, developing directly under hydrotheca, with pedicel of two segments. Female gonotheca pear-shaped, slightly curved or straight, length 0.8 to 0.9 mm, with truncated operculate end, base with two large nematothecae. Male gonothecae 0.6-0.7 mm long and with more rounded distal end and smaller or invisible lid.

Nematocysts: a) large microbasic mastigophore in nematophores, (10.5-13.5) × (4.0-5.0) μm, s = 0.8-0.9; b) almond-shaped capsule from tentacles, (4.5-5.5) × (2.0-3.0) μm; c) egg-shaped capsule, rare, (4.0-4.5) × (3.5) μm.

Type locality.— Mediterranean Sea.

Variation.— The length of the intersegments is extraordinarily variable. Also the dimensions of the hydrothecae are quite variable. This variability is even seen between colonies from the same locality (Broch, 1933). There are normally two nematothecae per intersegment, or its equivalent if fused to the main segment, but one to three can be present. Occasionally, irregularly branched forms similar to *Monostaechas* spec. can occur (Billard, 1913; Ryland & Gibbons, 1991).

Distribution.— Cosmopolitan species with distinct preference for temperate and

warmer localities. The species occurs from the littoral zone to at least 1250 m depth.

Ecology.— In the Mediterranean, *A. secundaria* occurs at a depth of 7 to 20 m, it is frequently found on algae, concretions, and other hydroids; the reproductive season is from August to October (Boero & Fresi, 1986). Riedl (1959) gives a fertile period from October to November for the Naples region, Broch (1933) from July to November for the Adriatic sea.

Remarks.— Calder (in press) will discuss the complicated history and synonymy of this species thoroughly; therefore it is not repeated here.

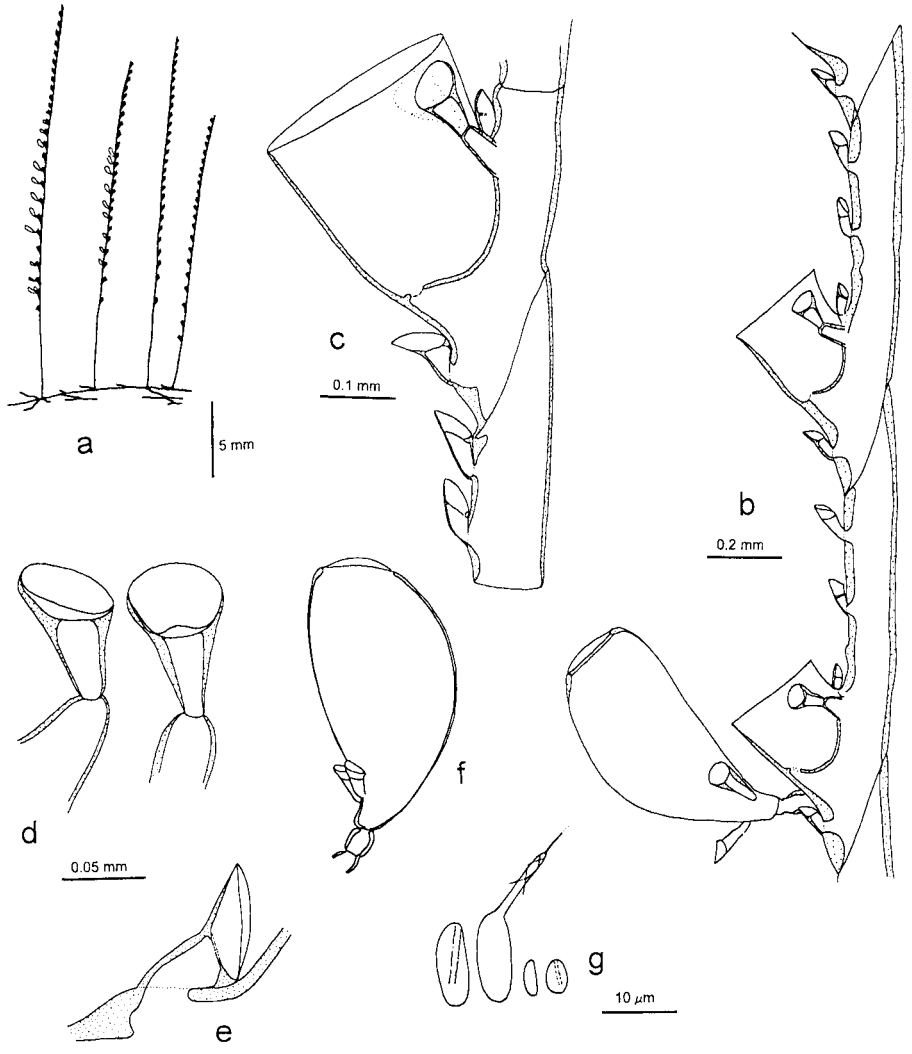

Fig. 3. *Antennella secundaria* (Gmelin, 1791); a-e, after sample no. 1, f-g, sample no. 7; a, part of fertile colony; b, part of stem with female gonotheca, note absence of transverse nodes; c, part of stem with complete segmentation; d, two lateral nematothecae showing extent of variation; e, median inferior nematotheca; f, female gonotheca; g, nematocysts: undischarged and discharged microbasic mastigophore, almond-shaped capsule from tentacles, rare egg-shaped capsule.

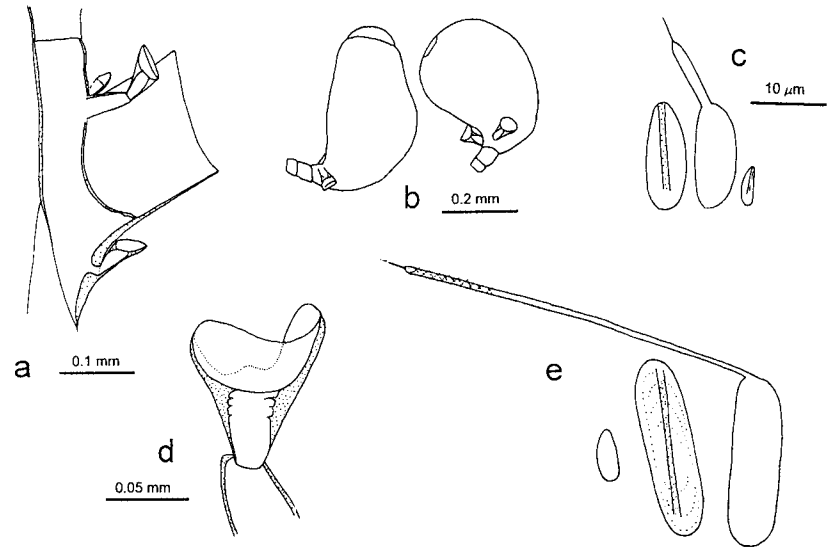

Fig. 4. *Antennella secundaria* (Gmelin, 1791); a-c, after material from Seychelles (sample no. 9), d-e, after material from Florida (sample no. 10); a, part of stem, note size difference of hydrotheca to fig. 1b; b, female (left) and male (right) gonotheca; c, nematocysts: undischarged and discharged microbasic mastigophore, almond-shaped capsule from tentacles, note that this is probably not the complete cnidome; d, lateral nematotheca; e, nematocysts: almond-shaped capsule from tentacles, undischarged and discharged microbasic mastigophore.

The holotype of *Antennella gracilis* Allman, 1877 was re-examined for this study. The type material is of somewhat limited value as it also contains fragmented material of *Monostaechas dichotoma* Allman, 1877 [= *M. quadridens* (McCrady, 1859)]. The inclusion of this species may be due to accidentally combining two samples (see Calder, in press). Although *Monostaechas quadridens* fragments can look exactly like *A. secundaria*, some differently coloured stems in the sample probably represent the material of *A. gracilis*. As already noted by Calder (in press), the description of Allman (1877) is not correct and the material of *A. gracilis* cannot be separated from *A. secundaria*. This view was also expressed by Bedot (1914) and Stechow (1919).

Type material of *Plumularia dubiaformis* Mulder & Trebilcock, 1911 has been re-examined by Watson (1973). Her description exactly fits *A. secundaria*. Watson (1973) maintained a subspecies *dubiaformis* on account of the presence of two nematothecae per intersegment. This, however, is the normal condition for this species and the variety *dubiaformis* is not recognised here (see also Rees & Vervoort, 1987).

The author agrees with Ramil & Vervoort (1992a) that García-Corrales et al. (1978) misidentified *A. secundaria* as *H. catharina*. Likewise it is not certain that all *A. secundaria* described previously were actually that species, because many authors did not pay attention to the nematotheca behind the hydrotheca.

The dimensions of *A. secundaria*, especially the size of segment and hydrotheca, vary greatly, even in samples from the same locality (Broch, 1933). As can be seen from table 1, the Indo-Pacific samples have considerably smaller dimensions and also the shape of the gonotheca seems to be slightly different (fig. 4). Significant differences were found in the size and type of the large mastigophore in the nemato-

Table 1. Variation and dimensions of *Antennella secundaria*, in µm if not stated otherwise.

sample no.	1	2	3	4	5	6	8	10
stem height [mm]	27	20	8	48	20	12	7	20
main segment length	460-530	480-640	290-350	720-760	580-720	430-500	260-370	490-560
intersegment length	390-760	420-900	320-400	640-1680	840-1280	420-480	230-410	460-750
diameter stem	100	110-120	60	160-180	70-110	60-80	60-70	100-140
abcauline length hydrotheca	230-260	220-250	160-180	340-390	230-270	180-220	140-150	290-320
free adcauline length hydrotheca	120-160	130-150	90-100	170-180	140-180	100-130	90-100	140-150
diameter of hydrotheca	260-280	230-250	150-160	350-420	300-350	210	170-190	260-290
female gonotheca length	800	900	-	800	-	-	-	-
nematothecae/intersegment	2	2	2	3-4	3-4	2	2	2
number tentacles (approximately)	-	-	-	-	12	14	18?	14-16

phores of material from Florida. They were much larger (size (19-23) × (5.5-6.5) µm), and had a shaft length that almost qualifies them as macrobasic mastigophores (fig. 4e). In the material from the Mediterranean, the Atlantic coast of Spain, or from the Seychelles the same type is much smaller and has a short shaft (fig. 3g). Also the lateral nematothecae of the material from Florida showed a clear difference to all other samples. These differences could indicate that in fact more than one species might be included in *A. secundaria*, and it is important that future investigations pay attention to the nematocysts. The difference in shape and size of the large mastigophore as found here would normally be enough to recognise distinct species in athecate hydroids. However, as the nematocysts could not be examined in the native condition and because gonothecae are absent in the material from Florida, it has not been described as a new species.

Antennella avalonia Torrey, 1902

Antennella avalonia Torrey, 1902: 74, pl. 10 figs 92-94. Billard, 1904: 484; Bedot, 1917: 125; 1921b: 4; Fraser, 1938a: 57; 1948: 263.

Type locality.— Avalon, Catalina Island, California, U.S.A.

Distribution.— Santa Rosa Island, Santa Catalina Island.

Remarks.— Billard (1904) suggested that *Antennella avalonia* is conspecific with *H. catharina*, which seems very unlikely. Bedot (1917) thought that *A. avalonia* is actually *A. siliquosa* (Hincks, 1877). This interpretation is formally correct, as Torrey's (1902) description of *A. avalonia* does hardly allow a distinction from *A. siliquosa*. According to Fraser (1946, cited by Calder, in press) *Antennella avalonia* is similar to *A. secundaria* but he distinguishes them on account of colony size, segment length, location of thecate segments, nematothecal arrangement, and gonothecal shape. These are rather variable characters and it seems likely that *A. avalonia* and *A. secundaria* can in fact not be separated. Torrey (1902) did not describe or depict an axillar nematotheca, although he stated that *A. avalonia* resembles *Monostaechas quadridens*, which has an axillar nematotheca. It is thus necessary to re-examine the type material of *A. avalonia* before further decisions can be made. Pending such an examination, *Antennella avalonia* is here kept separate from *A. secundaria*.

Antennella siliquosa group

Remarks.— This group contains *Antennella siliquosa, A. campanulaformis, A. tubulosa, and A. kiwiana.* All these species are similar and it is conceivable that at least some may prove conspecific as soon as more material provides further information on the variability within and between populations. The characters used to distinguish these four species at the present state of our knowledge are given in table 2.

Table 2. Distinguishing characters of the *Antennella siliquosa* group.

species character	*Antennella siliquosa*	*Antennella campanulaformis*	*Antennella tubulosa*	*Antennella kiwiana*
location of female gonotheca comp. to male one	proximal	distal	only known from separate stems	proximal
shape of female gonotheca	quadrangular	circular to slightly	circular to oval elongate	oval
size of female gonotheca [in mm]	1.2	0.6-0.7	0.55	1.2
number nematothecae on intersegments	2	1	1	1
hydrotheca: shape in side view	campanulate	cylindrical	cylindrical	cylindrical
hydrotheca: depth to diameter ratio	1.0-1.2	~0.9	1.4-2.1	1.1-1.4
pedicel of lateral nematotheca	as long as nematotheca	short	very short	as long as nematotheca

Antennella siliquosa (Hincks, 1877)
(fig. 5, table 3)

Plumularia siliquosa Hincks, 1877: 148, pl. 12 figs 2-6.
Antennella siliquosa; Billard, 1912: 468; Bedot, 1917: 125; Stechow, 1919: 112; Bedot, 1923: 220, fig. 12; Stechow, 1923b: 222; Riedl, 1959: 653; Medel & Vervoort, 1995.
Antennella simplex Bedot, 1914: 84, pl. 5 figs 2-5; 1917: 115 [not *Halopteris simplex* (Warren, 1914)]
Antennella diaphana f. *siliquosa*; Vervoort, 1959: 286, fig. 43; ? Redier, 1966: 89.
Halopteris diaphana f. *siliquosa*; ? Broch, 1933: 26 (material from locality 3); García-Corrales et al., 1978: 45, fig. 19; Ramil & Vervoort, 1992a: 148, fig. 38a.

Material examined.
- 1) Syntype material of *Antennella simplex* Bedot, 1914, MHNG, collection Bedot, three jars, all labelled as type, collected near Roscoff. Jar 294: 21.vii.1906, dredged 24 m, Baye de Morlaix, fertile. Jar 254: 13.vi.1910, 5 miles NNE of Roscoff, no depth given, infertile. Jar 276: 22.vi.1910, 2.5 miles NNW of Ile de Batz, infertile.
- 2) Atlantide stations 125, 68, and 44 (tropical Atlantic off West Africa, see Vervoort, 1959), RMNH Coel. 1241, 1269, 13061, as *Antennella diaphana* f. *siliquosa.*

Description.— Colony composed of ramified, tubular stolons from which rise upright, unbranched stems.

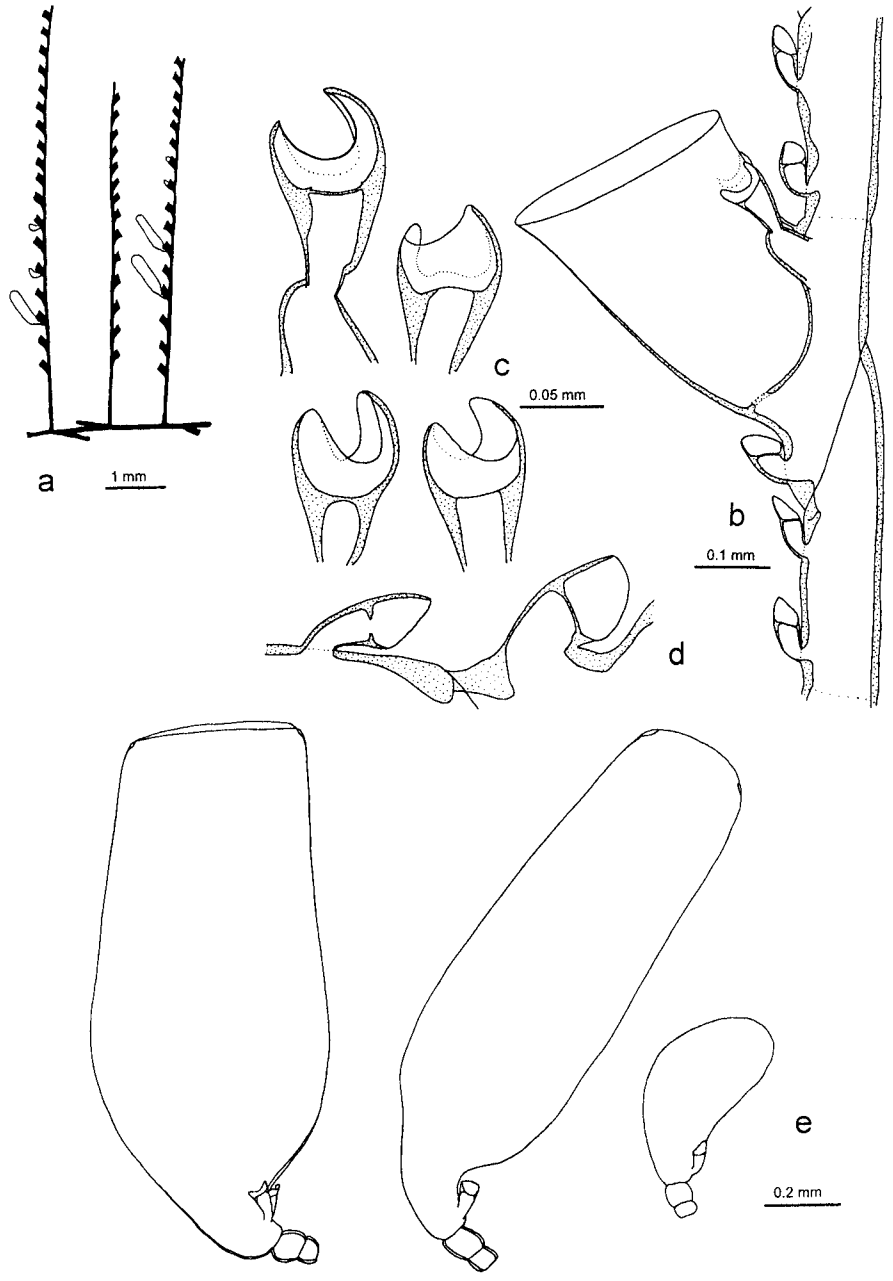

Fig. 5. *Antennella siliquosa* (Hincks, 1877) from Roscoff, except male gonotheca which is from Atlantide station 44; a, part of fertile colony; b, part of stem; c, several lateral nematothecae showing typical spanner-like shape; d, median inferior nematotheca (right); e, gonothecae, frontal view of female gonotheca, same in lateral view, male gonotheca.

Stems composed of a basal part, divided into a variable number of segments by means of transverse nodes, segments bearing up to five frontal nematothecae. Rest of stem composed of hydrothecate segments with oblique nodes. Occasionally a horizontal node may delimit an intersegment distally from the main segment.

Hydrotheca surrounded by three nematothecae: one median inferior not reaching hydrothecal base and one pair of laterals on well formed pedicels. Distal to hydrotheca there are two (one to three occasionally) nematothecae which may sometimes be placed on a separate intersegment. Hydrotheca campanulate, walls in side view only slightly curved, margin even, opening forming an angle of 35 to 45° with the main axis, adcauline side adnate for half of its length or less.

Nematothecae all two-chambered. Median nematothecae scoop-shaped with adcauline wall of upper chamber much lowered. Lateral nematothecae with inrolled upper chamber with a deep emargination on inner and outer side thus giving a spanner-like appearance (fig. 5c).

Gonothecae of both sexes on the same stem. Female gonotheca proximal to male ones, up to 1.4 mm long, sitting on a pedicel of two short segments; main body flattened (by a factor of approximately two), quadrangular, with straight walls, only extreme basal end curved, distal end truncated with inconspicuous annular thickening and almost flat lid. Basal part with two nematothecae. Male gonotheca only about $^1/_3$ the size of the female one, curved, distal end rounded, with pedicel of two segments, with one nematotheca near its base.

Type locality.— Coast of Guernsey, Channel Islands, United Kingdom.

Variation.— The population from the Channel seems to have two nematothecae on the intersegments or their homologues. This number is variable to some extent within one colony. In the examined material only $^3/_4$ of the intersegments had two nematothecae, the remaining $^1/_4$ had either one or three nematothecae with equal frequencies. Branching is not known in this species.

Distribution.— Atlantic coasts of England to France; Mediterranean; Atlantic coast of tropical West Africa.

Remarks.— Hincks (1872) provided a very good description and figures that leave no doubt on the identity of this species. Later, several authors (e.g. Broch, 1933; Vervoort, 1959) erroneously attributed this species to *Halopteris diaphana*. Recently, Medel & Vervoort (1995) and Calder (in press) considered the species valid again. Although *H. diaphana* can form *Antennella*-like stems (see p. 51), the two species can be separated on account of the shape of the female gonotheca and the shape of the upper chamber of the lateral nematotheca (compare figs 5c, e and 15 e-f). The walls of the female gonotheca of *A. siliquosa* are straight for most of their length and not cornucopia-shaped as in *H. diaphana*. The lateral nematothecae of *A. siliquosa* have both inner and outer walls of the upper chamber deeply emarginated, and not only slightly so on the inner side as in *H. diaphana*. Although the shape of the lateral nematothecae can be variable in some species, it is rather constant in both *A. siliquosa* and *H. diaphana*. *Antennella siliquosa* is also not known to form pinnate cormoids. Reexamination of Vervoort's (1959) material showed that it is identical with the material from the Channel. For further discussion and characters to distinguish *A. siliquosa* from similar species see also the discussions of *H. diaphana*, *A. campanulaformis*, *A. kiwiana*, and table 2.

Antennella simplex was described by Bedot (1914) as a new species, but he later (1917) realised that his material must obviously belong to *A. siliquosa*. Stechow (1925: 245) also reported that species from Australia. His observations were based on sterile material and it had only one nematotheca on the apparently well formed intersegment. It is thus much more likely that he actually studied immature colonies of *Halopteris campanula* or *Antennella campanulaformis*.

Table 3. Dimensions of *Antennella siliquosa* (Hincks, 1877), in µm if not stated otherwise.

sample no.	1
caulus height [mm]	12-16
hydrothecate segments	380-470
ahydrothecate segments	400-800
abcauline side of hydrotheca	270-410
free adcauline side of hydrotheca	150-210
diameter of hydrotheca	280-350

Antennella siliquosa has been synonymised with *A. secundaria* by Cornelius (1995), which seems unlikely and is not followed here.

Antennella tubulosa (Bale, 1894) (fig. 6, table 4)

Plumularia tubulosa Bale, 1894: 114, pl. 5 figs 2-5; Mulder & Trebilcock, 1909: 34.
Antennella tubulosa; Bedot, 1917: 126; Watson, 1973: 182, fig. 42.

Material examined.

- 1) Lectotype MVM slide F58752, ex collection Bale, original labels: W. M. Bale, Hydroida, Plumulariidae, *Plumularia tubulosa* W.M.B., Pt. Philip, Mr. J. B. Wilson, 1889. By inference from Bale (1894) this must be the specimen on which he based his description. It is designated here as the lectotype.
- 2) Port Philip Bay, Victoria, Australia, MVM, two slides F58753, ex collection Bale, identified as *Plumularia tubulosa*.

Description.— Colony forms upright, unbranched stems reaching 8 mm in height, arising from tubular stolons.

Stems with basal part with transverse nodes and one nematotheca per segment. Basal part ends in an oblique node. Distal part heteromerously segmented by alternating oblique and transverse nodes. Transverse nodes separating main- from intersegments often indistinct. Main segments with a hydrotheca and three nematothecae: one median inferior and one pair of laterals. There is no nematotheca in axil of hydrotheca. Intersegments with a single nematotheca only, rarely (2 out of 25 examined intersegments) with two nematothecae.

Hydrotheca cylindrical and very deep, walls in side view straight or with slight convexity below margin, rim often lowered laterally. Thickness of walls varies considerably, some thin, some thick, especially abaxial side. Hydrotheca reaches far beyond transverse node, angle of opening with axis of segment 50 to 60°.

Nematothecae all two-chambered. Median inferior nematotheca does mostly not reach hydrotheca, immovable, scoop-shaped, adaxial wall of upper chamber missing. Lateral nematothecae without or with short pedicel, conical, with strongly inrolled wall of upper chamber, inner and outer sides emarginated and thus looking like a spanner. Nematothecae on intersegments similar to median inferior ones.

Gonothecae of both sexes on different stems in the few examined fertile stems, difficult to distinguish as shape and size vary even within same stem. Female

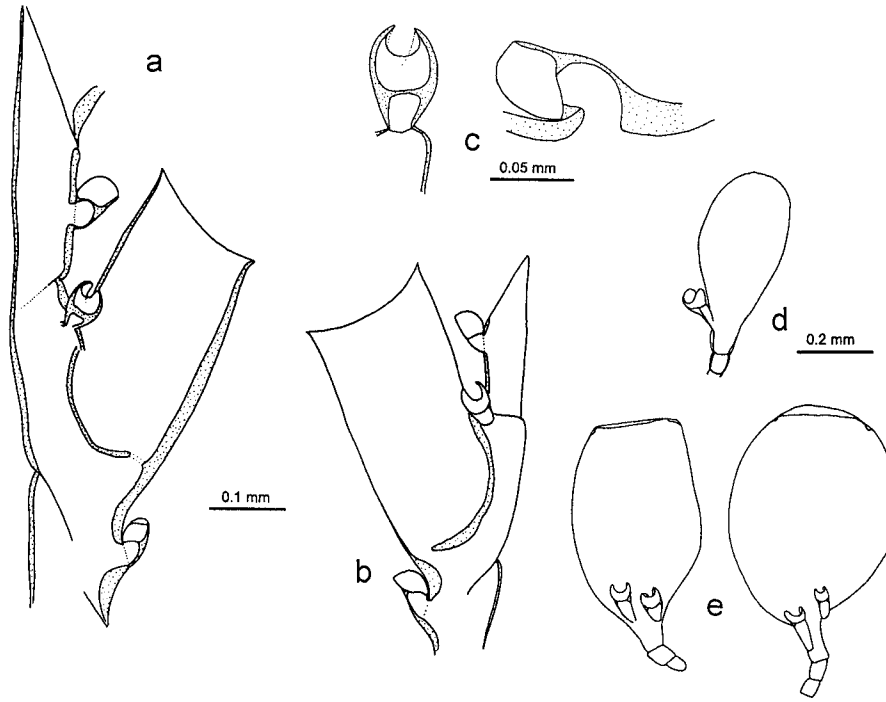

Fig. 6. *Antennella tubulosa* (Bale, 1894); a, part of stem, hydrotheca with thickened wall; b, part of other stem without thickened walls of hydrotheca, same scale as a; c, nematothecae, left: lateral one, right: median inferior; d- e, gonothecae, all same scale; d, male gonotheca; e, two female gonothecae showing extent of shape variation.

gonotheca up to 0.55 mm long, with tapering base and either rounded or quadrangular distally; distal end truncated and with lid, with two nematothecae near basis and with pedicel of two segments. Male gonotheca up to 0.5 mm long, rounded, more oblong than female one, with single nematotheca near basis; pedicel composed of one or two segments.

Nematotcysts: a) microbasic mastigophore, 15 × 5 µm, s~1, in nematophores; b) isorhizas, 3.5 × 1.5 µm, in tentacles.

Type locality.— Port Philip Bay, Victoria, Australia.

Variation.— The shape of the female gonotheca was found to be rather variable (cf. fig. 6e). The thickness of the hydrothecal wall is also very variable (cf. figs 6a and 6b).

Additional information.— The stems are either colourless (Bale, 1894) or yellow (Watson, 1973).

Distribution.— South Australia to Victoria, Australia.

Remarks.— Bale thought that *A. tubulosa* might be a form of *Halopteris campanula*. Both species resemble each other in structure and shape of the nematothecae. However, the characteristically deep hydrothecae of *A. tubulosa* immediately distinguishes it from all other species. Because the species has been found several times at different localities the opinion of Watson (1973) is here followed and *A. tubulosa* is

seen as a distinct species. Besides the long hydrotheca, *Antennella tubulosa* can be distinguished from the similar *A. kiwiana* by the height of the pedicels of the lateral nematothecae, the twice bigger female gonotheca, and the shape of the hydrotheca (see also table 2). The likewise similar *A. campanulaformis* is presently only securely distinguishable from *A. tubulosa* by the depth of the hydrotheca. More material of both species is needed to obtain more information on the extent of variation of the hydrothecal length. It is possible that both nominal species are actually only phenotypic modifications of the same species.

Table 4. Dimensions of *Antennella tubulosa*, in µm if not stated otherwise.

sample no.	1
caulus height [mm]	8
max. no. hydrothecae per stem	12
main segments	320-420
intersegments	210-410
abcauline side of hydrotheca	220-350
free adcauline side of hydrotheca	140-220
diameter of hydrotheca	160-170

Antennella campanulaformis (Mulder & Trebilcock, 1909) (fig. 7, table 5)

Plumularia campanulaformis Mulder & Trebilcock, 1909: 31, pl. 1 figs 6, 9, 10; Mulder & Trebilcock, 1911: 115.
Plumularia campanulaformis var. *dubia* Mulder & Trebilcock, 1911: 115, pl. 2 fig. 6.
Antenella dubia; Stechow, 1923b: 222; 1925a: 244.
Antennella siliquosa; ?Stechow, 1925a: 245.
Antennella campanuliformis; Watson, 1973: 182, figs 43-44 (subsequent incorrect spelling).
Halopteris diaphana; Millard & Bouillon, 1973: 82, fig. 10L-M.

Material examined.

- 1) Lectotype MVM slide F57966, ex collection Trebilcock (Stranks, 1993), original label: Type, R. E. Trebilcock, Kerang, Vict., Australia, *Plumularia campanulaformis* M. & T. Contains obviously the material figured with first description and designated here as lectotype; contains fragment of basal part of stem and one much compressed female gonotheca.
- 2) Torquay, Victoria, Australia, MVM slide F57983, *Plumularia campanulaformis* var. *dubia*, ex collection Trebilcock, labelled as type on original label, contains stem fragment as figured in original publication and also one plume of *Halopteris everta* Mulder & Trebilcock, 1909.
- 3) Pearson Island, South Australia, MVM slides F42015 and F42016, ex collection Watson (described by Watson, 1973), several fertile stems up to 6 mm high.
- 4) Amirante Isl., Seychelles, MACT no. 2.779, coll. J. Bouillon (described in Millard & Bouillon, 1973), labelled as *Halopteris diaphana*, contains a few well preserved unbranched stems up to 10 mm high, only female gonothecae present.

Description.— Colony forms upright, unbranched stems reaching 1 cm in height, arising from tubular stolons.

Stems with basal part with transverse nodes and without hydrothecae but with nematothecae. Basal part ends in oblique node. Distal part heteromerously segmented by alternating oblique and transverse nodes. Transverse nodes separating main- from intersegments often weak and indistinct. Main segments with hydrotheca and three nematothecae: one median inferior and one pair of laterals. There is no nematotheca in axil of hydrotheca. Intersegments with single nematotheca only.

Hydrotheca cylindrical, walls in side view straight or with slight convexity

below margin, rim smooth and sometimes sinuated. Abcauline wall thickened considerably, adcauline wall thin or also thickened. Hydrotheca reaches far beyond transverse node, angle of opening with segmental axis 30 to 50°.

Nematothecae all two-chambered. Median inferior nematotheca reaches to hydrotheca, conical, adaxial wall of upper chamber broadly emarginated down to bottom of upper chamber. Lateral nematotheca on pedicel that is much shorter than nematotheca itself, upper chamber with inrolled wall, inner and outer sides deeply emarginated, thus looking like a spanner. Nematothecae on intersegments similar to median inferior ones.

Gonothecae of both sexes on same stem, female gonothecae distal to male ones. Female gonotheca 0.6 to 0.7 mm in diameter, almost globular, flattened, with short conical base and terminal, oval lid, two nematothecae near basis, pedicel formed by one segment and an apophysis. Female gonotheca contains one egg only. Male gonotheca smaller, up to 0.3 mm long, ovate, with small terminal lid, with one nematotheca near basis, pedicel as above.

Type locality.— Barwon Heads, Victoria, Australia.

Distribution.— Southern Australia, Seychelles.

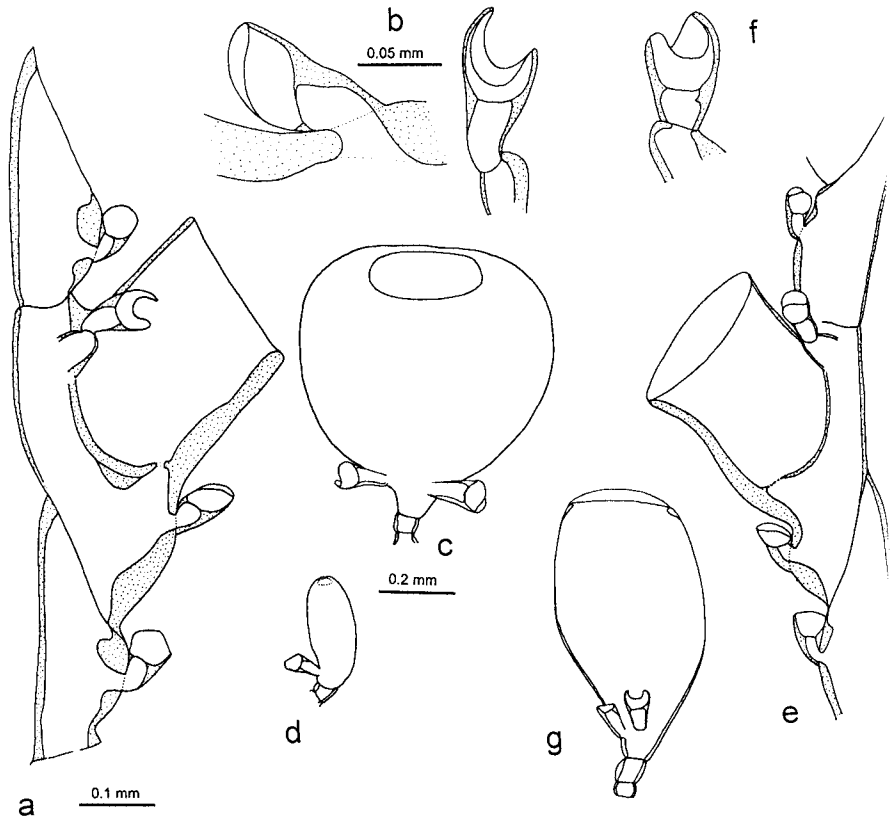

Fig. 7. *Antennella campanulaformis* (Mulder & Trebilcock, 1909); a-d, material from Pearson Island, Australia, e-g material from Seychelles; a, part of stem; b, median inferior and lateral nematothecae; c, female gonotheca; d, male gonotheca; e, part of stem, same scale as a; f, lateral nematotheca, same scale as b; g, female gonotheca, same scale as c.

Table 5. Dimensions of *Antennella campanulaformis*, in µm if not stated otherwise.

sample no.	3	4
caulus height [mm]	8	10
main segments	330-450	380-390
intersegments	290-380	330-450
abcauline side of hydrotheca	180-250	150-210
free adcauline side of hydrotheca	170-200	90-120
diameter of hydrotheca	280	210-250
tentacle number	-	18-22

Remarks.— As already noted by Watson (1973), the hydrothecae of *H. campanulaformis* are rather cylindrical than campanulate as described by Mulder & Trebilcock (1909). These authors studied a strongly compressed and distorted sample which may explain the discrepancy. Although the minute structure of *A. campanulaformis* shows a close resemblance to that of *H. campanula*, both species can be distinguished by the shape of the female gonotheca and the hydrothecae. *Antennella campanulaformis* also does not seem to form plumose colonies.

Antennella campanulaformis also resembles *A. siliquosa* (see p. 19); this species, however, has a different female gonotheca, has two nematothecae per intersegment, and differs in the shape of the hydrotheca. The new species *Antennella kiwiana* shows even a closer affinity to *A. campanulaformis*. The characters used to distinguish the two are discussed under the latter and also in table 2.

Plumularia campanulaformis var. *dubia* was described by Mulder & Trebilcock (1911) as different from the nominal species by being more robust with larger and more widely spaced hydrothecae. The material of this variety is presumably based on a single sample that was re-examined for this study. This type material consists of a small, compressed stem fragment with three hydrothecae. Although the hydrothecae lack the thickened walls, the differences were not seen as significant and the material considered insufficient to warrant the distinction of a separate variety. The material could as well belong to one of the numerous related species. Stechow's (1923b, 1925a) proposal to raise this variety to the species level therefore seems unnecessary.

The material described by Stechow (1925a) from Western Australia as *Antenella dubia* (sic) and *A. siliquosa* probably belongs to *A. campanulaformis*. Stechow's material identified as *A. siliquosa* had only a single nematotheca on its intersegments, thus resembling more the present species than *A. siliquosa*.

Material from the Seychelles described by Millard & Bouillon (1973) as *H. diaphana* was re-examined for this study. The material closely resembles *A. campanulaformis* and it is here tentatively assigned to this species (fig. 7e-g). The only difference found was the presence of an occasional second nematotheca on the intersegments and a more elongate female gonotheca. Male gonothecae were not present, therefore it could not be proved whether or not the female gonothecae develop proximally to the male ones. More material is needed to assess the extent of variation in the shape of the female gonothecae.

Antennella kiwiana spec. nov.
(fig. 8, table 6)

Material examined.— Schizoholotype RMNH Coel. 27609, slide 3299, made from one colony collected 7.viii.1991 by author on Echinoderm Reef, Leigh Marine Biological Station, Auckland, New Zealand, intertidal, several fertile stems; remainder of colony preserved in alcohol and deposited as holotype (RMNH Coel. 27609).

Description.— Colony approximately 2 cm in diameter, forming upright, unbranched stems reaching 1.5 cm in height that arise from reticulate, tubular stolons without nematothecae.

Stems with short basal part with up to three transverse nodes and without hydro-

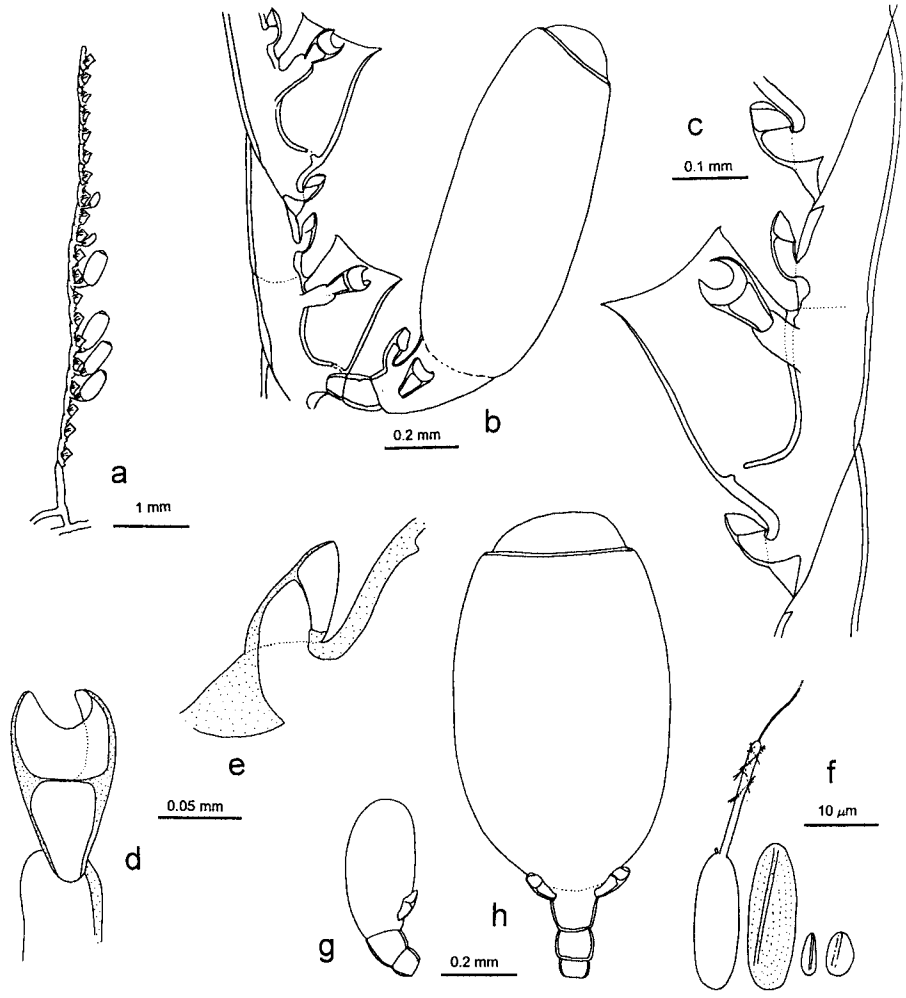

Fig. 8. *Antennella kiwiana* nov. spec.; after type material; a, fertile stem; b, part of stem in lateral view with female gonotheca; c, part of stem in lateral view; d, lateral nematotheca; e, median inferior nematotheca; f, nematocysts: discharged microbasic heteroneme, same undischarged, almond-shaped small capsule, egg-shaped small capsule; g, male gonotheca; h, female gonotheca in frontal view.

thecae but with zero to two nematothecae per segment. Basal part ends in oblique node. Distal part heteromerously segmented by alternating oblique and transverse nodes. Transverse nodes separating main- from intersegments often weak and indistinct. Main segments with a hydrotheca and three nematothecae: one median inferior and one pair of laterals. There is no nematotheca in axil of hydrotheca. Intersegments with single nematotheca only.

Table 6. Dimensions of *Antennella kiwiana*, in µm if not stated otherwise.

material	holotype
max. no. hydrothecae per stem	15
main segments	390-310
intersegments	350-400
stem diameter	100-140
abcauline side of hydrotheca	270-290
free adcauline side of hydrotheca	130-150
diameter of hydrotheca	170-200
pedicel of lateral nematothecae	60-70
length female gonotheca	1120-1200
length male gonotheca	460-500
tentacle number	18

Hydrotheca deep, cylindrical in side view, often with constriction near distal end, rim flaring, smooth, lowered laterally. Abcauline wall sometimes thickened, adcauline wall thin. Hydrotheca reaches far beyond transverse node. Angle of opening with stem axis 30 to 40°.

Nematothecae all two-chambered. Median inferior nematotheca does not reach hydrotheca, scoop-shaped, adaxial side shortened, adaxial wall of upper chamber lowered down to bottom of chamber. Lateral nematothecae on pedicels as long as nematotheca itself, with two chambers of equal size, upper chamber with much inrolled wall, inner and outer sides deeply emarginated, thus resembling a spanner. Nematothecae on intersegments similar to median inferior ones, but with longer adaxial wall.

Gonothecae of both sexes on same stem, female gonothecae proximal to male ones, developing singly or in pairs below hydrotheca. Female gonotheca about 1.2 mm long, flattened in frontal plane for a factor of about two, base curved. Main body of female gonotheca oval in frontal view, with truncated distal end bearing convex lid, base short, with two to three nematothecae. Pedicel of female gonothecae formed by two quadrangular segments. Male gonotheca up to 0.5 mm long, oblong and evenly rounded, with one nematotheca near base, pedicel formed by one or two segments.

Nematocysts: a) large microbasic euryteles, sometimes looking like mastigophores, spines only on distal half of shaft, (17-21) × (4.5-5.5) µm, s~1, found in nematophores; b) small, almond-shaped capsule, (5.5-6.5) × (1.5-2.0) µm, in tentacles; c) egg-shaped capsule, (5.0-5.5) × (3.0-3.5) µm, frequently in median nematophores.

Colour.— Transparent.

Type locality.— Echinoderm Reef Flat, near Leigh Marine Biological Laboratory, Northland, New Zealand.

Etymology.— The species name *kiwiana* is derived from the commonly used nick name for the New Zealanders.

Remarks.— *Antennella kiwiana* closely resembles *A. campanulaformis* (Mulder & Trebilcock, 1909). Both species are here kept separate because of the following differences (see also table 2): *Antennella kiwiana* has its female gonothecae proximal to the male ones while *A. campanulaformis* has a reversed order; the size of the female gonotheca differs for a factor two. Furthermore, the hydrothecae have a different

shape (cf. figs 7a and 8b). For the distinction of the likewise similar *A. tubulosa* see the remarks under this species and also table 2.

Antennella group with two pairs of lateral nematothecae

Remarks.— This group contains the following species: *Antennella quadriaurita, A. varians, A. sibogae* and *A. biarmata.* They are all characterised by the possession of two pairs of lateral nematothecae. *Antennella quadriaurita* is readily separated from the other species as it has its nematothecae other than the laterals in a single median row only and not two rows as in the other species. Those other species are less readily distinguishable and the descriptions must be consulted.

Antennella quadriaurita Ritchie, 1909
(fig. 9, table 7)

Antenella gracilis; Nutting, 1900: 77, misidentification after Stechow (1919).
Antenella quadriaurita Ritchie, 1909: 92, fig. 9; Bedot, 1917: 123; Stechow, 1919: 113; Bedot, 1921b: 5; 1923: fig. 2; Millard, 1966: 492; Millard, 1977: 123, fig. 8; 1978: 188; Calder, in press: fig. 6.
Antenella quadriaurita forma *africana* Broch, 1914: 26.
Antennella africana; Stechow, 1923b: 223; 1925b: 492, fig. 41; Millard, 1957: 226; Ralph, 1961: 23, figs 1a-c, f-g; Millard, 1962: 274; Rho, 1967: 344, fig. 4a-b; Millard, 1968: 273; 1975: 331, fig. 107A-E; 1977: 123;
Antennella ritchiei Totton, 1930: 211, fig. 52a-b; Ralph, 1961: 23, figs 1d-e, h.
Antennella serrata Totton, 1930: 212, fig. 53; Ralph, 1961: 25.
Antennella variabilis Fraser, 1936: 52, fig. 6a-c (syn. nov.) [not *Schizotricha variabilis* (Bonnevie, 1899)].
Halopteris quadriaurita; Stepanjants, 1979: 124, pl. 23 fig. 2.

Material examined.
- 1) Natal coast, SAM H-2880 (described in Millard, 1977; sample SM 103E), as *Antennella quadriaurita,* depth 680 m, several stems with female and male gonothecae, male ones lacking a nematotheca.
- 2) T. Mortensen expedition station 63 (34°09'S, 18°30'E, South Africa, sample described by Millard, 1968), ZMC, as *Antennella africana,* depth 29 m, with female and male gonothecae, males ones with one or two nematothecae.
- 3) T. Mortensen expedition station 64, (34°07'S 18°15'E, South Africa, sample described by Millard, 1968), ZMC, as *Antennella africana,* depth 24 m, with male gonothecae bearing one nematothecae; includes one detached stem with differently shaped nematothecae (fig. 8i).

Description.— Colonies with upright, unbranched stems arising separately or in clusters from tubular stolons. Stolons may bear nematothecae.

Stems reach 3 cm in height, consisting of short basal ahydrothecate part with variable number of transverse nodes and longer distal part. Distal part heteromerously segmented by alternating oblique and transverse nodes. Transverse nodes separating main- from intersegments can be weak and absent. Main segments with a hydrotheca and five nematothecae: one median inferior and two pairs of laterals. There is no nematotheca in axil of hydrotheca. Intersegments with one to four median nematothecae.

Hydrothecae deep, campanulate to nearly cylindrical in side view, abcauline wall sometimes thickened. Angle of opening with axis of segment 20 to 50°.

Nematothecae all two-chambered and movable. Median inferior nematotheca

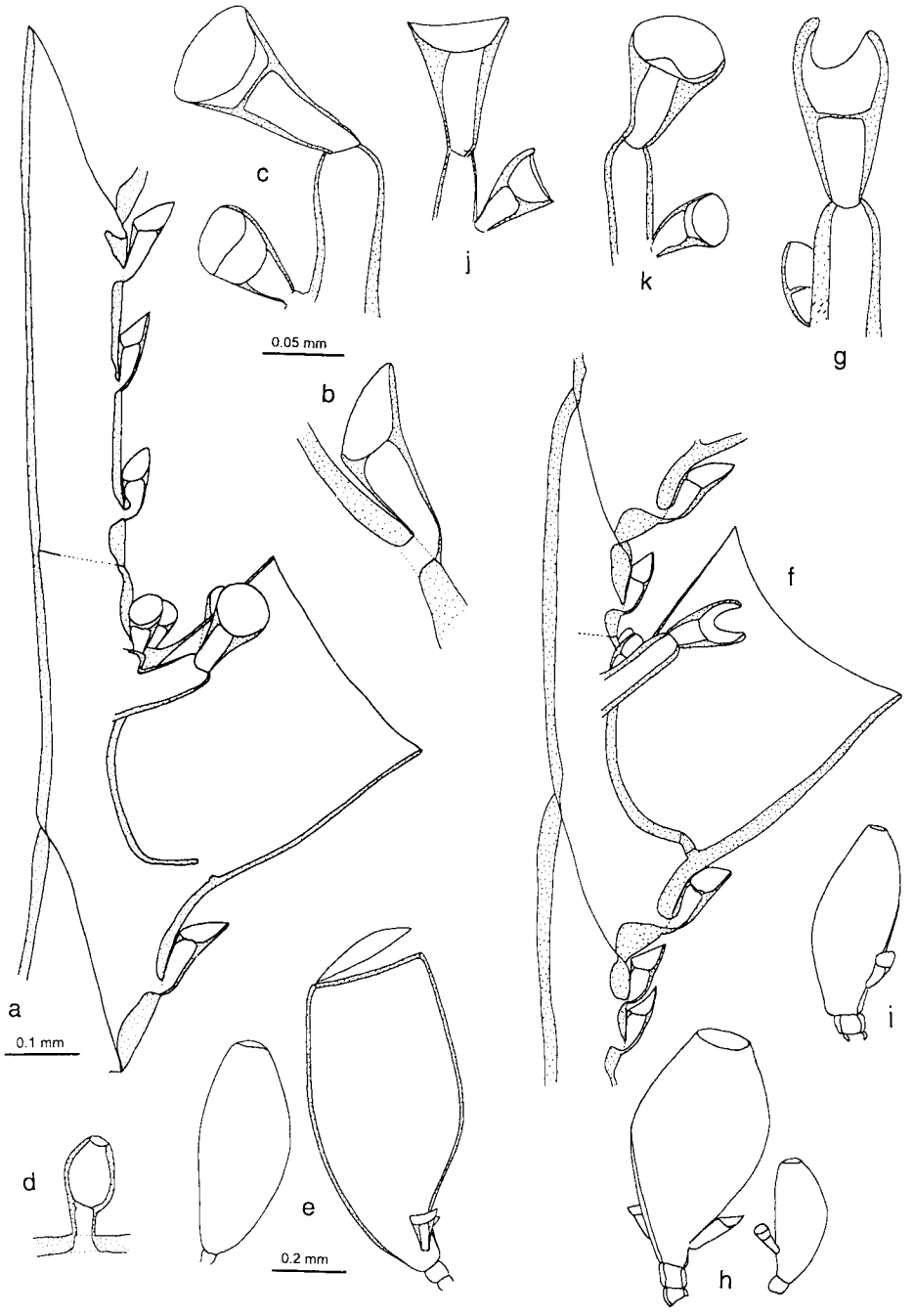

Fig. 9. *Antennella quadriaurita* Ritchie, 1909; a-e, from sample no. 1; f, g, i, j, from sample no. 3; k-h, from sample no. 2; a, part of stem; b, median inferior nematotheca; c, lateral nematothecae, same scale as b; d, nematotheca from stolons, same scale as b; e, male (left) and female (right) gonothecae; f, part of stem, note variability of nematothecae per intersegment, same scale as a; g, lateral nematothecae, same scale as b; h, female (left) and male (right) gonothecae, same scale as e; i, male gonotheca; j-k, lateral nematothecae, same scale as b.

does not reach or just reaches hydrotheca, scoop-shaped, adaxial side shortened, adaxial wall of upper chamber lowered. First pair of lateral nematothecae on pedicel that can be as long as nematotheca itself, not reaching hydrothecal margin, with lower chamber as long as or longer than upper one, shape varied: either with inrolled walls and inner and outer side emarginated (spanner-type), or with straight walls and inner side of upper chamber lowered, with or without adaxial tooth (bivalved). Second pair of lateral nematothecae smaller than first one, structure similar, placed at base of pedicel of first pair, either on upper side or more on inner side. Nematothecae on intersegments similar to median inferior ones.

Gonothecae of both sexes on same stem, female gonothecae proximal to male ones, developing singly or in pairs below hydrotheca. Female gonotheca around 0.6 to 0.8 mm long, pear-shaped, not curved, with wide operculate distal aperture, base with two nematothecae, pedicel composed of two segments. Male gonotheca smaller, spindle-shaped, not curved, bearing zero to two nematothecae near base, pedicel composed of one segment.

Variation.— The intersegments may vary considerably in their length which is also correlated with the number of nematothecae they carry (Millard, 1977).

Type locality.— Gough Island, South Atlantic.

Distribution.— Bermuda; Cuba; Tristan da Cunha group; tropical West Africa; Vema Seamount; South Africa; India; New Zealand, Japan; Korea.

Remarks.— A complete taxonomic history of *Antennella quadriaurita* will be published by Calder (in press). By analysing the variability of the number of nematothecae on the intersegments, Millard (1977) provides convincing arguments that *A. africana* cannot be separated from *A. quadriaurita* exclusively on this character. She thus sunk *A. africana* into the synonymy of *A. quadriaurita*, which is also accepted here. The present material, however, shows also considerable variation in the shape of the lateral nematothecae, their positioning, and also in the gonothecae (cf. fig. 9 a and f, c and g, table 7). It might thus well be that *A. quadriaurita* is nevertheless a complex of species. An allozyme study of the South African populations of *A. quadriaurita* could therefore be most rewarding.

Antennella ritchiei Totton, 1930 from New Zealand was kept distinct from *A. quadriaurita* by Totton (1930) on account of its more reduced nodes, the two nematothecae on the intersegments and the larger size of the thecate segments. Contrary to this,

Table 7. Variation and dimensions of examined *Antennella quadriaurita* samples, in µm if not stated otherwise.

sample no.	1	2	3
segment length (main + inter)	620-680	440-500	300-380
nematothecae/intersegment equivalent	2-3	1-2	1-2
abcauline side of hydrotheca	270-360	280-360	160-230
free adcauline side of hydrotheca	170-220	160-220	110-130
diameter of hydrotheca	320-370	310-360	230-240
shape of first lateral nematotheca	conical, inner side lowered	conical, bivalved	spanner type
nematothecae on male gonotheca	0	1-2	1

already Ralph (1961) noted that the nodes can be present to a varied degree, and Totton's (1930) and Ralph's (1961) measurements agree well with *A. africana*. The only remaining difference with Ralph's concept of *A. africana* is in the two nematothecae on the intersegments. But as shown by Millard (1977) this is also not a valid character and can vary from one to four in *A. quadriaurita*. Following Stepanjants (1979), *Antennella ritchiei* is therefore here also synonymised with *A. quadriaurita*.

The description and figures of *Antennella variablis* Fraser, 1936 from Japan exactly agree with *A. quadriaurita* having two nematothecae per intersegment; the species is therefore considered conspecific with *A. quadriaurita* and the name thus becomes a junior subjective synonym. This does not extend the known range of this widespread species, as it has already been reported from Korea (Rho, 1967; Rho & Park, 1986).

Antennella varians (Billard, 1911)
(figs 10 &11)

Plumularia varians Billard, 1911: 62, fig. 2; Van Praët, 1979: 930, fig. 72.

Plumularia balei Billard, 1911: 63, fig. 3 (syn. nov.) [not *Plumularia balei* Bartlett, 1907 = *Gattya balei* (Bartlett, 1907)].

Antennella varians; Billard, 1913: 11, fig. 4, pl. 1 figs 5, 8; Bedot, 1917: 124; Rees & Vervoort, 1987: 117, fig. 23c-d.

Antennella balei; Billard, 1913: 13, fig. 5, pl. 1 figs 6 & 9; Bedot, 1917: 124; 1921b: 4.

Material examined.

- 1) Holotype of *Plumularia varians* Billard, 1911, ZMA Coel. 4925, Siboga station 166, 2°28.5'S 131°3.3'E (close to New Guinea), depth 118 m, colony reaching 6 cm, with gonothecae, type designation by Billard (1913).
- 2) Siboga stations 80, 99, 117, 125, 133, 153, 164, 257, all from Indonesia, for localities see Billard (1913), ZMA Coel. 4924, as *Plumularia varians*.
- 3) Holotype of *Plumularia balei* Billard, 1911, ZMA Coel. 5264, Siboga station 164, 1°42.5'S 130°47.5'E (close to New Guinea), depth 32 m, without gonothecae, type designation by Billard (1913).
- 4) Île Europe, Madagascar, RMNH Coel. 8103, as *Antennella balei*, coll. P. Vasseur, depth 50 m.

Description.— Colonies forming simple stems clustered into tufts, arising either directly from creeping stolons or from short, erect stem formed by bundled stolons (*Corhiza* form).

Stems thick, stiff, 5 to 8 cm high; segmentation sparse and irregular, only most proximal hydrotheca often proximally and distally with oblique nodes. Not all first hydrothecae from one tuft constructed like this. Several oblique and also transverse nodes can be dispersed irregularly along stem. Also most proximal parts of stems devoid of regular segmentation; basal regions of stems may bear transverse nodes and numerous nematothecae, but they lack hydrothecae.

Hydrothecae cup-shaped in side view, abaxial walls of variable thickness and shape, opening perpendicular to stem or angle even larger than 90°, adaxial wall adnate to stem for all its length, either completely fused to it (proximal stem region) or free for about $^1/_5$ of its length (distal stem region). Arrangement of nematothecae variable. On each side of hydrotheca there are two nematothecae, first one on long pedicel, second one near base of this pedicel. In between successive hydrothecae there are four, rarely six, nematothecae in double row, often in pairs at same level,

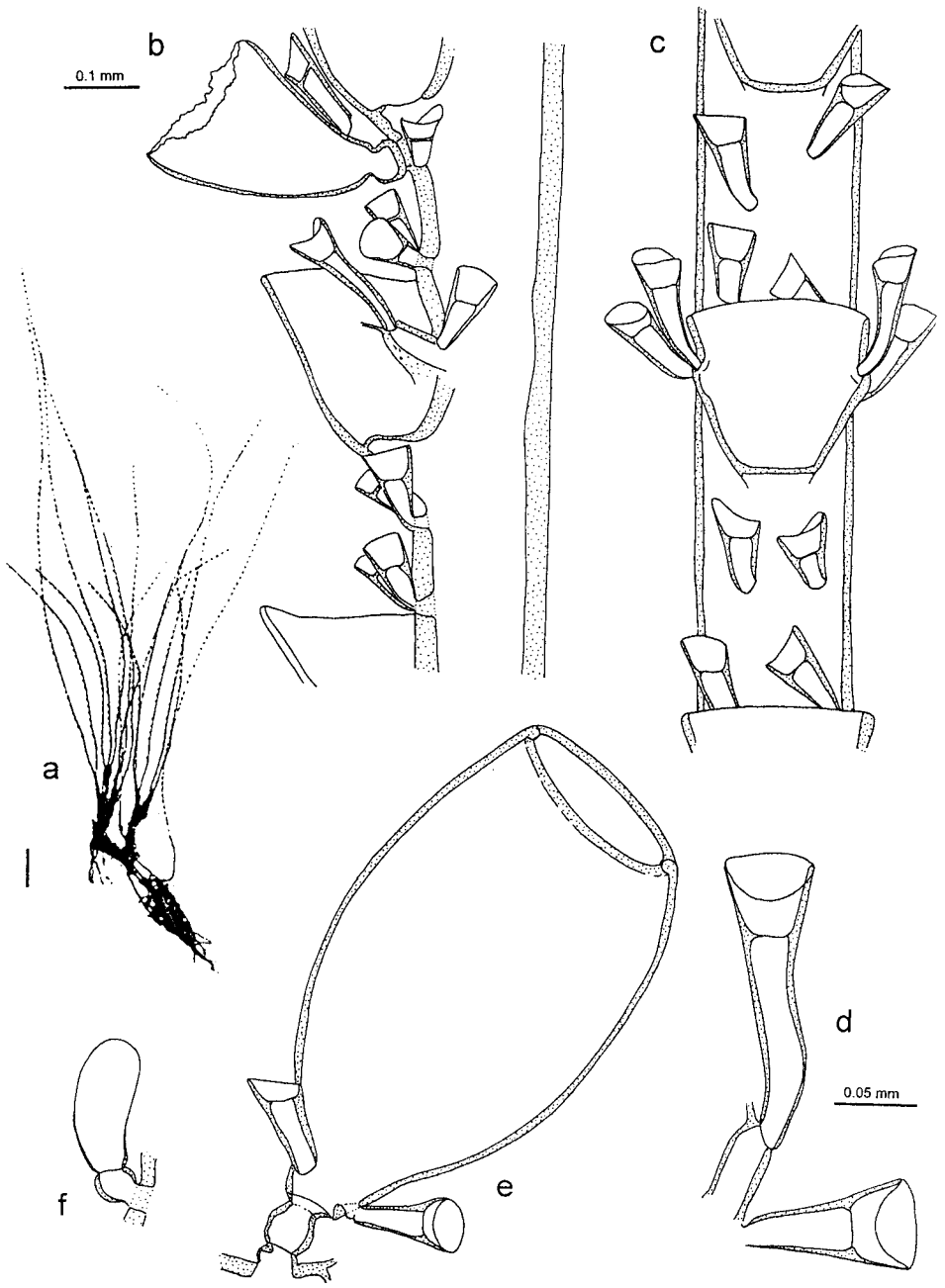

Fig. 10. *Antennella varians* (Billard, 1911); after holotype material; a, whole colony (modified after Billard, 1913), note growth in tufts, scale bar 5 mm; b, stem in lateral view, with eroded gonotheca; c, stem in frontal view, note absence of median inferior nematothecae, same scale as b; d, two lateral nematothecae viewed from adaxial; e, female gonotheca, same scale as b; f, possible male gonotheca, same scale as b.

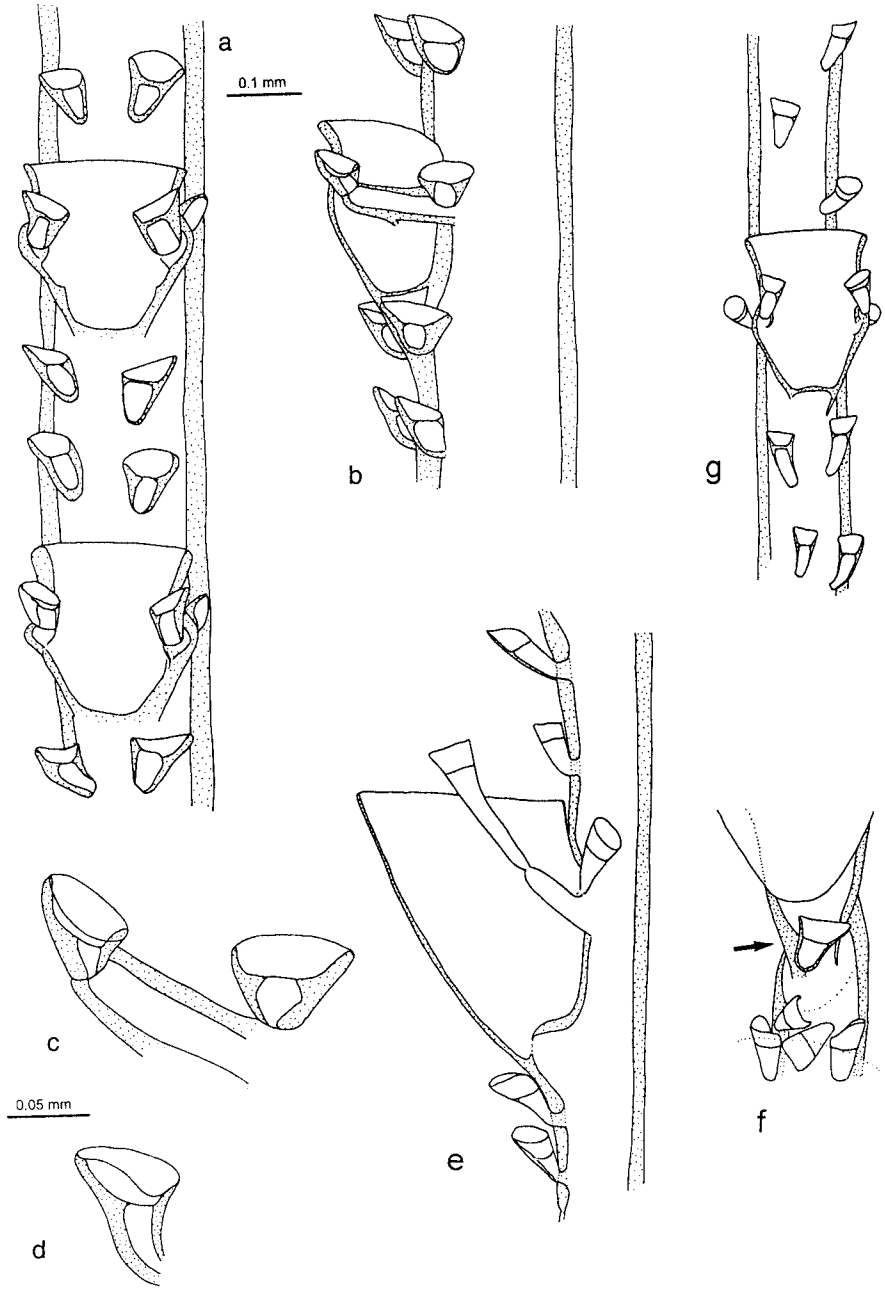

Fig. 11. *Antennella varians* (Billard, 1911); a-d, after type material of *P. balei* Billard, 1911; e, as *A. varians* from Siboga station 153; f, as *A. varians* from Siboga station 164; g, from sample no. 4; a, frontal view of stem; b, lateral view of stem, same scale as a; c, lateral nematothecae; d, lateral inferior nematotheca, same scale as c; e, distal part of stem, note single row of nematothecae and free adaxial part of hydrotheca, same scale as a; f, part of stem in proximal region with oblique node, note presence of median inferior nematotheca (arrow), same scale as a; g, part of stem, same scale as a.

but frequently also not on same level but on alternate sides. Median inferior nematothecae rare, frequently occurring above oblique nodes, especially above two most proximal ones. In extreme distal region of stem there are two median nematothecae in between successive hydrothecae.

Nematothecae all two-chambered and movable, length varies considerably, longer ones curved, conical to funnel-shaped, wall of upper chamber straight, lowered or with broad emargination on inner side.

Gonothecae of both sexes on same colony, developing below hydrothecae in positions otherwise occupied by median inferior nematotheca. Female pear-shaped, length 0.5 to 0.7 mm, with operculate, truncated end, two to three nematothecae near base, pedicel composed of one or two segments. Putative male gonotheca small, sac-shaped, distal end rounded, without nematotheca, pedicel one- segmented.

Additional information.— The length of the abaxial side of the hydrotheca varies between 175 and 500 µm (Billard, 1913), most values are in the range of 210-280 µm.

Type locality.— 2°28.5'S 131°3.3'E, depth 118 m.

Distribution.— Zanzibar; Madagascar; Malayan Archipelago; Japan.

Remarks.— *Antennella varians* (Billard, 1913) grows in dense tufts and is a quite characteristic species among its congeners. Notably, the regular absence of median inferior nematothecae makes it very distinct. It can also grow short, polysiphonic stems that would qualify the colony as belonging to the genus *Corhiza*. The variability of this character once more undermines the validity of the genus *Corhiza* (see also under *Halopteris campanula*, p. 102).

Billard (1911) established *Plumularia balei*, a species that closely resembles *A. varians*. *Plumularia balei* Billard, 1911 is an invalid junior homonym of *P. balei* Bartlett, 1907 = *Gattya balei* (Bartlett, 1907). Billard (1913) regarded *A. balei* (Billard, 1911) as distinct from *A. varians* because of the following two characters: the first hydrotheca is not framed by two oblique nodes and the lateral nematothecae are shorter. However, even in the material of *A. varians* that was available to Billard, not all stems of one tuft have their first hydrotheca framed by oblique nodes. This seems to be a variable character and of limited value only. The length of the nematothecae is here considered as unsuitable to define *A. balei* because this character too is highly variable. In a sample from Madagascar (no. 4) there are no oblique nodes framing the first hydrotheca, but the nematothecae are long and resemble more those seen in the type of *A. varians* (cf. figs 10b-d, and 11f-g). The validity of *A. balei* has also been questioned by Rees & Vervoort (1987) after observations made on African material. The Indonesian material of *A. varians* and *A. balei* also has the same characteristic macroscopic appearance (see Billard, 1913: pl. 1 figs 5, 6, 8). For all these reasons, *A. balei* is here synonymised with *A. varians*, the latter becoming the valid name for this species.

Antennella sibogae (Billard, 1911)
(fig. 12)

Plumularia sibogae Billard, 1911: 62, fig. 1.
Antennella sibogae; Billard, 1913: 9, figs 2-3, pl. 1 figs 4, 7; Bedot, 1917: 124; 1921b: 5.

Material examined.
- 1) Holotype of *P. sibogae* Billard, 1911, ZMA Coel. 5263, Siboga station 310, 8°30'S 119°7.5'E (Flores

Sea, Indonesia), one tuft 2 cm high composed of 5 stems plus detached stem, without gonotheca.
- 2) West coast of Lombok (Indonesia), RMNH Coel. 746, as *Antennella sibogae*, coll. Tydeman, May 1909, infertile tuft 3 cm high.

Description.— Colonies with simple stems clustererd to tufts.

Stems up to 3 cm high, basal part without hydrotheca but with transverse nodes and many nematothecae in two rows. Stem above basal part throughout distinctly homomerously segmented by oblique nodes. Each repeat with hydrotheca and nine nematothecae: one median inferior, two pairs of laterals, and four superior nematothecae in double row. Median inferior nematothecae always present.

Hydrothecae cup-shaped, abaxial walls of variable thickness and shape, opening perpendicular to stem or angle larger than 90°, adaxial wall adnate to stem for all its length, either completely fused to it or free for about $^1/_5$ of its length.

Nematothecae all two-chambered and movable. First pair of lateral nematothecae on pedicel, second pair at base of this pedicel. First pair of lateral nematothecae conical, wall mostly straight, lower chamber longer than upper one, wall of upper chamber emarginated on sides (bivalved appearance). Other nematothecae conical, size variable, adaxial wall of upper chamber lowered or emarginated.

Further data.— The presumed female gonotheca is oblong, 1.2 to 1.35 mm long, with up to five nematothecae near base, pedicel composed of one segment (Billard, 1913).

Type locality.— 8°30'S 119°7.5'E, depth 73 m.

Distribution.— Indonesia.

Remarks.— *Antennella sibogae* is only slightly different from *A. varians*. Contrary to the latter it is regularly segmented by oblique nodes, its hydrothecae are always associated with a median inferior nematotheca, and the gonotheca seems to be larger with more nematothecae. Billard (1913, material station 144) noted, that in *A. sibogae* too the segmentation can be less distinct. *Antennella varians* has only occasional oblique nodes and median inferior nematothecae. However, above oblique nodes there is frequently also an median inferior nematothecae (fig. 11f). The occurrence of a median inferior nematotheca thus seems to be correlated with the presence of an oblique node and it is probably not an independent character. Therefore, the only distinct character that separates *A. sibogae* from *A. varians* is the larger

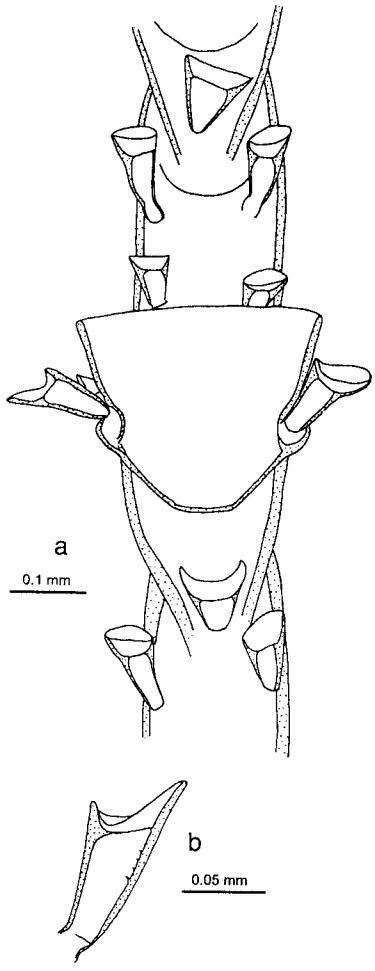

Fig. 12. *Antennella sibogae* (Billard, 1911); after type material; a, part of stem in frontal view; b, lateral nematotheca in lateral view.

gonotheca and the more regular segmentation. Although it is highly probable that *A. sibogae* is nothing but a growth form of *A. varians*, it is here kept separate due to the difference of the gonotheca. More observations will hopefully clarify the picture.

Antennella sibogae also resembles other species, namely *A. quadriaurita* Ritchie, 1909, *Corhiza bellicosa*, *C. pannosa* and *Monostaechas natalensis*. The double row of nematothecae and the angle of the hydrothecal rim readily separate *A. sibogae* from *A. quadriaurita*, *C. pannosa*, and *M. natalensis* and the absence of lateral inferior nematothecae distinguishes it from *C. bellicosa* (cf. fig. 108 A-D in Millard, 1975).

Antennella biarmata Nutting, 1927

Antennella biarmata Nutting, 1927: 226, pl. 44 fig. 5 [not *Plumularia biarmata* Fraser, 1938a].

Diagnosis (after Nutting, 1927).— Simple stems arising from stolons, segmentation homomerous, nodes sometimes indistinct, hydrotheca four-fifths adnate, aperture perpendicular to stem, with two pairs of lateral nematothecae; one pair sitting on long pedicels originating opposite middle of hydrotheca, second pair almost sessile above bases of pedicels of other pair. Two to three pairs of nematothecae in between each pair of hydrothecae, gonothecae not observed.

Type locality.— Davao Bay, Philippines.

Distribution.— Known from type locality only.

Remarks.— The description of Nutting (1927) makes this species indistinguishable from *Antennella sibogae* (Billard, 1911) or *Antennella varians* (Billard, 1911). Nutting's description and figure do not agree concerning the site of the second pair of lateral nematothecae as they are absent in his figure. The lateral nematothecae are frequently lost in *A. sibogae* and *A. varians* and it seems that Nutting figured what he actually saw. Pending an examination of the type material - which was not available for this study - *A. biarmata* is here kept separate. However, it is likely that Nutting's material will be referable to *A. varians*.

Antennella group composed of various species

Remarks.— This left-over group includes *Antennella allmani*, *A. compacta*, *A. curvitheca*, *A. microscopica*, and *A. recta*. With the exception of *A. curvitheca*, these nominal species are either not well defined or not adequately known and hardly recognisable. Some could prove to be conspecific with other species when type material will be examined.

Antennella allmani Armstrong, 1879

Antennella allmani Armstrong, 1879: 102, pl. 12; Mammen, 1965: 296.

Description (after Armstrong, 1879).— Colony with simple stems reaching 1.3 cm in height. Stems with homomerous segmentation by oblique nodes, one hydrotheca and four nematotheca per segment: one median inferior, one pair of laterals, one superior on distal end of segment (homologue of intersegment). Hydrotheca cam-

panulate, slightly flaring. Lateral nematothecae conical, long and overtopping hydrotheca, aperture circular. Gonothecae unknown.

Type locality.— Off Cape Comorin (92 m) and off the coast of Cheduba Island (15-18 m), India.

Remarks.— Already Bedot (1917) considered *Antennella allmani* as insufficiently described and this still holds true. *Antennella allmani* has long lateral nematothecae that could characterise this species. However, the length of the lateral nematothecae can vary considerably in other species and it may well be that *A. allmani* is a form of another *Antennella* or even only a juvenile form of a species of *Halopteris*. *Antennella allmani* must be collected again from the original localities and knowledge of the gonothecae is needed to establish its validity.

Antennella compacta Fraser, 1938b

Antennella compacta Fraser, 1938b: 57, pl. 13 fig. 65.

Description (after Fraser, 1938b).— Colony small, 6 to 7 mm high; with one or two proximal segments, long and without hydrothecae, that have a varying number of nematothecae. Remainder of hydrocladium divided into alternating hydrothecate and non-hydrothecate segments; hydrothecate segments with proximal transverse node and distal oblique node, having usual type of hydrotheca for genus, with median nematotheca just proximal to it (like that of *A. gracilis*), and much larger pair of laterals, one on each side, with trumpet-shaped distal section (like those of *A. secundaria*). Intersegment short, with single nematotheca. Gonothecae arising from hydrothecate segment, just proximal to median nematotheca, obovate and curved, tapering at base into short pedicel; two nematothecae were gonotheca joins pedicel.

Type locality.— South Bay, Cerros Island, Lower California.

Distribution.— Only known from first description.

Remarks.— To his original description, Fraser (1938b) added two figures of limited value, also he did not discuss what distinguishes his species from the many other known species of *Antennella*. *Antennella compacta* therefore remains unrecognisable until the type material has been re-examined.

Antennella curvitheca Fraser, 1937a
(fig. 13, table 8)

Antenella curvitheca Fraser, 1937a: 4, pl. 2 fig. 7.
Antenella curvitheca; Van Gemerden-Hoogeveen, 1965: 56, figs 32-33.

Material examined.— Nevis Island, Fort Charles, Caribbean, RMNH Coel. 1637, as *A. curvitheca*, material described by Van Gemerden-Hoogeveen, 1965, contains a few stems and fragments, collected 28.vi.1949.

Description.— Colonies forming simple, 3 mm high stems developing from creeping hydrorhiza.

Stems with short basal part devoid of hydrothecae, divided by transverse nodes, last one oblique, few or no nematothecae present. Stem above basal part segmented

heteromerously by alternating oblique and transverse nodes, nodes distinct. Main segments long, with hydrotheca in middle, each main segment with four nematothecae: one median inferior, a pair of laterals, and a superior one. Lateral nematothecae placed quite distal, inserting at level of upper axil of hydrotheca. Distal end of main segment rather long and margin of hydrotheca not reaching beyond transverse node. Superior nematotheca situated towards distal end of segment, thus clearly not axillar. Intersegments bear one median nematotheca only.

Hydrothecae cup-shaped, adnate for about half their length, angle of opening with stem axis 45 to 60°, abcauline side straight, adcauline side with distinct concave curvature, walls thickened, adcauline wall with more or less distinct internal tooth projecting into cavity, abcauline side often with small internal tooth near its base.

Nematothecae all two-chambered. Median inferior nematotheca reaches hydrothecal base, short and curved, adaxial side very short, adaxial side of upper chamber much lowered. Lateral nematothecae arise on pedicels much shorter than nematotheca; nematotheca conical, walls straight, inner side of upper chamber lowered to halfway of outer side.

Gonothecae known only in damaged condition, sex unknown, pedicel composed of two segments, base of gonotheca with internal annular thickening, one nematotheca.

Type locality.— North of Puerto Rico, 18°24.5'N, 65°38.5'W, depth 16 m.

Distribution.— Puerto Rico, Nevis Island, Caribbean.

Remarks.— Although Fraser's (1937a) description and especially his figures are not accurate, there is little doubt that the material described by Van Gemerden-Hoogeveen (1965) belongs to *A. curvitheca*. The combination of the curved adcauline side of the hydrotheca and the long distal end of the main segments bearing a nematotheca make this species quite distinct. The internal tooth was not observed by Fraser (1937a), but it is either not con-

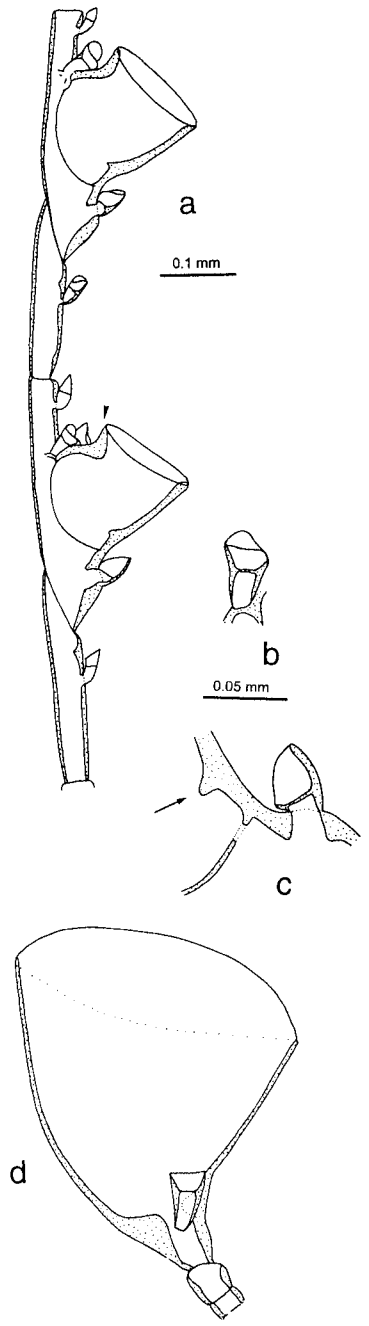

Fig. 13. *Antennella curvitheca* Fraser, 1937a; after material from Nevis Island; a, part of stem, note curvature of adcauline side of hydrotheca and internal projection (arrowhead); b, lateral nematotheca; c, median inferior nematotheca and abcauline base of hydrotheca showing internal cusp (arrow), same scale as b; d, part of gonotheca, same scale as a.

stant in its presence or was neglected by Fraser. Both known samples of this species are from neighbouring localities.

Van Gemerden-Hoogeveen (1965) described the gonothecae of her sample as male. A re-examination of her material could not confirm this. The gonothecae are either immature or eroded, so that the precise shape remains unknown.

Table 8. Dimensions of *Antennella curvitheca*, in µm.

material	Nevis Isl.
length main segments	250-290
length intersegment	320-350
diameter stem	35-40
abcauline side hydrotheca	140-160
adcauline side hydrotheca	70-80
diameter hydrotheca	140-150

Antennella curvitheca is almost identical to unbranched stems of *Halopteris pseudoconstricta* (cf. p. 96 and fig. 34). However, as the material of *A. curvitheca* showed no signs of branching and was mature, it seems to be a separate species. An internal tooth on the abaxial wall of the hydrotheca is only present in *A. curvitheca* and not in *H. pseudoconstricta*.

Antennella microscopica (Mulder & Trebilcock, 1909)

Plumularia microscopica Mulder & Trebilcock, 1909: 30, pl. 1 fig. 4; Stranks, 1993: 12.
Antennella microscopica; Bedot, 1917: 116; 1921b: 5.

Description (Mulder & Trebilcock, 1909).— Hydrocaulus (sic) a mass of matted tubes; shoot monosiphonic, erect, simple, slender, divided by non-oblique joints into segments; segments (with the exception of the lowest, which is short) long and slender; hydrothecae borne on upper half of the segments, and lying at an angle of about 30 degrees to it, tubular, margin plain and at right angles to stem; sarcotheca bithalmic, canaliculate, with slender base, one immediately above the hydrotheca, and large in proportion to it. Gonotheca unknown.

Type locality.— Thompsons Creek (= Bream Creek), Torquay, Victoria, Australia (Stranks, 1993).

Distribution.— Only known from type locality.

Remarks.— Mulder & Trebilcock (1909) based their description of *Antennella microscopica* on a small stem fragment bearing only a single hydrotheca. The available information concerning *A. microscopica* is insufficient and the species most probably can not be recognised anymore. The Museum of Victoria owns a slide of *A. microscopica* donated by Trebilcock (MVM F7964). This slide could be examined for this study. According to its label it should contain the type specimen of *P. microscopica* growing on *Sertularella divaricata*. However, no trace of a plumularid could be found in this preparation, although the *Sertularella* species is present. It must therefore be assumed that there is no type material of *A. microscopica* left.

Antennella recta Nutting, 1927

Antennella recta Nutting, 1927: 227, pl. 44 figs 6-7.

Diagnosis (after Nutting, 1927).— Simple stems with indistinct segmentation, nodes transverse. Hydrothecae with adcauline wall adnate for half its length. Lateral

nematothecae conical and rather distal to hydrotheca, one median inferior nematotheca and one or two nematothecae in between successive hydrothecae.

Type locality.— 21°33'N 116°13'E (near Hong Kong), depth 182 m.

Distribution.— Only known from first description.

Remarks.— Nutting (1927) separated this species from all other *Antennella* species on account of the sole presence of transverse nodes, the absence of intersegments, and the bell-shaped hydrotheca. Nutting (1927) thought that *A. miscrocopica* (Mulder & Trebilcock, 1909) is the only species that resembles *A. recta*. The figure given by Nutting (1927) is somewhat inadequate and it may be difficult to recognise this species.

Genus *Halopteris* Allman, 1877

Heteroplon Allman, 1883: 31-32; type: *Heteroplon pluma* Allman, 1883.
Acladia Marktanner-Turneretscher, 1890: 261; type: *Acladia africana* Marktanner-Turneretscher, 1890.
Thecocaulus Bale, 1915: 294; type: *Plumularia catharina* (Johnston, 1833).
See detailed discussion in Calder (in press).

Diagnosis.— Halopteridídae forming pinnate cormoids that arise from creeping hydrorhiza. Hydrocaulus usually monosiphonic, rarely polysiphonic, bearing hydrothecae and pinnately arranged hydrocladia. In polysiphonic stems, all tubes can give rise to cormidia. Hydrocladia unbranched or branched, alternate or in opposite pairs, but usually with at least first one or two pairs opposite, sometimes (as secondary growth-form) arising independently from hydrorhiza. Hydrotheca cup-shaped, margin smooth or one abcauline cusp.

Type species.— *Halopteris carinata* Allman, 1877.

Remarks.— Allman (1877) created this genus for the rather unique *Halopteris carinata*. Stechow (1926) was the first author to observe the cauline hydrothecae in this species, noticing its differences with the family Plumulariidae; he also synonymised *Thecocaulus* Bale, 1915 with *Halopteris*. Unfortunately, most later authors followed Stechow's proposal (e.g. Totton 1930; Ralph 1961; Millard 1962). *Halopteris carinata* thus became the type species for a genus of which most other members look quite different. *Halopteris carinata* seems to present more affinities with certain species of the genus *Gattya* (cf. figs 49-50). Calder (in press) put forward similar considerations. The definition of *Halopteris* used here is broader than that commonly used (e.g. by Millard, 1975; Bouillon 1985) as it also includes species with branched hydrocladia. This point, and the differences between *Schizotricha* and *Halopteris*, are discussed under the genus *Schizotricha* (p. 133).

The name *Halopteris* is also used for a genus of brown algae (Sphacelariales, Stypocaulaceae, after Adams, 1994). Though this is allowed under the Code for Zoological Nomenclature (Mayr & Ashlock, 1991), it may create confusion in ecological studies. Algae of the genus *Halopteris* are common in shallow water and rather large (5 to 30 cm; Riedl, 1983; Adams, 1984). They also serve as a substratum for hydroids (unpublished observations). A more comprehensive phylogenetic analysis of the Plumularoidea may show the feasibility of reserving the genus *Halopteris* for those species that are closely allied to *Halopteris carinata* and to re-establish *Acladia* or *Thecocaulus* for the remaining species now in *Halopteris*.

Plumularia sulcata Lamarck, 1816 (= *Plumularia aglaophenoides* Bale, 1884) was included in *Halopteris* by Watson (1973). Judging from the descriptions of Bale (1884: 126, pl. 10 fig. 6; 1887: 22; 1914b: 172, pl. 35 figs 6-7) and Briggs (1915: 306, pl. 11 fig. 1) this species is better referred to the genus *Polyplumularia*.

Some species of *Halopteris* are quite similar and difficult to distinguish. Therefore, where possible, resembling species of *Halopteris* are here clustered into groups, which should not be interpreted as taxonomic units (see p. 12). The groups are only conceived to facilitate comparisons.

Halopteris diaphana group

Remarks.— This group contains the following species: *Halopteris alternata, H. billardi, H. diaphana, H. tenella,* and *Halopteris platygonotheca* nov. spec. Most of these species are rather similar and they have been treated as conspecific by some authors. Although they are distinguishable by minute details only, their comparatively small degree of variation allows rather accurate identifications.

The distinguishing characters of the species involved are tabulated in table 9.

Table 9. Comparison of species of the *Halopteris diaphana* group, data of *H. billardi* from Billard (1904).

species	*Halopteris alternata*	*Halopteris billardi*	*Halopteris diaphana*	*Halopteris tenella*	*Halopteris platygonotheca*
stem polysiphonic	no	yes	no	no	no
hydrocladia branched	no	no	no	yes	rarely
axillar nematotheca above cauline hydrothecae	regularly found	absent	absent	absent	absent
cauline segmentation	mostly homomerous	mostly homomerous	hetero-merous	homo-merous	homo-merous
female and male gonotheca on same stem	yes	?	not observed so far	?	yes
number of nematothecae on cauline intersegments	1	1?	2-3	2-4	1-4
number of nematothecae on hydrocladial intersegments	1	1	1	1	1-2
shape of female gonotheca	fusiform, straight	?unknown	cornu-copia	cornu-copia	flat, curved only near base
size of female gonotheca [mm]	0.6-0.7	-	0.7	?	0.9-1.1
abcauline length of hydrotheca [µm]	180-240	200-240	120-150	140-150	180-200
unbranched *Antennella* form known	no	no	yes	no	no

Halopteris alternata (Nutting, 1900) (fig. 14, table 10)

Plumularia alternata Nutting, 1900: 62, pl. 4 figs 1-2.
Not *Plumularia alternata;* Billard, 1904: 484, fig. 4 (= *H. billardi*).

Not *Plumularia alternata*; Billard, 1912: 468, fig 5.
?*Plumularia diaphana*; Billard, 1913: 31.
Not *Plumularia diaphana*; Jarvis, 1922: 345, pl. 25 fig. 16, (= *H. peculiaris* in part).
Not *Plumularia diaphana*; Fraser, 1938a: 62, pl. 14 fig. 71.
Thecocaulus diaphanus; Vannucci-Mendes, 1946: 576, pl. 5 fig. 46-47 [not *Halopteris diaphana* (Heller, 1868)]
Schizotricha billardi Vannucci, 1951: 88, pl. 3 figs 19-20 (in part, Brazilian material only).
Antennella diaphana diaphana; Van Gemerden-Hoogeveen, 1965: 49, figs 23-28 (in part).
Halopteris diaphana diaphana Vervoort, 1968: 58, fig. 27.
Halopteris diaphana; Calder, 1996.

Material examined.

- 1) Turin Cays, Belize, ROMIZ B2239, 3.ii.1987, coll. D. Calder, identified as *Halopteris diaphana*, many fertile plumes.
- 2) San Sebastian, Cigarras Beach, São Paulo, Brazil; RMNH Coel. 18818 (coll. date 12.viii.1991), many plumes intertidal on rocks, labelled *Halopteris diaphana*.
- 3) San Sebastian, Praia de São Fransisco, São Paulo, Brazil; coll. A. Migotto, 16.vi.1992, intertidal on *Galaxaura* spec., many plumes with gonothecae. In addition a sample from the same locality, 19.v.1988, coll. A. Migotto (RMNH Coel. 27611), intertidal on rocks, with gonothecae, as *Halopteris diaphana*.
- 4) Klein Bonaire, Caribbean, RMNH Coel. 1633 (described in Van Gemerden- Hoogeveen, 1965; station. 1049B), labelled as *Antennella diaphana* f. *typica*, coll. 13.ix.1948, infertile plumes 7 to 9 mm high.
- 5) Florida, Dry Tortugas, U.S.A., RMNH Coel. 364, 3610, 1622, 1623, infertile plumes up to 11 mm, labelled as *Halopteris diaphana* or *Antennella diaphana* (no. 3610 described by Vervoort, 1968).
- 6) Kingston, Jamaica, RMNH Coel. 3570, 1 plume 15 mm, infertile, labelled *Halopteris diaphana* (described by Vervoort, 1968).
- 7) Puerto Colombia, Columbia, Caribbean, RMNH Coel. 3611, on Pier; 3.i.1923, 2 infertile plumes max. 10 mm high, labelled as *Halopteris diaphana* (described by Vervoort, 1968).
- 8) Aruba, Boekoeti reef, Caribbean, RMNH Coel. 362 & 1618 (described in Van Gemerden-Hoogeveen, 1965; station 1006), labelled *Antennella diaphana* forma *typica*, coll. 25.vi.1930, infertile plumes up to 15 mm high.
- 9) St. Martin, Simson Bay Lagoon, Caribbean, RMNH Coel. 1626 (described in Van Gemerden-Hoogeveen, 1965; station 1131), labelled *Antenella diaphana diaphana*, coll. 2.viii.1949 on *Rhizophora*, intertidal.
- 10) St. Kitts, Frigate Bay, Caribbean, RMNH Coel. 1632, (described in Van Gemerden-Hoogeveen, 1965; station 1397), coll. 20.vii.1955, small infertile plumes, labelled *Antenella diaphana diaphana*.
- 11) St. John, Turner Bay, Caribbean, RMNH Coel. 1619 (described in Van Gemerden-Hoogeveen, 1965; station 1407), labelled *Antenella diaphana diaphana*, coll. 18.vi.1955, infertile plumes up to 6 mm high.
- 12) Bonaire, Poeloe Lechi, Caribbean, RMNH Coel. 1624, (described in Van Gemerden-Hoogeveen, 1965; station 1056B), labelled *Antenella diaphana diaphana*, coll. 4.ix.1948, intertidal, infertile plumes up to 6 mm high.

Description.— Colony forming up 7 to 20 mm high plumes arising from creeping, ramified, tubular stolons.

Hydrocaulus monosiphonic, unbranched, often geniculate, with basal part ($^1/_4$) devoid of hydrothecae and hydrocladia. Basal part divided into segments by two to three transverse nodes, last node oblique, segments with several nematothecae. Caulus above basal part homomerously segmented by oblique nodes, only towards distal end transverse nodes can separate main- from intersegments. Hydrocladia alternate, only most proximal pair can be opposite, up to 13 per side. Cauline main seg-

ments or their equivalents bear one hydrotheca and three or four nematothecae: one median inferior, one pair of laterals, and one smaller in upper axil of hydrotheca. Axillar nematotheca can be missing in distal part of stem. Cauline intersegments or their equivalents with single nematotheca only.

Hydrocladia thick in relation to stem, inserting on well formed apophyses lateral to cauline hydrothecae, thus placing one lateral nematotheca into axil of hydrocladium. First segment quadrangular, without nematotheca, with transverse nodes. Second segment elongate, with one nematotheca on upper side, with distal oblique node. Remaining part of hydrocladium heteromerously segmented by alternating oblique and transverse nodes. Main segments with three nematothecae: one median inferior and one pair of laterals. No nematotheca in upper axil of hydrotheca. Intersegments with single nematotheca.

Hydrotheca cup-shaped, rim smooth, reaching beyond transverse node, abcauline and adcauline walls rather straight in side view, converging downwards. Adcauline wall adnate for about half its length, angle of opening with segment axis 40 to 50°.

Nematothecae of stem and hydrocladia all two-chambered. Median inferior nematotheca far below hydrotheca, conical, immovable, with short adcauline wall and wall of upper chamber much lowered on adcauline side. Lateral nematothecae on short and broad pedicel, movable, conical, wall of upper chamber straight, rim uneven, variably lowered on adcauline side down to half height. Nematothecae on intersegments similar to median inferior ones but with longer adcauline wall and movable. Nematotheca in upper axil of cauline hydrotheca movable, two chambered, one side of wall of upper chamber lowered to bottom.

Gonothecae of both sexes on same plumes, females both on caulus and hydrocladia, males on hydrocladia, both arising below hydrothecae. Female gonotheca up to 0.8 mm long and 0.32 mm in diameter, spindle-shaped, sometimes slightly flattened, straight, only extreme base curved, distal end truncated, with convex lid, gonothecal wall along lid thickened, two nematothecae near base, with pedicel of two segments. Female gonotheca with single egg. Male gonotheca smaller, oblong, with rounded distal end with small opening, one nematotheca near base, pedicel of one segment.

Nematotcysts: a) microbasic mastigophores in nematophores, (16.5-18.0) × (5.0-6.5) µm, s = 0.85; b) smaller capsules in tentacles, (4.5-6.0) × (1.5-2.0) µm.

Type locality.— Barracuda Rocks, West Indies, Caribbean.

Variation.— *Halopteris alternata* seems not to occur in the simple *Antennella*- like form. Branched hydrocladia were not observed. The nematotheca in the upper axil of the cauline hydrotheca is frequently absent in the more distal and younger portions of the plumes, probably it develops only after the hydrotheca has reached a certain age. There is only a single nematotheca on all intersegments or their equivalents if fused to the main segment. Almost no variation of this number was observed in the numerous colonies examined. The length of the intersegments, however, may vary considerably (table 10).

Distribution.— Florida, Caribbean, Brazil.

Remarks.— Nutting (1900) based his description of *Plumularia alternata* on a single, infertile plume. Nutting's description and figures are not very detailed and it is therefore not surprising that Bedot (1914) synonymised *P. alternata* with *H. diaphana*.

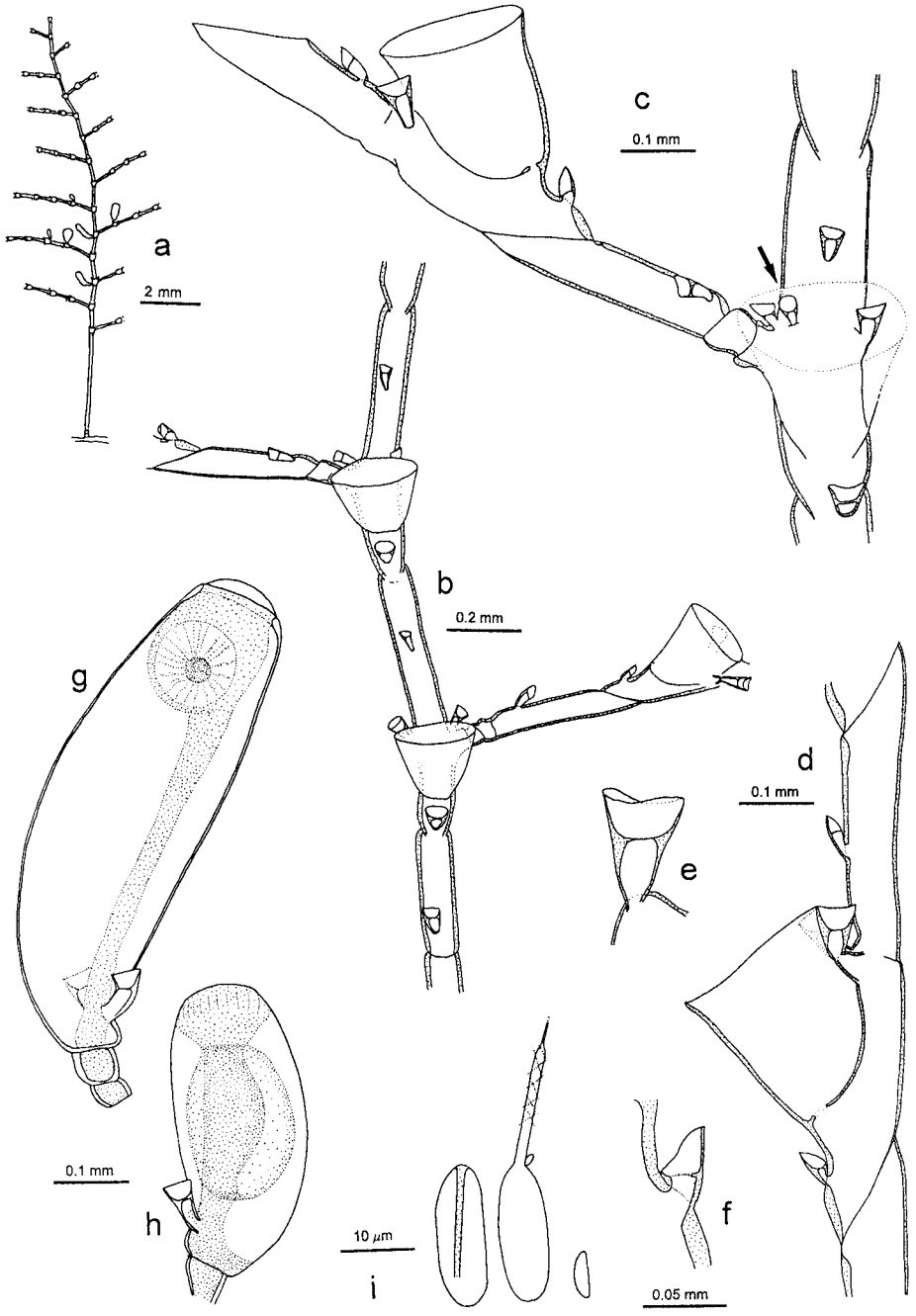

Fig. 14. *Halopteris alternata* (Nutting, 1900); after sample from Belize (sample no. 1), except c which is from sample no. 4; a, single plume with gonothecae; b, part of hydrocaulus with proximal parts of hydrocladia; c, part of hydrocaulus indicating position of axillar nematotheca (arrow); d, part of hydrocladium; e, lateral nematotheca; f, median inferior nematotheca; g, female gonotheca with contents; h, male gonotheca with contents; i, nematocysts: undischarged and discharged microbasic mastigophore and smaller capsule found in tentacles.

Table 10. Variation and dimensions of *Halopteris alternata*, in µm if not stated otherwise.

sample no.	1	2
stem height [mm]	22	15
hydrocladia per side	11	13
length cauline repeats	780-800	550-610
hydrocladial main segments	320-400	310-320
hydrocladial intersegments	420-530	180-260
second cladial segment	400-420	160-340
abcauline side of hydrotheca	200-240	180-220
free adcauline side of hydrotheca	90-100	90-100
diameter of hydrotheca	220-230	220-230
tentacle number	12	14-16

Many other authors accepted his proposal (Stechow, 1919; Fraser, 1938a). The present samples assigned to *H. alternata* were thought to belong to another species than *H. diaphana* on account of the following differences: the female gonotheca is straight for most of its length, female and male gonothecae occur on the same plume, a small nematotheca frequently occurs in the upper axil of the cauline hydrothecae, and a single nematotheca occurs on the cauline intersegments or their equivalents if fused to the main segment. *Halopteris diaphana* has a characteristically cornucopia-shaped female gonotheca, female and male gonotheca so far have not been found on the same stem, it never has axillar nematothecae, and it has almost always two or more nematothecae on the cauline intersegments. The number of nematothecae on intersegments may vary considerably in some species. However, the examined samples of *H. alternata* are from a considerable geographic range and show little variation in the number of nematothecae. Furthermore, both species differ considerably in their dimensions, *H. alternata* being more robust and larger. *Halopteris alternata* seems also not to form simple *Antennella*-like stems besides the normal plumose stems. Colonies of *Halopteris alternata* and *H. diaphana* were also found at the same locality (São Sebastião, Brazil), which shows that they are not mere geographic variants or subspecies (Mayr & Ashlock, 1991). The present samples were assigned to the nominal species *Halopteris alternata* (Nutting, 1900) on account of their single nematotheca on the intersegments; their occurrence also includes the type locality. Nutting's type specimen of *H. alternata* is lost (A.B. Johnston, MCZH, pers. comm). A neotype is not designated here, as no material from the original type locality was available.

Halopteris alternata also closely resembles *H. platygonotheca* nov. spec. *Halopteris platygonotheca* was separated from *H. alternata* because of the shape of the female gonotheca (cf. figs 14g and 17f), which in *H. platygonotheca* is broad and strongly flattened like the blade of an oar.

The material assigned by Jarvis (1922) to *P. alternata* and originating from the Indian Ocean was re-examined by Millard (1962); she found it to be a mixture of *H. peculiaris* (as *H. glutinosa* in Millard, 1962) and another species of *Halopteris*, most probably the species described here as *H. platygonotheca*).

Fraser (1938a) assigned some samples from the Pacific Ocean to *Plumularia alternata*. However, his material had a nematotheca in the axil of the hydrocladium and a

cornucopia-shaped gonotheca. It is therefore most probably another species and neither *H. alternata* nor *H. diaphana*.

The gonothecae of *H. alternata* were unknown until Vannuccci (1951) found gonothecae on Brazilian material and noted the difference with *H. diaphana*. However, she did not assign her material to *H. alternata*, but identified it with material described by Billard (1904) as *Plumularia alternata*, originating from the Gulf of Aden. Vannucci (1951) gave Billard's material the new name *Schizotricha billardi* (Billard, 1904). This is nomenclatorially incorrect, as Vannucci (1951) did not create a new name but a new species. Billard's (1904) material of *P. alternata* is here seen as distinct from *H. alternata* and the species name *billardi* of Vannucci (1951) for this material is here preserved (see under *H. billardi*, below). Vannucci's (1951) figures, however, and also the new material examined from Brazil, make it clear that this population actually belongs to *H. alternata* as defined here and not to *H. billardi*.

Most material examined for this study has been described by Van Gemerdeen-Hoogeveen (1965) as *Antennella diaphana diaphana*, although not all the material originally assigned by Van Gemerdeen-Hoogeveen to this species actually belongs to *H. alternata*. Some of her samples proved to belong to *Monostaechas quadridens* and *Halopteris gracilis* (see also there).

Halopteris billardi (Vannucci, 1951)

Plumularia alternata; Billard, 1904: 484, fig. 4.
Schizotricha billardi Vannucci, 1951: 88 (except Brazilian material = *Halopteris alternata*).

Type locality.— Obock, Clochetterie reef, Gulf of Aden.

Remarks.— Vannucci (1951) proposed the new name *Schizotricha billardi* for Billard's (1904) material of *P. alternata* from Obock and also referred her material from Brazil to this species. Vannucci (1951) created this new species because she thought that *H. alternata* (Nutting, 1900) is a synonym of *H. diaphana* (Heller, 1868); therefore it should have cornucopia-shaped female gonothecae. Vannucci's (1951) description and figures, however, leave no doubt that her material was actually *Halopteris alternata* (see p. 42). Billard's (1904) sample, which he referred to as *Plumularia alternata*, closely resembles *H. alternata* as described above, however, the gonotheca seems to be different. Furthermore, Billard (1904) describes the stem as polysiphonic (see also table 9). Following Bedot (1914: 92) and Vannucci (1951), Billard's material from Obock is assigned to a separate species, for which Vannucci proposed the species name *billardi*. Billard's (1904) description and figure are somewhat inadequate and it might be difficult to recognise the species again. It may well belong to *H. platygonotheca* nov. spec. At present, the available information on the shape of the gonothecae and the polysiphonic stem distinguish this species from *Halopteris platygonotheca* nov. spec.

Halopteris diaphana (Heller, 1868)
(fig. 15, table 11)

Anisocalyx diaphana Heller, 1868: 42, pl. 2 fig. 5.
Plumularia cornu-copiae Hincks, 1872: 389, pl. 21 figs 1-3; Kirchenpauer, 1876: 27, pl. 1 fig. 17, pl. 3 fig. 17.

Plumularia diaphana; Kirchenpauer, 1876: 27, pl. 1 fig. 13; Stechow, 1912: 363, fig. E; Bedot, 1914: 89, pl. 5 figs 14-16; Hamond, 1957: 318, fig. 25.
Plumularia alternata; Billard, 1912: 468, fig. 5 [not *Plumularia alternata* Nutting, 1900].
Thecocaulus diaphanus; Stechow, 1923: 224.
?*Antennella diaphana* forma *typica*; Broch, 1933: 24 (in part).
?not *Plumularia diaphana*; Fraser, 1948: 277.
?*Halopteris diaphana*; Pennycuik, 1959: 177; Gibbons & Ryland , 1991: 528, fig. 3.
Not *Thecocaulus diaphanus* Riedl, 1959: 654, pl. 11 fig. 7.
Not *Antennella diaphana* f. *siliquosa* Vervoort, 1959: 286, fig. 43 [= *A. siliquosa*].
Not *Antennella diaphana diaphana* Van Gemerden-Hoogeveen, 1965: 49, figs 23-28 [in part *H. alternata*, *H. gracilis* and *Monostaechas quadridens*].
?*Schizotricha diaphana*; Mammen , 1965: 303, fig. 100.
?*Halopteris liechtensternii*; Riedl 1966: fig. 84, Gili & Castello, 1985: 18, fig. 6E.
Not *Halopteris diaphana*; Cooke, 1975: 100, pl. 5 fig. 1; Calder, 1996 [= *H. alternata*].
Halopteris diaphana diaphana; García-Corrales et al., 1978: 42, fig. 18; Boero & Fresi, 1986: 145.
Not *Halopteris diaphana* f. *siliquosa*; García-Corrales et al., 1978: 45, fig. 19; Ramil & Vervoort, 1992a: 148, fig. 38a [= *A. siliquosa*].
?*Halopteris constricta*; Park, 1990:83 fig. 5.

Material examined.

- 1) Naussa, Island of Paros, Greece, Mediterranean, several colonies on *Padina pavonia* (brown algae), depth 1 m, Sept. 1990, collected by author, fertile female colonies, with branching and non-braching stems in same colony.
- 2) Banyuls-sur-Mer, Anse du Troc, France, Mediterranean, several colonies collected by author, January 1992 and 14.ix.1995, depth around 2 m, all infertile, mostly pinnate cormoids.
- 3) Dubrovnik, Croatia, Mediterranean, RMNH Coel 1446, on *Posidonia* leaf, 2.ix.1960, several stems, only one branched stem, several stems with male gonothecae.
- 4) Jaraba Point, São Paulo, Brazil, RMNH Coel. 18815, as *H. constricta*, collected by A. Migotto, 3.xi.1992, fertile males, on *Codium decorticatum*, mostly pinnate stems, some simple stems also present. In addition a sample from Praia de Cabelo Gordo-parque, São Sebastião, Brasil, collected by A. Migotto, 03.xi.1992, RMNH Coel. 27612.
- 5) Marcambrils, near Barcelona, Spain, Mediterranean, several colonies from depth 1 m, on wave breaker, all infertile, collected 13.ix.1995 by author, unbranched and pinnate forms in same colony.

Description.— Colonies consisting of mixture of up to 12 mm high plumes, plumes with reduced number of hydrocladia, and simple *Antennella*-like cauli. Fertile colonies always have at least few cauli with few hydrocladia. Stems arise from tubular, ramified, creeping stolons. Stolons bear nematothecae and can have stretches with regular internal thickenings.

Hydrocaulus monosiphonic, unbranched, with short basal part ($^1/_6$) devoid of hydrotheca. Basal part with transverse nodes and several nematothecae. Basal part ends in oblique node. Caulus above basal part heteromerously segmented by alternating oblique and transverse nodes, transverse nodes always distinct. Hydrocladia alternate in plumose cormoids, only most proximal pair can be opposite. Cauline main segments bear one hydrotheca and three nematothecae: one median inferior and one pair of laterals. No nematothecae in axil of hydrotheca or on hydrocladial apophysis. Intersegments of stem typically with two nematothecae, exceptionally with one or three.

Hydrocladia thin and slender, inserted on well formed apophysis below lateral cauline nematothecae. First segment quadrangular and lacking nematothecae. Sec-

ond segment long, ending in oblique node, with two nematothecae on upper side. Remainder of hydrocladia organised like stem with alternate main segments and intersegments, up to four main segments per hydrocladium, but usually less. Main segments shorter than intersegments, with three nematothecae as on caulus. Intersegments long, with single nematotheca. Sometimes quadrangular segment without nematotheca inserted between main- and intersegment.

Hydrotheca cup-shaped, shallow, as deep as broad, rim straight and smooth, sometimes slightly everted, reaching to transverse node. Walls in side view straight, converging proximally. Adcauline wall adnate for about half its length, angle of opening with hydrocladial axis 50 to 60°.

Nematothecae of stem and hydrocladia all two-chambered and movable. Median inferior nematothecae not reaching hydrotheca, conical, adaxial wall of upper chamber emarginated to bottom of chamber. Lateral nematothecae on very short pedicel, movable, conical, with long lower chamber, walls straight, adaxial wall of upper chamber only slightly lowered or emarginated. Nematothecae of intersegments resembling median inferior ones, but with less lowered adaxial wall. Nematothecae of stolons resembling laterals.

Gonothecae of the two sexes only seen in separate colonies. Gonothecae arise from stems and hydrocladia. Also simple stems without hydrocladia as part of colony with branched stems may bear gonothecae. Female gonotheca up to 0.7 mm long, inserted by means of pedicel of two quadrangular segments, evenly curved for its entire length and thus forming semi-circle, smoothly tapering towards base over its entire length. Distal end truncated and provided with convex lid, two to four nematothecae near base. Male gonotheca up to 0.5 mm, inserted by means of pedicel of two quadrangular segments, only slightly curved, oblong, with two nematothecae near base. Developing male gonothecae obliquely truncated.

Nematotcysts: a) microbasic heteronemes observed as mastigophores or eurytetes, in nematophores only, (16-18.5) × (6.0-7.0) µm, s = 0.8; b) smaller capsule in tentacles (isorhiza ?), almond-shaped, (6.0-6.5) × (1.5-2.5) µm.

Colour.— transparent.

Type locality.— Capocesto, Dalmatian Coast, Mediterranean.

Additional notes on variation.— Unbranched stems also bear two nematothecae on their intersegments, thus indicating that these stems are homologues of the caulus. Branched hydrocladia were not observed in the present material. In both the material from the Mediterranean and Brazil certain areas of the stolons were provided with frequent internal pegs resembling the stolons of *Halopteris minuta*.

Distribution.— Mediterranen, Brazil.

Remarks.— *Halopteris diaphana* has a rather complicated taxonomic history and very often other species have erroneously been allocated to this species. Many single records, especially from outside Europe, are most probably incorrect as they are based on too broad a concept of this species. *Halopteris diaphana* was first described by Heller (1868) as *Anisocalyx diaphana* from the Adriatic Sea. His description and especially figures are somewhat inadequate. He described the gonotheca as pyriform and figured a small, indistinct but straight gonotheca on a hydrocladium. He probably observed male gonothecae on the plumes. Type material could not be located, but the concept of *H. diaphana* as given above is compatible with Heller's description.

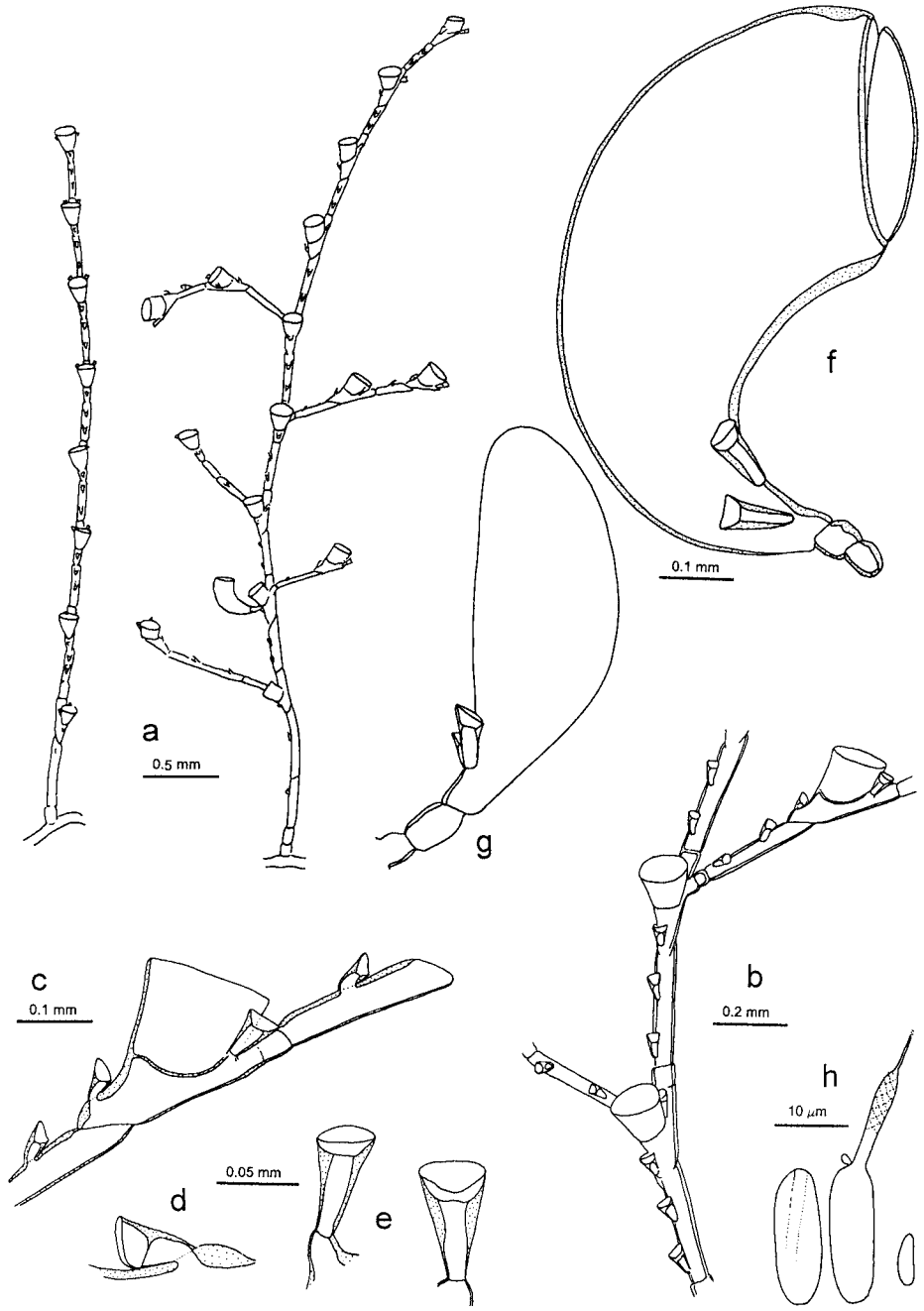

Fig. 15. *Halopteris diaphana* (Heller, 1868); all after material from Paros, Greece (sample no. 1), except g which is from Adriatic Sea (sample no. 3); a, different forms of stems, left simple form, right plumose form, note that also plumes with many more hydrocladia can regularly be found; b, part of stem with bases of hydrocladia, c, part of hydrocladium; d, median inferior nematotheca; e, lateral nematothecae, same scale as d; f, female gonotheca; g, male gonotheca, same scale as f; h, nematocysts: undischarged and discharged microbasic heteroneme, smaller capsule found in tentacles.

Table 11. Variation and dimensions *Halopteris diaphana*, in µm if not stated otherwise.

sample no.	1	4	5
stem height [mm]	6	10	12
cauline main segments	300-400	320-390	260-420
cauline intersegments	240-330	320-390	380-480
nematothecae/cauline intersegment	2	2 (rarely 1-3)	2 (rarely 3)
hydrocladial main segments	240-350	310-330	290-310
hydrocladial intersegments	220-240	250-280	280-330
nematothecae/cladial intersegment	1	1	1
second cladial segment	320-340	350-370	360-410
abcauline side of hydrotheca	120-140	120-130	120-150
free adcauline side of hydrotheca	70-80	60-80	70-80
diameter of hydrotheca	130-140	130-150	140-150
tentacle number	12-14	12	-

The only known *Halopteris* species from the Mediterranean, that could possibly have been present in Heller's material is *H. liechtensternii*. However, Heller (1868) clearly describes his species as having a heteromerously segmented caulus with intersegments longer than the main segments and widely spaced hydrocladia. This almost certainly excludes *H. liechtensternii*. *Halopteris diaphana* remained somewhat doubtful until Stechow (1912) redescribed the species from Mediterranean material and he also figured the female gonothecae which is characteristically curved (cornucopia-shaped). This made evident that the well described *Plumularia cornucopiae* Hincks, 1872 must be a synonym of *H. diaphana* (cf. Bedot, 1914). Bedot (1914) further incorrectly synonymised *H. alternata* Nutting, 1900 with *H. diaphana*, a conclusion based exclusively on the similarity of the trophosome because the gonothecae of the Caribbean *H. alternata* were not known at that time. Bedot (1914) carefully compared the descriptions of *H. alternata* and *H. diaphana* and found both inseparable. The arguments discussed by Bedot are indeed insufficient to separate the two species, however, new traits used here demonstrate the validity of both species. Also *Plumularia tenella* (Verrill, 1874) was synonymised with *H. diaphana* by Bedot (1914) on account of the similar female gonotheca, a proposal not followed here. Broch (1933) correctly noted that some of the stems of *H. diaphana* can occur in the simple *Antennella*-like form (fig. 15a) and then erroneously included also *Antennella siliquosa* (Hincks, 1877) in *H. diaphana*, although *A. siliquosa* has a straight gonotheca and also differs in other details (see p. 21). Possibly Broch also had *H. liechtensternii* in his material. Later authors followed Broch in uniting *A. siliquosa* with *H. diaphana* (e. g. Vervoort, 1959; Cornelius 1995), but others did not (e. g. Medel & Vervoort, 1995; Calder, in press). Also Fraser (1938) referred *H. alternata* to *H. diaphana* as he found strongly curved gonotheca in material from the Pacific. But Fraser's material had nematothecae in the axils of the hydrocladia, thus it must be another species, neither *H. diaphana* nor *H. alternata*. *Halopteris diaphana* thus became an assemblage of several species and so ill-defined that later authors added even more species (cf. Van Gemerden-Hoogeveen, 1965; Millard & Bouillon, 1973). Numerous samples and re- examination of original material made it possible to separate *A. siliquosa*, *H. alternata*, and *H. tenella* from *H. diaphana*.

Halopteris diaphana closely resembles several other *Halopteris* species, but a combination of characters allows a distinction (see table 9). The most characteristic trait of *H. diaphana* is the cornucopia-shaped female gonotheca[2].

Other characters that separate *H. diaphana* from similar species are discussed in table 9 and under *A. siliquosa*, *H. alternata*, *H. platygonotheca*, *H. pseudoconstricta*, and *H. tenella*. No records of *H. diaphana* from outside Europe mention the characteristic female gonotheca, with the exception probably of Park (1990). All these records are here considered slightly doubtful because they are mostly based on descriptions of *H. diaphana* that included several other species. Infertile material, especially from outside Europe, should only be allocated to *H. diaphana* with great care.

The material described by Park (1990) as *H. constricta* certainly has been misidentified. It closely resembles *H. diaphana* and could also belong to it, but the chances of it being a new species are also great. The only apparent difference that can be lifted from Park's (1990) description is the single nematotheca on the cauline intersegments.

In all material examined and also in reliable descriptions of fertile *H. diaphana* (Hincks 1872; Billard 1906 as cited in Bedot 1914: 94; García-Corrales et al. 1978) gonothecae of the two sexes were never found on the same stem. This could either mean that gonophores of the two sexes develop in one colony at different times, or each sex is found in separate colonies. Because no vestiges of gonothecae of the opposite sex were found in male or female colonies examined so far, the second hypothesis is here favoured. This is rather unusual for Halopteridídae and new investigations should address this problem again.

H. diaphana and *H. liechtensternii* were frequently found together by the author. In the field, *H. liechtensternii* is easily distinguished from *H. diaphana* by its yellow colour, larger size, and more robust appearance. Because of the delicacy of the plumes, *Halopteris diaphana* is not as easily detected in the field as *H. liechtensternii*.

Ecology.— In the Mediterranean, *Halopteris diaphana* is frequently found in shallow waters and at well-illuminated sites (see also under *H. liechtensternii*, p. 76). According to Boero & Fresi (1986) it matures in June, but during this study mature colonies were also found in September. Mature colonies seem to be fairly rare.

Halopteris tenella (Verrill, 1874)
(fig. 16, table 12)

Plumularia tenella Verrill, 1874: 731.
Schizotricha tenella; Nutting, 1900: 80, pl. 4 figs 4-5; Vanhöffen, 1910: 338; Calder, 1983: 18, fig. 10.
Halopteris tenella; Vervoort, 1968: 108.

Material examined.— Younges Island, South Carolina, U.S.A., ROMIZ accession number 1990-076, as *Schizotricha tenella*, depth 7 m, coll. vi.1974, D. Calder, plumes up to 26 mm height, with eroded gonothecae.

Description (after above material; Calder, 1983, and Nutting, 1900).— Colony forming 2 to 5 cm high plumes arising from tubular, ramified stolons.

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[2] (= horn-shaped, the names derives from a goat's horn in Greek mythology).

Hydrocaulus monosiphonic, unbranched, geniculate in younger cauli, with basal part ($^1/_6$) devoid of hydrothecae and hydrocladia, and divided into segments by transverse nodes; last node oblique. Basal segments with nematothecae. Caulus above basal part homomerously segmented by oblique nodes. Only in distal region repeats are subdivided by an indistinct transverse node delimiting distal intersegment. Hydrocladia in alternate positions. Each repeat with up to seven nematothecae: one median inferior, one pair of laterals, and two to four superior nematothecae in one or two rows. These superior nematothecae are all located on separate intersegment if transverse node is present.

Hydrocladia almost all branched once or twice. Hydrocladia inserted on long apophyses lateral to cauline hydrothecae. Most proximal segments quadrangular, normally only one, but up to three may be present. Next segment elongate, with one nematotheca. Remainder of hydrocladium formed by repeats with oblique nodes. Repeats often subdivided into three segments: one main segment with a hydrotheca, a short quadrangular segment without nematotheca, and an elongate intersegment with one or rarely none or two nematothecae. This subdivision inconstant: short quadrangular segment not always present and intersegment may be fused to main segment without vestiges of a transverse node. Main segments with three nematothecae: one median inferior and a pair of laterals.

Hydrotheca cup-shaped, walls straight in lateral view and converging proximally, rim even, opening at an angle of 50 to 60° to hydrocladium, adcauline wall adnate for half its length.

Nematothecae all two-chambered and movable. Median inferior far below hydrotheca, conical, lower chamber long, with inner wall of upper chamber only slightly lowered. Lateral nematothecae on short pedicel, conical, walls straight, adaxial side of upper chamber emarginated to half its height. Nematothecae of intersegments similar to median inferior ones.

Presumed female gonotheca cornucopia-shaped with three nematothecae near base, 0.56 to 0.69 mm long, pedicel composed of two segments.

Nematotcysts.— a) microbasic eurytele, in nematophores, (14-15) × (5-6) µm, s = 0.8; b) small almond-shaped capsule in tentacles, 4 × 1µm; c) rare oval capsule of uncertain status, 4 × 2.5 µm.

Type locality.— Vineyard Sound, U.S.A.

Distribution.— Massachusetts to Caribbean Sea; Eastern Pacific from Southern California to Panama (Calder, 1983).

Ecology.— *Halopteris tenella* is the most widespread plumularian hydroid in temperate estuaries of the east coast of the United States. It is both euryhaline, penetrating up-estuary to a salinity of about 15‰, and eurythermal, having been collected over a temperature range from 9 to 32°C (Calder, 1983).

Remarks.— *Halopteris tenella* was here included in the genus *Halopteris* and not *Schizotricha* for reasons discussed under *Schizotricha* (see p. 133 and Totton, 1930). The minute structure of *Halopteris tenella* resembles very closely *H. diaphana*. Especially striking is also the similarity of the gonothecae. Stechow (1919), Bedot (1921b), and Vervoort (1968) therefore regarded *H. tenella* as conspecific with *H. diaphana*. Calder (1983) kept both species separate because of the presence of three types of segments in the hydrocladia. However, this argument looses somewhat of its weight as the

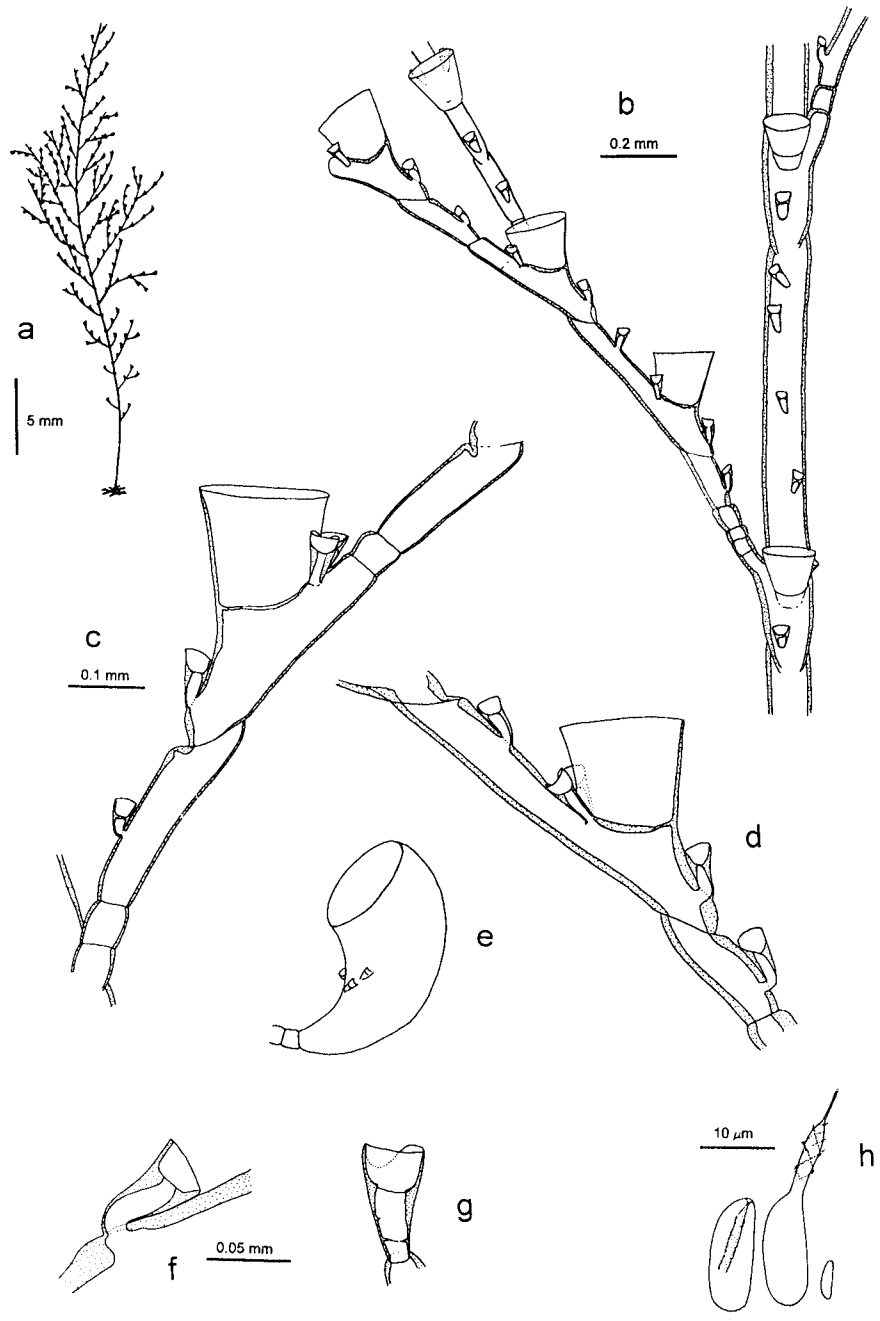

Fig. 16. *Halopteris tenella* (Verrill, 1874); after sample from South Carolina; a, single plume; b, part of stem and branched hydrocladia; c, basal part of hydrocladium, note short anematothecate segment distal to main segment; d, hydrocladial repeat without transverse nodes, same scale as c; e, female gonotheca after Nutting (1900), no scale given; f, median inferior nematothe ca, note long adaxial side; g, lateral nematotheca seen from outer side, same scale as f; h, nematocysts: intact eurytele, same discharged, small almond- shaped capsule.

short, anematothecate segment in between main- and intersegment is not always present and the intersegment can even be fused to the main segment (see fig. 16d). Moreover, also *H. diaphana* can occasionally have such an intercalating segment. Both species were here nevertheless concived as distinct on account of the following differences: *H. tenella* has regularly branched hydrocladia in many known samples while *H. diaphana* probably never has branched hydrocladia; the caulus of *H. tenella* is typically homomerously segmented and has more nematothecae above the hydrotheca; *H. tenella* forms larger plumes. *Halopteris tenella* can also tolerate reduced salinity, which is not known for *H. diaphana*.

Table 12. Dimensions *Halopteris tenella*, in µm.

material	ROMIZ
cauline main segments	270-580
cauline intersegments	390-490
diameter of caulus	80-110
length of apophysis	80-100
length of 2nd cladial segment	240-430
cladial main segments	250-330
cladial intersegments	370-430
abcauline side of hydrotheca	140-150
free adcauline side of hydrotheca	90-100
diameter of hydrotheca	150-160
tentacle number	12-14
stolon diameter	100

Halopteris platygonotheca spec. nov.
(fig. 17, table 13)

Plumularia alternata; Billard, 1913: 31 [not *P. alternata* Nutting, 1900].
Halopteris glutinosa; Schmidt, 1971: 38 [in part, not *H. glutinosa* (Lamouroux, 1816)].

Material examined.

- 1) Holotype, RMNH Coel. 8125, Comores, internal slope of reef of Dzaudzi, Île Mayotte, coll. P. Vasseur, July 1964, identified originally as *Halopteris diaphana*, depth 2 m, colony with many plumes, up to 3 cm high, with many female and male gonothecae.
- 2) Paratypes, slide and alcohol preparation, RMNH Coel. 8123, Comores, internal slope of reef of Dzaudzi, Île Mayotte, 2 m, coll. P. Vasseur, identified as *Halopteris diaphana*, female and male gonothecae present; contains several plumes 2-3 cm high.
- 3) Comores, barrier reef of Île Mayotte, RMNH Coel. 8122, coll. P. Vasseur July 1964, identified as *Halopteris diaphana*, depth 15 m, many plumes, 2-3 cm high, female and male gonothecae present.
- 4) Comores, barrier reef of Île Mayotte, RMNH Coel. 8126, coll. P. Vasseur, July 1964, identified as *Halopteris diaphana*, depth 9 m, infertile.
- 5) Comores, Longogori Passage, barrier reef of Île Mayotte, RMNH Coel. 8124, coll. P. Vasseur, July 1964, identified as *Halopteris diaphana*, depth 9 m, two broken plumes with female gonothecae.
- 6) Madagascar, Île Europa, RMNH Coel. 8127, coll. P. Vasseur, 1965-1966, identified as *Halopteris diaphana*, depth 50 m, several plumes, up to 2.5 cm high, one with female gonotheca.
- 7) Seychelles, Ternang Bay, Mahé, MACT 2.700 (described by Millard & Bouillon, 1973), few infertile plumes in sample containing mostly *H. polymorpha*.
- 8) Siboga station 77, Borneo, 3°27'S 117°36'E, ZMA Coel. 4078, material described by Billard (1913) as *Plumularia alternata*, two plumes, up to 15 mm high, with female and male gonothecae.
- 9) Island of Lucipara, Indonesia, Siboga station 225, material described by Billard (1913) as *Plumularia alternata*, ZMA Coel. 4078, one plume, 5 mm high, infertile.
- 10) Elath, Gulf of Aqaba, RMNH Coel. 6772 and 6773, 1-4 m depth, material collected 27.iii.1970 and described by Schmidt (1971) as *Halopteris glutinosa*, up to 12 mm high plumes, 6773 with female and male gonothecae. One further slide labelled *H. glutinosa* also collected by Schmidt from the same locality (RMNH Coel. 6774) is *Plumularia setacea* and does not belong here.
- 11) Wasset, Sinai, Red Sea, RMNH Coel. 6869, coll. L. Fishelson, 8.x.1968, with fertile plumes 2 to 4 cm high, labelled as *Halopteris* cf. *glutinosa*.

Description.— Colony forming 1 to 4 cm high plumes arising from tubular stolons.

Hydrocaulus monosiphonic, unbranched, with basal part (1/4) devoid of hydrocladia and hydrothecae. Basal part divided into segments by several transverse nodes, last node oblique, segments with nematothecae. Caulus above basal part homomerously segmented by oblique nodes, only at very distal end heteromerous segmentation by additional transverse nodes that delimit intersegments from main segments. First pair of hydrocladia opposite, others alternate, up to 12 per side. Cauline segments bear up to seven nematothecae: one median inferior, one pair of laterals, and one to two (rarely up to four) on distal part of segment (fused intersegment). No nematotheca behind hydrotheca.

Hydrocladia inserted on short apophysis lateral to cauline hydrothecae. First segment quadrangular, without nematotheca, sometimes indistinctly delimited from following segment. Second segment long with two nematothecae on upper side, ending in oblique node. Remaining part of hydrocladium heteromerously segmented by alternating oblique and transverse nodes with up to eight repeats, transverse nodes are often weak or even absent. Each repeat with a hydrotheca and five nematothecae: one median inferior, one pair of laterals, and one to two median on distal part of segment, the latter on separate intersegment when transverse node is present.

Hydrotheca cup-shaped, rim smooth, abcauline and adcauline walls straight in lateral view, converging proximally. Adcauline wall adnate for about half its length. Angle of opening at 50 to 60° to hydrocladium.

Nematothecae of stem and hydrocladia all two-chambered. Median inferior nematotheca does not reach hydrotheca, immovable, with short adcauline wall and adcauline wall of upper chamber much lowered. Lateral nematothecae on pedicel shorter than nematotheca itself, movable, broadly conical, wall of upper chamber straight, rim not lowered and either almost straight or slightly sinuated. Nematothecae distal to hydrotheca movable, conical, with adaxial wall of upper chamber lowered to half its abaxial height.

Gonothecae of both sexes on same stem, both types developing on caulus and hydrocladia. Female gonotheca up to 1.1 mm long, with pedicel composed of two quadrangular segments. Main body of gonotheca strongly flattened, rectangular, straight except for most proximal part that is tapering and curved 90°. Distal end truncated transversely and provided with concave lid. Two nematothecae on curved basal part. Male gonotheca oblong, up to 0.45 mm in length, evenly rounded at both ends, with one nematotheca near base, and with pedicel composed of one segment.

Nematotcysts: a) microbasic mastigophores in nematophores, (22-23.5) × (6.0-8.5) μm, s = 0.9; b) smaller capsule in tentacles, (4-5) × (1.5-2) μm.

Variation.— Rarely some hydrocladia are branched. In one sample (sample no. 10 from Elath) there was rarely a nematotheca in the upper axil of the cauline hydrotheca.

Type locality.— Internal slope of reef of Dzaudzi, Île Mayotte, Comores; depth 2 m.

Etymology.— The species name *platygonotheca* refers to the strongly flattened female gonotheca that distinguishes the species from other similar halopterids (fig. 17f).

Distribution.— Comores Islands, Madagascar, Seychelles, Red Sea, Indonesia.

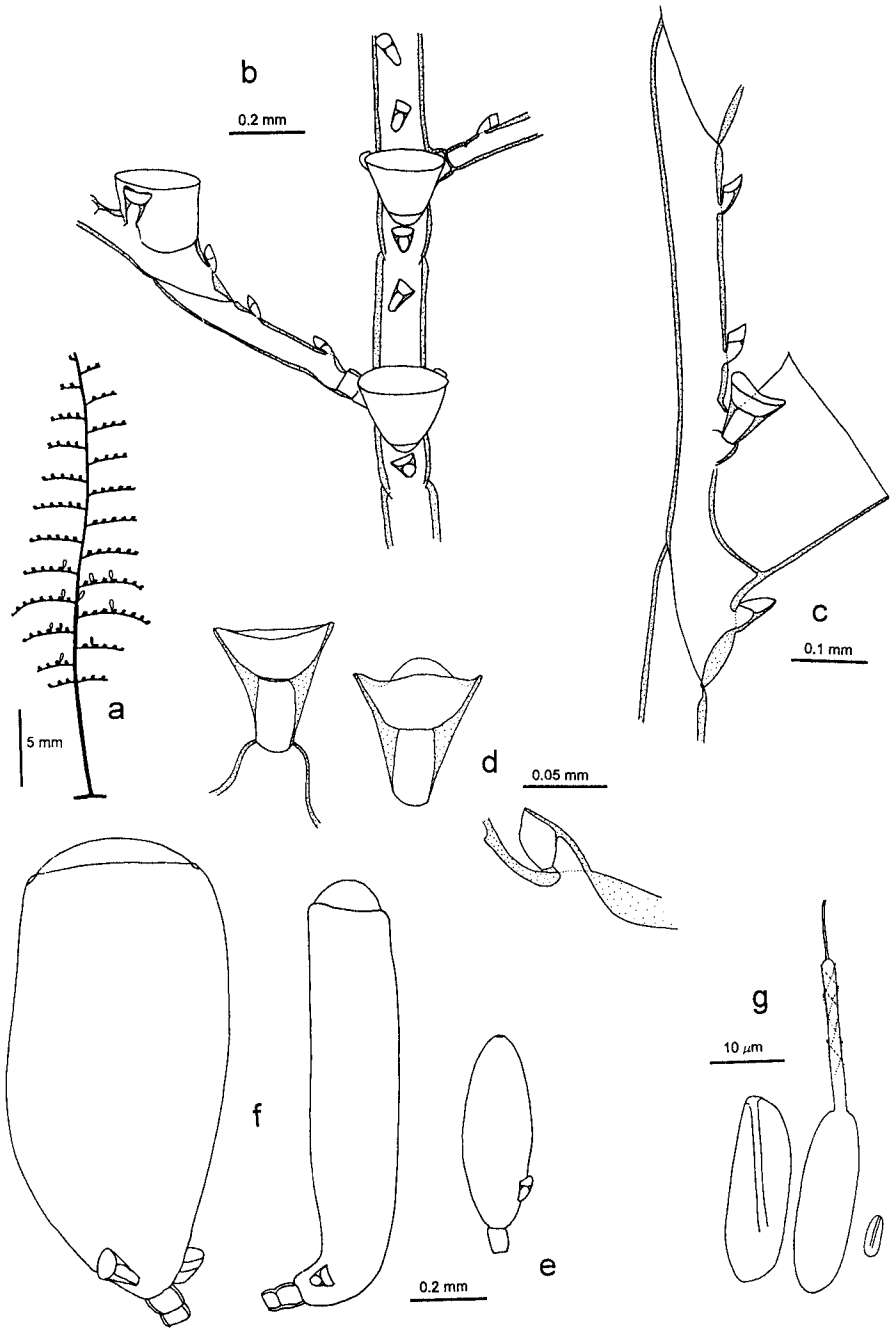

Fig. 17. *Halopteris platygonotheca* nov. spec.; after material from Comores Islands (sample no. 4); a, single plume; b, part of caulus with two hydrocladia; c, part of hydrocladium; d, lateral (top) and median inferior nematothecae, note variation of lateral ones; e, male gonotheca; f, female gonothecae, left in frontal view, right in lateral view, note strong flattening; g, nematocysts: undischarged and discharged microbasic mastigophores and smaller capsule from tentacles.

Table 13. Variation and dimensions *Halopteris platygonotheca*, in µm if not stated otherwise.

sample no.	1	8
stem height [mm]	30	15
cauline segments	500-800	540-1100
diameter caulus	100-140	110-170
hydrocladia per side	12	8
hydrocladial main segments	330-400	400-410
hydrocladial intersegments	380-500	280-390
nematothecae/intersegment	2	1
second cladial segment	480-620	380-450
abcauline side of hydrotheca	180-200	200-210
free adcauline side of hydrotheca	90-110	110-130
diameter of hydrotheca	210-220	230-240

Remarks.— *Halopteris platygonotheca* closely resembles *H. alternata* and *H. diaphana*, and it can only reliably be distinguished from those species by the female gonotheca, which is strongly flattened and only curved for a short distance near its base (see also fig. 17f and table 9). Plumes of *Halopteris platygonotheca* attain also about twice the size of *H. alternata* or *H. diaphana*. Furthermore, *Halopteris platygonotheca* has its distribution in the Indo-Pacific oceans, whereas *H. diaphana* and *H. alternata* are Atlantic species. The material assigned by Billard (1913) to *P. alternata* was re-examined for this study. It has well formed gonothecae that leave no doubt that this material actually belongs to *H. platygonotheca*. Schmidt (1971) erroneously attributed some samples from the Gulf of Aqaba to *H. glutinosa*. A re-examination of Schmidt's material showed that it is partly *H. platygonotheca* and partly *Plumularia setacea*.

A nematotheca in the upper axil of the cauline hydrothecae was only seen in material from Elath and only on rare occasions. Such a nematotheca, however, was regularly seen in the distal parts of cauli of *H. alternata*.

Halopteris buskii group

Remarks.— This group clusters the following species: *Halopteris buskii, H. polymorpha, H. crassa, Halopteris tuba, H. peculiaris, H. liechtensternii,* and *H. glutinosa*. Several are extraordinarily variable nominal species that are often not well separable, or are separated on rather unreliable characters. The present status is very unsatisfactory, but it is not clear whether more material will help to resolve the ambiguities. Table 14 gives the criteria by which the species are distinguished here. Revision by another taxonomist and based on a larger material might easily lead towards differing results.

Halopteris buskii (Bale, 1884)
(figs 18, 19, table 15)

Plumularia obconica Kirchenpauer, 1876: 46, pl. 1 fig. 5, pl. 3 fig. 5, pl. 5 fig. 5 (syn. nov.).
Heteroplon pluma Allman,1883: 32, pl. 8 figs 1-3 (syn. nov.).
Plumularia armata Allman, 1883: 22, pl. 4 figs 3-4 (syn. nov.).

Plumularia buskii Bale, 1884: 125, pl. 10 fig. 3, pl. 19 figs 34-35; 1887: 22; Bartlett, 1907: 42; Briggs, 1915: 304; Hodgson, 1950: 45, fig. 75.

Not *Plumularia buskii* Hartlaub, 1901a: 374, pl. 22 figs 22, 32, 36; Billard, 1913: 21, fig. 11, pl. 1 fig. 15 (= *H. polymorpha*).

Heteroplon pluma; Billard 1909: 327; 1910: 36, fig 16 (only the Challenger material).

Plumularia armata; Billard, 1910: 31; Van Praët, 1979: 916, fig. 85.

Not *Plumularia nuttingi* Billard, 1911: 64, fig. 8 (= *H. polymorpha*).

? *Plumularia alternatella* Mulder & Trebilcock, 1911: 121, pl. 3 figs 1, 1a, 2; Billard, 1913: 23; Vervoort & Vasseur, 1977: 75.

Not *Plumularia buski* var. *peculiaris* Billard, 1913: 23, fig. 12, pl. 1 fig. 17 [= *Haloperis peculiaris* (Billard, 1913)].

Thecocaulus armata; Bedot, 1921b: 8.

Thecocaulus obconicum; Bedot, 1921b: 9.

Halopteris buskii; Watson, 1973: 184.

Not *Halopteris buskii* Vervoort & Vasseur, 1977: 72, figs 31c, 32; Rees & Vervoort, 1987: 119, figs 24, 25a-b, tabs 22-23; Gibbons & Ryland, 1991: 527, fig. 2 [= *H. polymorpha*].

Material examined.

- 1) Lectotype, MVM slide F58822, label: W. M. Bale, Hydroida, Plumulariidae, *Plumularia buskii* (WMB), Griffiths' Pt, July 1880. Contains two fragments of plumes, c. 1.5 cm and 3 cm high, with female and male gonothecae, in good condition.
- 2) Syntype material of *Plumularia armata* Allman, 1883 from Challenger collection, slide from Trebilcock's collection (see history in Stranks, 1993), MVM F60321. Contains basal 12 mm of larger plume, without gonothecae. Original label: *Plumularia armata* Allm., off Port Jackson, 30- 35 fathoms.
- 3) Schizoholotype of *Heteroplon pluma* Allman, 1883, MVM F60324, Challenger expedition station 162, East of Moncoeur Island (Bass Strait, Tasmania, Australia), 70-73 m depth, coll. 2.iv.1874, slide originally in collection Trebilcock (see history in Stranks, 1993). Contains basal part (22 mm) of a single plume with stolons, no gonotheca present, well stained.
- 4) Schizoholotype of *Heteroplon pluma* Allman, 1883, MNHN type L 1186, slide made by Billard (1909, 1910), contains stained distal part of plume.
- 5) Syntype specimen of *Plumularia alternatella* Mulder & Trebilcock, 1911, MVM F57991, from collection Trebilcock (see Stranks, 1993), original label: Type 31, *Plumularia alternatella*, Spring Creek. Contains fragments of a small plume, with tubular stolons, basal part without hydrocladia, with hinge joint, stem heteromerous, no gonothecae.

Description.— Colony forming up to 7.5 cm high plumes arising from tubular stolons.

Hydrocaulus monosiphonic, occasionally branched, without segmentation in proximal part, or with transverse nodes. Last segment of basal part with distal oblique hinge-joint. Above basal part segmentation lacking, distally becoming homomerously segmented by oblique nodes, each segment with one hydrotheca and a hydrocladium. Hydrocladia originate on alternate sides of cauline hydrothecae. Each hydrotheca associated with up to eight nematothecae: one median inferior, one pair of laterals, one (or two?) small reduced nematotheca behind free wall of hydrotheca, and one to four superior ones.

Hydrocladia inserted on well-formed apophysis, placed laterally to cauline hydrothecae. Apophysis without nematotheca. First segment short, quadrangular, without nematothecae. Second segment elongated, with one median nematotheca on upper side. Remaining part of hydrocladium homomerously segmented by oblique nodes, up to 12 hydrothecae per hydrocladium. Sometimes a transverse node subdi-

Table 14. Distinguishing characters of the *Halopteris buskii* group.

species	*Halopteris buskii*	*Halopteris polymorpha*	*Halopteris liechtensternii*	*Halopteris crassa*	*Halopteris peculiaris*	*Halopteris tuba*	*Halopteris glutinosa*
max. size of plume	50 mm	70 mm	22 mm	150 mm	180 mm	220 mm	80 mm
hydrothecae of stem in double row	no	no	no	no	generally not	yes	no
axillar nematothecae behind cauline hydrothecae	1	mostly 1	2	1	1	2	1
axillar nematothecae behind hydrocladial hydrothecae	1	mostly 1	2	1 or a nematophore only	1	nematophore only	1
nematothecae above cauline hydrotheca	2	2 (up to 5 possible)	2-5	2	0-2	0	2
nematothecae on distal end of cladial segments or intersegments	2	1 to 2	1 to 2	always lacking	0-1, very variable	always lacking	1
size of female gonotheca	1.2 mm	0.65 to 1.2 mm	1 mm	2 to 2.5 mm	1.5 to 3.7 mm	2.8 to 3.4 mm	unknown
nematothecae on female gonotheca	up to 12 along entire length	2-3 near base	2 near base	3 near base	2-5 near base	3 near base	unknown

vides repeats into main- and intersegment. Thickness of perisarc variable, but no internal ridges or septae present in individual segments. Main segments, or their equivalent, with four nematothecae: one median inferior, one lateral pair, and a small nematotheca in upper axil of hydrotheca. Intersegments, or their equivalents if no node is present, with one nematotheca, rarely two.

Hydrotheca cup-shaped, rim reaching beyond transverse node when present, occasionally with slight abcauline process, abcauline and adcauline walls straight in lateral view and converging proximally. Hydrotheca adnate for half of adcauline length, angle of opening with hydrocladium 30 to 55°.

Nematothecae of stem and hydrocladia all two-chambered. Median inferior nematothecae do not reach hydrotheca, curved, solid and immovable; adcauline wall of upper chamber lacking. Lateral nematothecae on pedicels of similar height as nematotheca itself, reaching almost to rim of hydrotheca, mobile, conical, wall of upper chamber straight, lower chamber slightly longer than upper one, rim of upper chamber on inner side with broad notch, reaching bottom of upper chamber. Nematothecae of intersegments and occasional superior ones on caulus similar to median inferior nematothecae but with longer free adcauline wall and mobile.

Gonothecae of both sexes on same plumes. Female gonotheca arising singly below side of cauline hydrothecae. Male gonothecae arising on hydrocladia in corresponding position as female ones. Female gonothecae with pedicel composed of one to two indistinct segments. Female gonotheca up to 1.2 mm long, flattened, oval, with tapering base and truncated end with a rounded to nearly polygonal lid, and with two longitudinal rows of up to 12 nematothecae, some of them also on the lid.

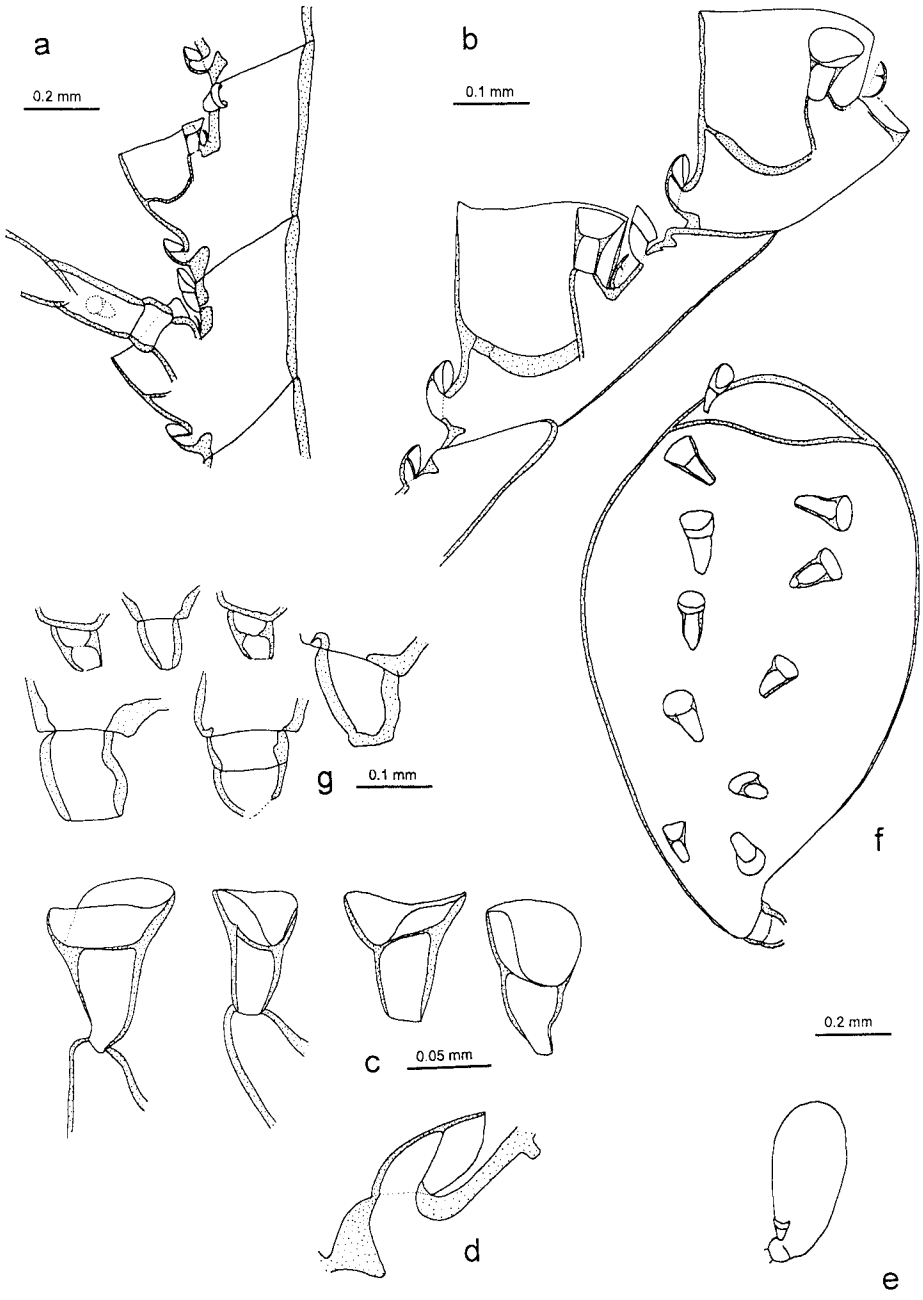

Fig. 18. *Halopteris buskii* (Bale, 1884); after type material of *P. buskii*; a, lateral view of segmented part of caulus; b, distal end of hydrocladium; c, several lateral nematothecae that demonstrate extent of variation; d, median inferior nematotheca; e, male gonotheca; f, female gonotheca, note presence of a double row of nematothecae, same scale as e; g, pedicels of female gonothecae, note variation.

Male gonotheca sac-shaped, without lid, thin walled, about 0.4 mm long, with indistinct, one-segmented pedicel and one to two nematothecae near its base.

Additional observations.— After Watson (1973) the colour of the plumes is varied from orange to yellow in specimens from shallow water, while colonies from deeper waters are intensely scarlet.

Type locality.— Griffiths' Point, Victoria, Australia.

Distribution.— Geraldton (Western Australia) to Nambucca Heads (New South Wales) (Dr. J. Watson, pers. comm.).

Remarks.— Type material of the nominal species *Heteroplon pluma* Allman, 1883, *Plumularia armata* Allman, 1883, and *Plumularia buskii* Bale, 1884 was re-examined. Bale did not designate a type specimen for *Plumularia buskii* (cf. Stranks, 1993). However, Bale's (1884) description is probably based mainly on a slide kept now in the Museum of Victoria. It dates from 1880 and is from the type locality. It is designated as co-type in the register to the collection (Stranks, 1993). This slide (MVM F58822) is herewith designated the lectotype. All type slides of the above mentioned three nominal species contain *Halopteris* species that are indistinguishable. Also the measurements agree very well (table 15). They certainly all belong to the same species. Additionally, the figure of the female gonotheca in Allman (1883) leaves little doubt that *P. armata* Allman, 1883 is conspecific with *P. buskii* Bale, 1884. It is surprising that Allman created a new genus for his *Heteroplon pluma*. Allman (1883) argued that the latter had median inferior nematothecae different from those found in the other species. However, Billard (1910), who re-examined the type material of *Heteroplon pluma*, observed that Allman had incorrectly figured those nematothecae. Billard (1910) further synonymised *Aglaophenia glutinosa* Lamouroux, 1816 and *Heteroplon pluma* Allman, 1883. Although this may be correct, Billard's proposal is not followed here (see under *H. glutinosa*). Billard (1910, 1913) figured and described *H. pluma* without axillar nematothecae, which is not correct. Billard's slide was from the distal end of a plume of the original Challenger material kept in the British Museum (Natural History). This slide is now in possession of the MNHN in Paris and it was re-examined. Although visible in only a few cases, this material clearly has axillar nematothecae and agrees well with the other material of *H. pluma* (sample 3, see fig. 19). Though *H. buskii* is at present only separable from *H. polymorpha* by its female gonotheca and as the material of *H. pluma* is infertile, it is here nevertheless referred to *H. buskii* for zoogeographic reasons (see Briggs, 1973). All reliable records of *H. buskii* published so far are from the area between South-western Australia and Sydney. The material of *H. pluma* was dredged

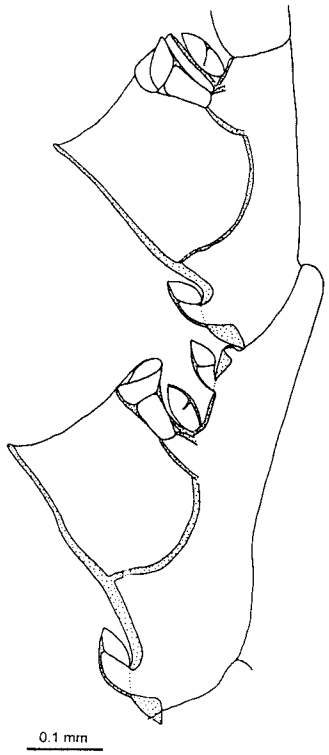

Fig. 19. *Halopteris buskii* (Bale, 1884); after type material of *Heteroplon pluma* Allman, 1883; part of hydrocladium, note the presence of axillar nematothecae.

Table 15. Variation and dimensions of *Halopteris buskii*, in µm if not stated otherwise.

sample no.	1 (*P. buskii*)	2 (*P. armata*)	3 (*H. pluma*)
diameter caulus	300-330	170-240	350-420
cauline superior nematotheca	1-4	2-4	1-4
cladial main segments	370-400	360-420	370-390
cladial intersegments	200-230	170-250	170-200
nematothecae / intersegments	1	1	1
hydrothecae/cladium	10	6	-
abcauline side of hydrotheca	150-180	210-260	210-250
free adcauline side of hydrotheca	90-110	80-120	80-90
diameter of hydrotheca	200-210	210-270	210-220
tentacle number	1	~ 14	-

in Bass Strait, lying more or less in the middle of this area and close to the type locality of *H. buskii*.

Allman (1883) indicated that also *Plumularia obconica* Kirchenpauer, 1876 is very similar to his *P. armata*. Kirchenpauer's *Plumularia obconica* originated from the Gulf of St. Vincent (Adelaide, South Australia) and also has the characteristic female gonothecae with many nematothecae. Allman (1883) kept *P. obconica* distinct from *P. armata* on the following arguments: shallower hydrothecae with plicate margin, conical lid and one-chambered nematothecae of the female gonotheca. These differences are here seen as insignificant and most probably derive from the inadequate description or sampling artefacts (Kirchenpauer probably had dried specimens; see Stranks, 1993). The type material of *P. obconica* is probably lost (but see Stranks, 1993). Although the description of Kirchenpauer (1876) is only sketchy, it is compatible with the present concept of the nominal species *Plumularia buskii*. Therefore also *P. obconica* is included in the synonymy of the present species. The identity of the four nominal species is further supported by their respective type localities which all lie rather closely together on the south to south-east coast of Australia. The oldest available name for this species would therefore be *Halopteris obconica* (Kirchenpauer, 1876) and also *H. armata* (Allman, 1883) is a senior synonym of *H. buskii* (Bale, 1884). However, *Halopteris obconica* and *H. armata* are virtually unknown names and they have not been used since their introduction more than a hundred years ago. Therefore, the frequently used and well known, although probably often incorrectly applied, name *H. buskii* (Bale, 1884) is here preferred, pending a decision by the International Commision on Zoological Nomenclature to overrule the Principle of Priority (Code of Zoological Nomenclature, ed. 3, article 79c).

Billard (1913) and Vervoort & Vasseur (1977) synonymised *Plumularia alternatella* Mulder & Trebilcock, 1911 with *H. buskii*. The type slide of *P. alternatella* was re-examined for this study. It contains a fragment of a juvenile *Halopteris* species that cannot be identified with certainty. Its structure, however, is compatible with that of *P. buskii* and therefore it is here tentatively synonymised with the latter. Also Mulder & Trebilcock (1911) considered this a possibility.

Billard's (1913) material of *Plumularia buskii* is here assigned to *Halopteris polymorpha*. The reasons for this are discussed under *H. polymorpha*.

The type material of *Plumularia buskii* shows perfectly the characteristic female gonotheca (fig. 18f). Contrary to the opinion of Ryland & Gibbons (1991), the pedicel of it is not composed of two segments. It is of rather varied shape and consist of one or two indistinct segments (fig. 18g). The variability even within one plume precludes its use as diagnostic character.

Several authors also identified material as *Halopteris buskii* from other localities than southern Australia, mostly from tropical waters (e.g. Billard, 1913; Nutting, 1927; Redier, 1966; Vervoort & Vasseur, 1977; Ryland & Gibbons, 1991). However, none of them noted the peculiar female gonotheca. Some authors found gonothecae without the double row of nematothecae. As also the trophosomes of these samples are deviating, as for instance the abcauline cusp in the material described by Vervoort & Vasseur (1977), these populations probably belong to another species and are here referred to *H. polymorpha* (for discussion see there).

Halopteris polymorpha (Billard, 1913)
(figs 20-23, table 16)

Plumularia nuttingi Billard, 1911: 64, fig. 8 (syn. nov.).

Plumularia polymorpha Billard, 1913: 24, figs 14-15.

Plumularia buski; Billard, 1913: 21, fig. 11, pl. 1 fig. 15; Nutting, 1927: 22; Redier, 1966: 90, pl. 2 figs 1, 3, pl. 3 fig. 1 [not *Plumularia buskii* Bale, 1884].

Halopteris polymorpha; Pennycuik, 1959: 178; Vervoort, 1966: 132, fig. 35; Millard & Bouillon, 1973: 83, 10F-J; Millard, 1975: 354, fig. 112G-L; 1978: 193; Ryland & Gibbons, 1991: 530, fig. 4

Halopteris buskii; Rees & Thursfield, 1965: 160; Vervoort & Vasseur, 1977: 72, figs 31c, 32; Gibbons & Ryland; 1991: 527, fig. 2.

Halopteris buskii; Rees & Vervoort, 1987: 119, fig. 25a-b, tab. 22 (in part, only material from station 112).

Material examined.

- 1) Lectotype, ZMA Coel. 4044, as *Plumularia polymorpha*, Siboga station 80 (2°25'S 177°43'E, Borneo, Indonesia), depth 40-50 m, on fine coralline sand, one plume 12 mm high, with gonothecae (presumably female), designated here lectotype of *P. polymorpha*.
- 2) Siboga station 77 (3°27'S 117°36'E, Borneo, Indonesia), ZMA Coel. 4044, as *Plumularia polymorpha*, depth 59 m, on fine coralline sand, one plume fragment 8 mm long, intersegments shorter than in lectotype, often with one nematotheca only, infertile.
- 3) Siboga station 299 (10°52.4'S 123°1.1'E, Indonesia), ZMA Coel. 4044, as *Plumularia polymorpha*, depth 34 meters, corals and *Lithothamnion*, one infertile plume, 15 mm high, resembling lectotype, stem proximally with indistinct segmentation.
- 4) Siboga station 164 (1°42.5'S 130°47.5'E, Indonesia), depth 32 meters, ZMA Coel. 4045 as *Plumularia polymorpha* var. *sibogae*, 2 infertile plumes up to 9 mm high, with long lateral nematothecae, hydrocladial intersegments mostly with 1 nematotheca.
- 5) Neotype of *Plumularia nuttingi* Billard, 1911, ZMA Coel. 5241, Siboga station 80, identified by Billard (1913) as *Plumularia buskii*, one plume 17 mm high and some hydrocladia, with many female, and at distal end of plume two male gonothecae, designated here the neotype of *Plumularia nuttingi*.
- 6) Siboga station 80, ZMA Coel. 4071, identified by Billard (1913) as *Plumularia buski*, several plumes up to 14 mm high, with female gonothecae, colony growing on polychaete tube.
- 7) Siboga station 93, ZMA Coel. 4071, identified by Billard (1913) as *Plumularia buskii*, contains four plumes.
- 8) Siboga station 125 (Island of Siau, Indonesia), ZMA Coel. 4045, identified by Billard (1913) as *Plumularia buskii*, several infertile plumes up to 25 mm high.

- 9) Siboga station 162 (between Loslos and Broken Island, Indonesia), ZMA Coel. 4070, identified 26.ii.1923 by Billard as *Plumularia buskii*, depth 35 meters, contains one infertile plume 15 mm high.
- 10) Siboga station 164 (see above), ZMA Coel. 4045, identified by Billard (1913) as *Plumularia buskii*, a few fragments.
- 11) Mahe, Seychelles, MACT 2.700 and 2.777 (described by Millard & Bouillon 1973), as *Halopteris polymorpha*, numerous plumes 1.5 to 7 cm high, with male and female gonothecae.
- 12) Amirantes, Seychelles, MACT 2.775 (described by Millard & Bouillon, 1973), as *Halopteris polymorpha* var. *sibogae*, a few small plumes.
- 13) Galathea expedition station 196 (see Vervoort 1966), 29°55'S 31°20'E (off Durban, South Africa), RMNH Coel. 3758, as *Halopteris polymorpha*, coll. 13.ii.1954, fragments 2 and 2.5 cm high in two slides, infertile, conical nematothecae with straight walls, adaxial side only slightly lowered, intersegments of hydrocladia with one nematotheca.
- 14) Ponta do Baleerio, São Sebastião, Brazil, ROMIZ B1259, as *Halopteris polymorpha*, coll. A. Migotto 18.viii.1988, depth 6 m, on rocks, several fertile plumes up to 25 mm high, with one nematotheca on hydrocladial intersegments, often with a pair of axillar nematothecae on caulus.
- 15) Ponto do Baleeiro, São Sebastião, Brazil, on rocks, 6-8 m, coll. A. Migotto 8.x.1987, originally identified as *Halopteris buskii*, one slide stained with Fast Green and Carmine and one sample preserved in alcohol (RMNH Coel. 27613).
- 16) Takapoto, Tuamoto Archipelago, French Polynesia (described by Vervoort & Vasseur, 1976 as no. 52), RMNH Coel. 11576, as *Halopteris buskii*, many plumes up to 2.5 cm high, with female and male gonothecae.

Description (after lectotype and material originally identified by Billard (1913) as *P. polymorpha*, sample nos 1 to 3).— Colonies forming up to 1.5 cm high plumes that arise from ramified, tubular stolons. Plumes with alternate hydrocladia, except first pair that can be opposite.

Hydrocaulus monosiphonic, unbranched, with basal part devoid of hydrothecae and hydrocladia, and a longer distal part. Basal part with variable number of nematothecae in two rows. Stem above basal portion segmented homomerously by oblique nodes. In proximal region segmentation can be indistinct or absent. Each segment with a hydrotheca, hydrocladium, and six nematothecae: one median inferior, one pair of laterals, one small axillar, and two (rarely one to three) on distal end of segment. Superior nematothecae either almost in median plane of distal region of stem or alternately displaced laterally.

Hydrocladia arising on long apophysis placed lateral to cauline hydrothecae. Apophysis followed by short, quadrangular segment, both without nematothecae. Next segment long, with two median nematothecae on upper surface. Remaining part of hydrocladium heteromerously segmented with main- and intersegments and alternate oblique and transverse nodes. Sometimes transverse nodes can be absent and then intersegment fused to previous main segment. Main segments with a hydrotheca and four nematothecae: one median inferior, one pair of laterals, and an axillar one. Intersegments about as long as main segments, with one to two nematothecae.

Hydrotheca cup-shaped, placed in middle of main segment, rim reaches beyond transverse node if present, abcauline and adcauline walls quite straight and parallel in lateral view. Hydrotheca adnate for about half its length, rim smooth and flat, sometimes gently flaring, opening forming an angle of c. 50 to 60° with hydrocladium.

Nematothecae of stem and hydrocladia typically two-chambered, axillar ones can be one-chambered. Median inferior nematotheca of main segments conical, adcauline wall of upper chamber slightly lowered. Lateral nematothecae on pedicel that is shorter than nematotheca itself, reaching rim of hydrotheca, conical with distal walls straight, lower chamber longer than upper one, wall of upper chamber lowered, sinuated, or with emargination on inner side. Remaining nematothecae and those of intersegments similar to median inferior ones but with longer lower chamber.

Presumed female gonothecae c. 0.65 mm long and 0.4 mm diameter, straight, base tapering, with two or three nematothecae near base. Pedicel formed of two segments. Male gonotheca not seen.

Nematocysts: microbasic mastigophore, c. 17 × 6 μm, s~0.8, smaller capsules also present.

Type locality.— 2°25'S 177°43'E, Borneo, Indonesia, depth 40 to 50 m, on fine coralline sand.

Distribution.— Indonesia; Polynesia; Seychelles; South Africa; Brazil.

Variation and additional observations.— The length of the intersegments can vary considerably, after Billard (1913) from 0.19 to 0.47 mm. The lateral nematothecae can have a much elongated lower chamber and then project beyond the rim of the hydrotheca [seen in samples 4 and 12, see fig. 22e, var. *sibogae* of Billard (1913)].

The material originally described as *P. nuttingi* Billard, 1911 (fig. 21) differs only in the shape of the lateral nematothecae: the wall of the upper chamber is rolled inwardly and it has an emargination on inner and outer sides (spanner type). Most intersegments of the hydrocladia have only one nematotheca, although two can also be observed. The length of the intersegments again is variable and falls in the range given above. The presumed male gonothecae are found distally of the female ones, they are smaller, have only a single nematotheca near the base, and a one-segmented pedicel.

The material of sample 9 differs from the type material by the regular occurrence of a pair of one-chambered axillar nematothecae and by the presence of a sinuated rim of the hydrothecae that occasionally produces a cusp on the abcauline side. The lateral nematothecae conform to the type material of *H. polymorpha*.

The material from French Polynesia (sample 16, fig. 23) differs in being more delicate and also by the regular presence of an abcauline cusp formed by the rim of the hydrotheca (see also Vervoort & Vasseur 1976). There is mainly a single axillar nematotheca, however, rarely a pair could be seen. The lateral nematothecae are long, resembling Billard's var. *sibogae*.

Remarks.— Billard (1913) described two species and a variety that are quite close: *Plumularia polymorpha, Plumularia polymorpha* var. *sibogae* and *Plumularia buski* (incorrect subsequent spelling). The material referred to *P. buski* was described earlier as a new species: *Plumularia nuttingi* Billard, 1911. In 1913, Billard then synonymised *P. nuttingi* with *H. buskii* (as *P. buski*), a proposal not followed here. *Plumularia buskii* of Billard (1913) will here again be referred to as *P. nuttingi* and synonymised with *H. polymorpha* (see also under *H. buskii*). Billard (1913) noted only one type of gonothecae in his samples of *P. nuttingi* and incorrectly interpreted those as male (cf. fig. 21d). This may have induced him to synonymise this sample with *H. buskii*, which

indeed mainly differs in the female gonotheca (cf. figs 18f and 21d, Billard's sample also differs from *H. buskii* in the shape of the lateral nematothecae on which he placed so much weight to distinguish it from *H. polymorpha*, cf. figs 18c and 21f). If one considers only the material of *H. nuttingi* and *H. polymorpha* available to Billard (1913) his distinction of two separate species seems plausible. However, after the study of more material, also from other regions, such a separation becomes difficult or even impossible (cf. also Ryland & Gibbons, 1991). Billard's nominal species *P. nuttingi* and *P. polymorpha* are here regarded as insufficiently separable because their distinction is based on too variable characters. Billard (1913) kept his *P. polymorpha* distinct from his *P. nuttingi* (as *P. buski*) only on account of the shape of the lateral

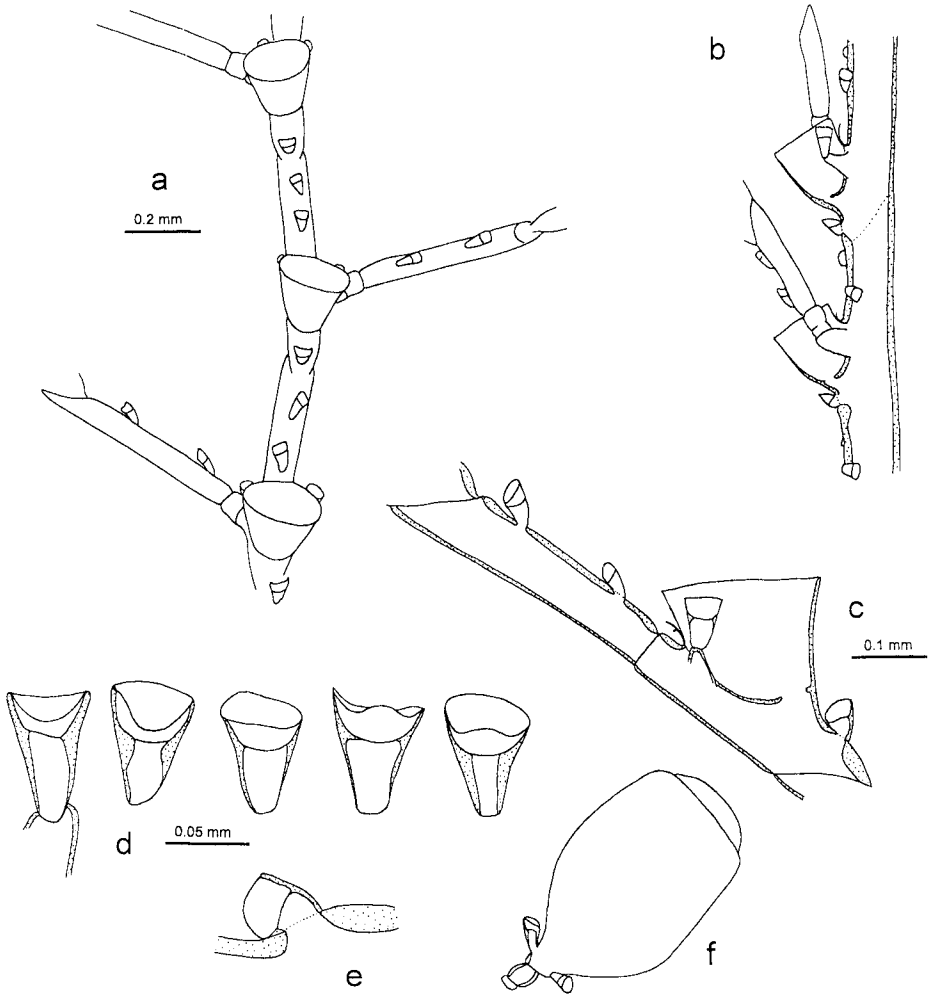

Fig. 20. *Halopteris polymorpha* (Billard, 1913); after lectotype of *P. polymorpha* Billard, 1913, except b which is from sample 3; a, part of caulus with basal parts of hydrocladia; b, lateral view of caulus in part with reduced segmentation, same scale as a; c, part of hydrocladium; d, several lateral nematothecae that demonstrate extent of shape variation; e, median inferior nematotheca, same scale as d; f, female gonotheca, same scale as a.

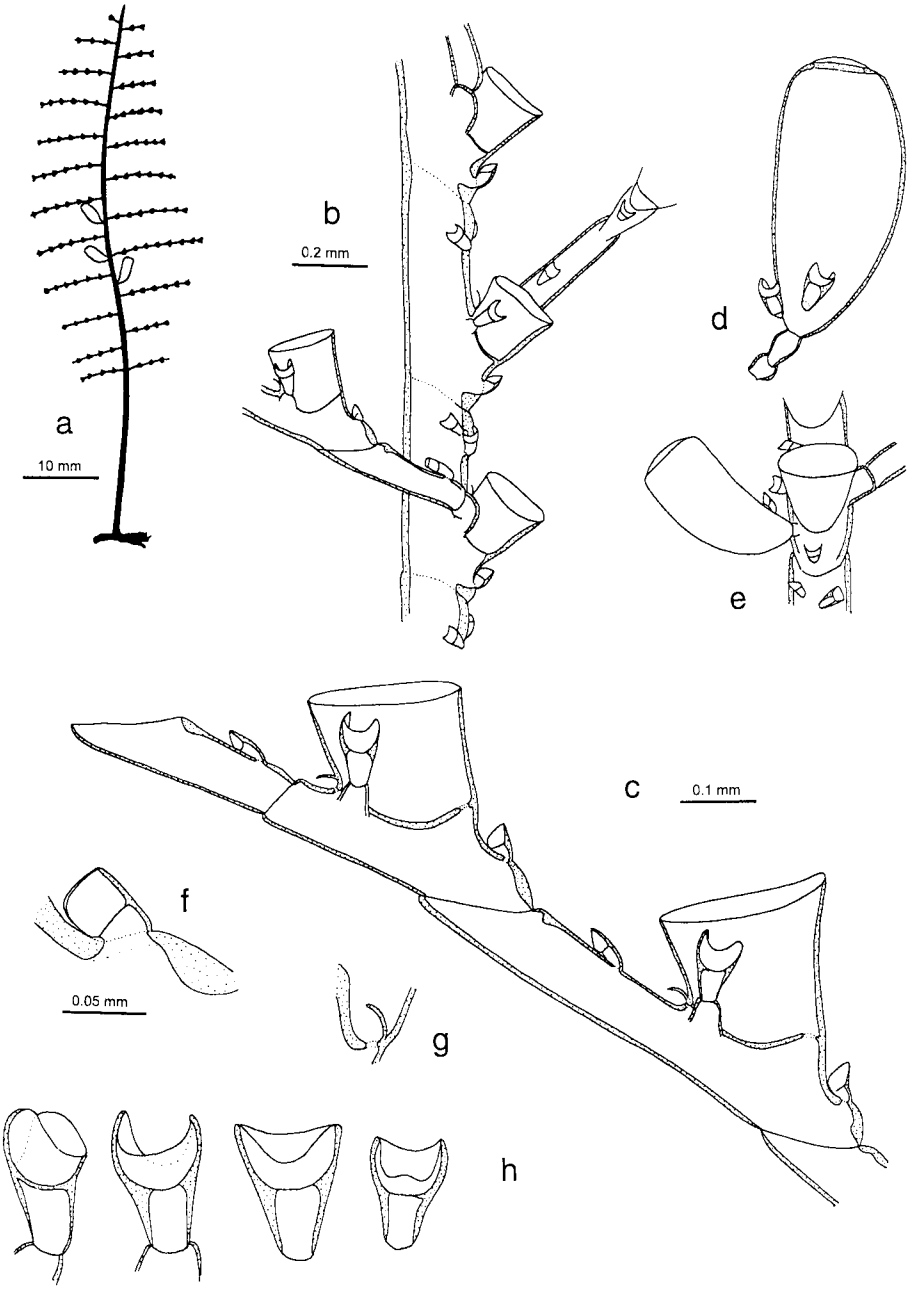

Fig. 21. *Halopteris polymorpha* (Billard, 1913); all after material from Siboga station 80 (sample 6), except last two nematothecae in h, which are from sample 7; this material was described as *P. nuttingi* and *P. buski* by Billard (1911, 1913); a, one plume with gonothecae; b, lateral view of caulus with hydrocladia; c, part of hydrocladium, note presence or absence of transverse nodes; d, female gonotheca, same scale as b; e, caulus in frontal view with possible male gonotheca, only one nematotheca is present, distal end may be not accurate, same scale as b; f, median inferior nematotheca; g, axillar nematotheca, same scale as f; h, several lateral nematothecae that show extent of shape variation, same scale as f.

nematothecae. Most lateral nematothecae in *P. nuttingi* have inwardly rolled walls and an emargination on both inner and outer sides (fig. 21h, spanner type), whereas those of *P. polymorpha* mostly have straight walls and only an emargination on the inner side (fig. 20d). It seems that Billard himself did not consequently adhere to distinction as he later identified some material (sample 9) as *P. buski*, despite its lateral nematothecae having straight walls. The species distinction based on the shape of the lateral nematothecae was also questioned by Ryland & Gibbons (1991). Shape of the lateral nematothecae can be used in some species as a reliable diagnostic character, in some species, however, it is notoriously variable (see *Antennella quadriaurita*). The re-examination of the type material showed that the shape of the lateral nematotheca shows variation in both samples identified by Billard as either belonging to *P. nuttingi* or *P. polymorpha* (figs 20d and 21h). Although the majority of the nematothecae in each nominal species shows a clear difference, enough variation is present to align both sets in a single, continuous row and thus invalidate this character as a useful diagnostic feature. Ryland & Gibbons (1991) used the relative length of the segments, the shape of the hydrotheca and the number of segments of the gonothecal pedicel to distinguish two nominal species that correspond to Billard's *P. polymorpha* and *P. nuttingi*. The re-examination of the type material of those nominal species does not support the suggestion of Ryland & Gibbons (1991) either. The length of the pedicel is too variable and the gonothecae are indistinguishable (cf. figs 20 and 21, table 16). The number of segments of the female gonotheca is also not a reliable character. In both type series the pedicels of the gonothecae have two segments (cf. figs 20f and 21d), although in *P. polymorpha* the proximal one is smaller. Experience with other species (e.g. see fig. 18g), indicates that also the number of segments in the gonothecal pedicel can be variable. The first segment can sometimes look like a simple stem apophysis, which some might consider a segment and others not. Such a situation is found in the sample from the Seychelles (sample 11, fig. 22d). This material was probably also used for Millard's (1975) description of *H. polymorpha*. Millard (1975) described *H. polymorpha* as having a female gonotheca with a pedicel of one segment. The shape of the male gonotheca observed in the material of *P. nuttingi* (fig. 21e) might suggest a difference with that found in other samples (figs 22d and 23b). However, only three gonothecae could be observed and they could not be examined with the desired accuracy. Future observations have to re-address this point.

Because *P. nuttingi* Billard, 1911 and *P. polymorpha* Billard, 1913 are here considered conspecific, formally *Halopteris nuttingi* would become the oldest available name and *H. polymorpha* a junior synonym. However, the species name *nuttingi* has not been used anymore since its original description more than eighty years ago. Therefore, the familiar and frequently used name *Halopteris polymorpha* (Billard, 1913) is applied here instead for nomenclatural stability, pending a decision of the International Commission on Zoological Nomenclature. This name also characterises the species rather accurately, although Billard based the description on a few plumes only showing considerably less variation than is now known.

The forma *sibogae* described by Billard (1913) as a form of *H. polymorpha* differs only in the length of the lateral nematothecae. As this length is also quite variable and both morphs apparently occurred in the same colony (see Millard & Bouillon, 1973: 85) no separate name should be applied. Names for varieties are misleading as

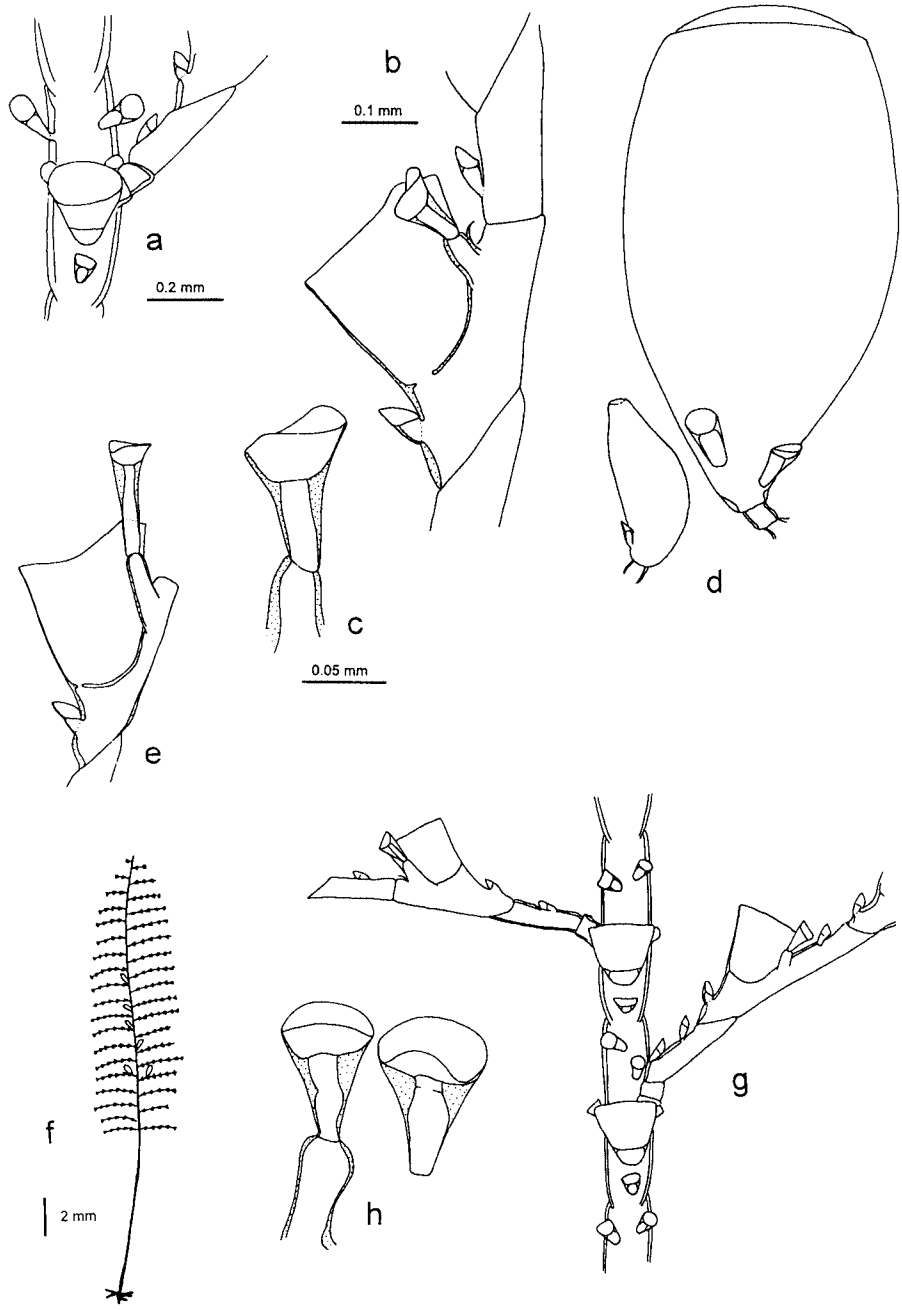

Fig. 22. *Halopteris polymorpha* (Billard, 1913); a-e after material from Seychelles (samples 11 & 12), f - h from Brazil (sample no. 14); a, part of caulus; b, part of hydrocladium; c, lateral nematotheca; d, male (left) and female (right) gonotheca, same scale as a; e, main segment of var. *sibogae* (sample 12); f, single plume; g, frontal view of part of caulus, same scale as a; h, variation of lateral nematothecae, same scale as c.

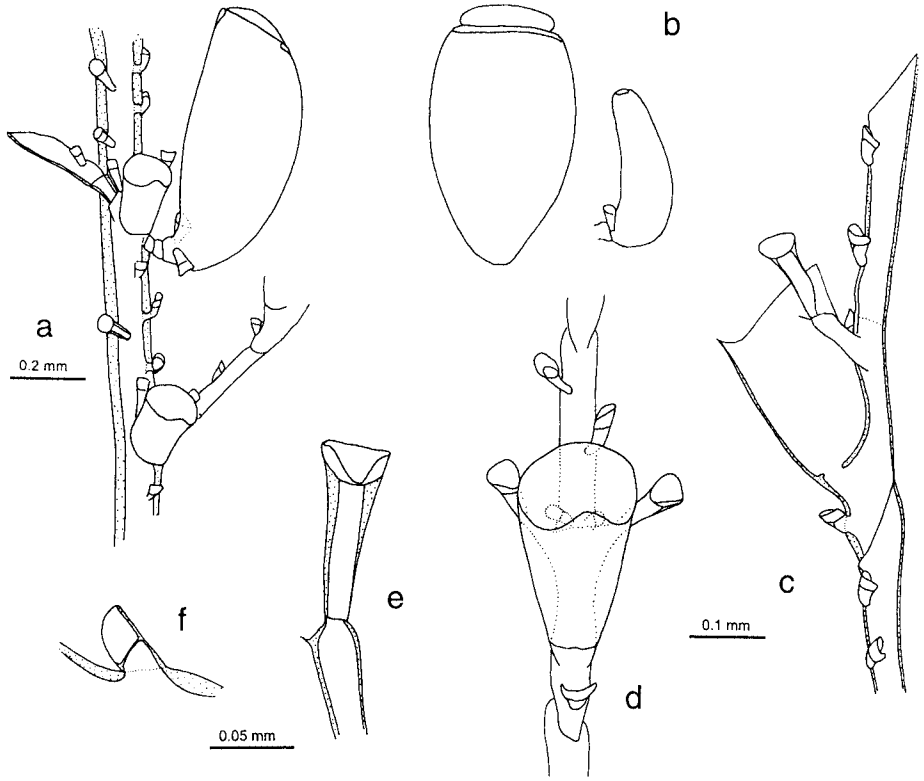

Fig. 23. *Halopteris polymorpha* (Billard, 1913); after material from French Polynesia (sample 16); a, frontal view of caulus with hydrocladia and female gonotheca in lateral view; b, female gonothecae (left) in frontal view (pedicel not shown) and male gonotheca at right, same scale as a; c, part of hydrocladium, note abcauline cusp of hydrotheca; d, frontal view of main segment showing a rare occasion of paired axillar nematothecae (dotted line), same scale as c; e, lateral nematotheca, note elongated lower chamber; f, median inferior nematotheca, same scale as e.

they can incorrectly suggest a subspecific status. The same form was also found in the Seychelles (sample 12; Millard & Bouillon, 1973). In that material, the rim of the hydrotheca also shows a sinuated outline which was not seen in the Siboga material.

The material described by Billard (1913) as *Plumularia buski* var. *peculiaris* differs distinctly from the type material of *P. nuttingi* and *P. polymorpha* by having very thick (0.4 mm) and high (up to 7 cm) hydrocauli (cf. figs 21 and 29). The height of the plumes is thus around three times the size of the typical *H. polymorpha*. Also the female gonotheca is much larger (2 mm compared to 0.7 mm). The intersegments of the hydrocladia, or their homologues if fused to the main segments, frequently lack a nematotheca; there is a single one in the type series referred to above. The material is here recognised as a separate species: *H. peculiaris* (tab. 14 and p. 84)

The material from French Polynesia described by Vervoort & Vasseur (1977) as *Halopteris buskii* was re-examined (sample 16, fig. 23) and it was tentatively assigned to *H. polymorpha*, although it could also be a separate species. The sample differs from material referable to *H. polymnorpha* in the following aspects: it has rather deli-

Table 16. Dimensions of *Haloperis polymorpha*, in µm if not stated otherwise.

sample no.	1	2	3	6	14
max. caulus height [mm]	12	-	15	14	25
hydrocladial main segments	320	330	300-350	325-360	300-350
hydrocladial intersegments	340-400	300	270-330	290-400	170-210
abcauline side of hydrotheca	150-160	200	200-220	180-200	190-210
free adcauline side of hydrotheca	80-90	110	100-110	130-150	90-110
diameter of hydrotheca	200-210	180	160-170	210-230	170-180
nematothecae/intersegment of hydrocladium (majority)	2	1	2	1	1
length female gonotheca [mm]	0.65	-	-	0.67-0.70	0.76

cate plumes, there are up to five nematothecae above each cauline hydrotheca instead of two only, the abcauline rim of the hydrotheca forms a distinct cusp, and the lateral nematothecae are as long as in var. *sibogae*. Contrary to the observations of Vervoort & Vasseur (1977), there is rarely a pair of nematothecae in the upper axil of the hydrocladial hydrothecae, but the majority of the axillar nematothecae are single. The material from French Polynesia could easily be interpreted as a distinct species, however, it is also connected with *H. polymorpha* by intermediate forms. A sample from the Siboga expedition (sample no. 9) that was identified by Billard after his publication of 1913, shows some intermediate characters. Billard identified it as *P. buskii* although its straight lateral nematothecae rather conform to his concept of *H. polymorpha*. Some, but not all, hydrothecae of Billard's sample have a sinuated rim with an abcauline cusp and shallow lateral elevations, reminiscent of the genus *Gattya*. The cauline and the hydrocladial hydrothecae often have a pair of axillar nematothecae. A sinuated rim was also seen in one sample from the Seychelles (sample no. 14), and also other samples showed a tendency towards an abcauline marginal cusp. Ryland & Gibbons (1991) also observed occasional paired axillar nematothecae in their material identified as *H. buskii*. In conclusion, it seems again impossible to draw an objective line of distinction and Vervoort & Vasseur's material is here also tentatively assigned to *H. polymorpha*.

Other samples agree rather well with the characteristic form of *H. polymorpha*. The plume from South Africa (no. 12) must have been rather tall (> 5 cm). Its lateral nematothecae are conical with straight walls, but they are somewhat longer and tend towards Billard's (1913) forma *sibogae*. The material from the Seychelles (samples 11 & 12) agrees well with Billard's material. Differences were only seen in the larger female gonotheca (length 1.2 mm) and the much larger colonies from station 2.700 that reached 7 cm in height. The other, smaller colonies (1.5 cm) have the same type and size of female gonothecae as the larger plumes. The samples from Brazil (fig. 22) agrees very well in all details with the typical form of *H. polymorpha*. The female gonothecae measure 0.75 mm in length, have a pedicel composed of two segments and contain a single egg only. Occasionally there was a pair instead of a single axillar nematotheca. This variation could be seen within the same plume, and conforms again with similar observations made by Ryland & Gibbons (1991) on material from Fiji. The Brazilian material may possibly differ in the large nematocysts of the nema-

tophores that resemble atypical euryteles. Unfortunately too little suitable material was available and a future investigation must address this problem again.

The extent of variation in *Halopteris polymorpha* makes it difficult to delimit other similar species, notably *H. buskii, H. peculiaris,* and *H. liechtensternii* (see also table 14). *Halopteris buskii* (Bale, 1884) (fig. 18f) is objectively only distinguishable by the numerous nematothecae in a double row that decorate the female gonotheca. Also the known biogeographical distribution pattern supports a separation of the species: while *H. polymorpha* is a species predominantly occurring in tropical waters, *H. buskii* is confined to the temperate waters of southern Australia (for marine zoogeographical zones see Briggs, 1973). The relationship of *H. polymorpha* to *H. peculiaris* and *H. liechtensternii* is discussed under those species.

In order to facilitate future revisions of this difficult species, nearly all variations described above are here illustrated in several figures (figs 20 to 23).

Halopteris liechtensternii (Marktanner-Turneretscher, 1890) (fig. 24, table 17)

Plumularia liechtensternii Marktanner-Turneretscher, 1890: 257, fig. 2-2a; Motz-Kossowska, 1908: 55, figs 1-3.

Heterotheca liechtensterni; Stechow, 1923b: 233.

Antenella diaphana forma *typica*; ? Broch, 1933: 24 (only fertile material from Prizidnice).

Thecocaulus diaphanus; Riedl, 1959: pl. 11 fig. 7; Riedl, 1966: fig. 84; Gili, 1982: 81, fig 39 [not *Halopteris diaphana* (Heller, 1868)]

Halopteris liechtensterni; Medel & Vervoort, 1995: 39, fig. 16.

Material examined.

-1) Lectotype, NHMV inventory number 1132, microslide prepared by Marktanner-Turneretscher, label: *Plumularia liechtensterni* n. sp., one fertile plume. Designated here as lectotype.
- 2) Île de Bendor (Bandol, French Riviera, Mediterranean), several plumes collected June 1991 by D. Geiger, 6 m depth, in cave, fertile, originally coloured yellow, in collection of author, one slide as RMNH Coel. 27615.
- 3) Naussa (Island of Paros, Greece), several infertile plumes, collected by author, September 1990, depth 1-2 m.
- 4) Porto Pollo (Corsica, France), several fertile plumes collected by author 30.vi.1992, depth 2 m.
- 5) Banyuls-sur-Mer, Grotte du Troc, France, Mediterranean, MHNG, no number, as *Schizotricha liechtensternii*, collection Bedot, collected by Pruvot, 2 infertile plumes, no date given.
- 6) Banyuls-sur-Mer, Anse du Troc, several infertile colonies collected 14.ix.1995, by author.
- 7) Marcambrils, near Tarragona, Spain, Mediterranean, many infertile colonies collected 13.ix.1995, by author.

Description.— Colony forming up to 22 mm high plumes, arising from creeping, ramified stolons without nematothecae. First pair of hydrocladia opposite, others alternate.

Stems monosiphonic, generally unbranched, with a basal part ($^1/_5$ of total length) devoid of hydrothecae and hydrocladia and a longer distal part bearing hydrothecae and hydrocladia. Basal part divided into segments by several straight nodes, last node oblique. Segments of basal part with up to nine nematothecae in two rows. Caulus above basal part homomerously segmented by oblique nodes, only at extreme distal end heteromerous segmentation by additional transverse nodes that

delimit intersegments from main segments. Hydrothecate segments bear one hydrocladium each, only most proximal segment may bear two opposite hydrocladia. Cauline hydrothecae in one row on front of stem. Each hydrothecate segment normally with seven nematothecae: one median inferior, one on each side of hydrotheca, two

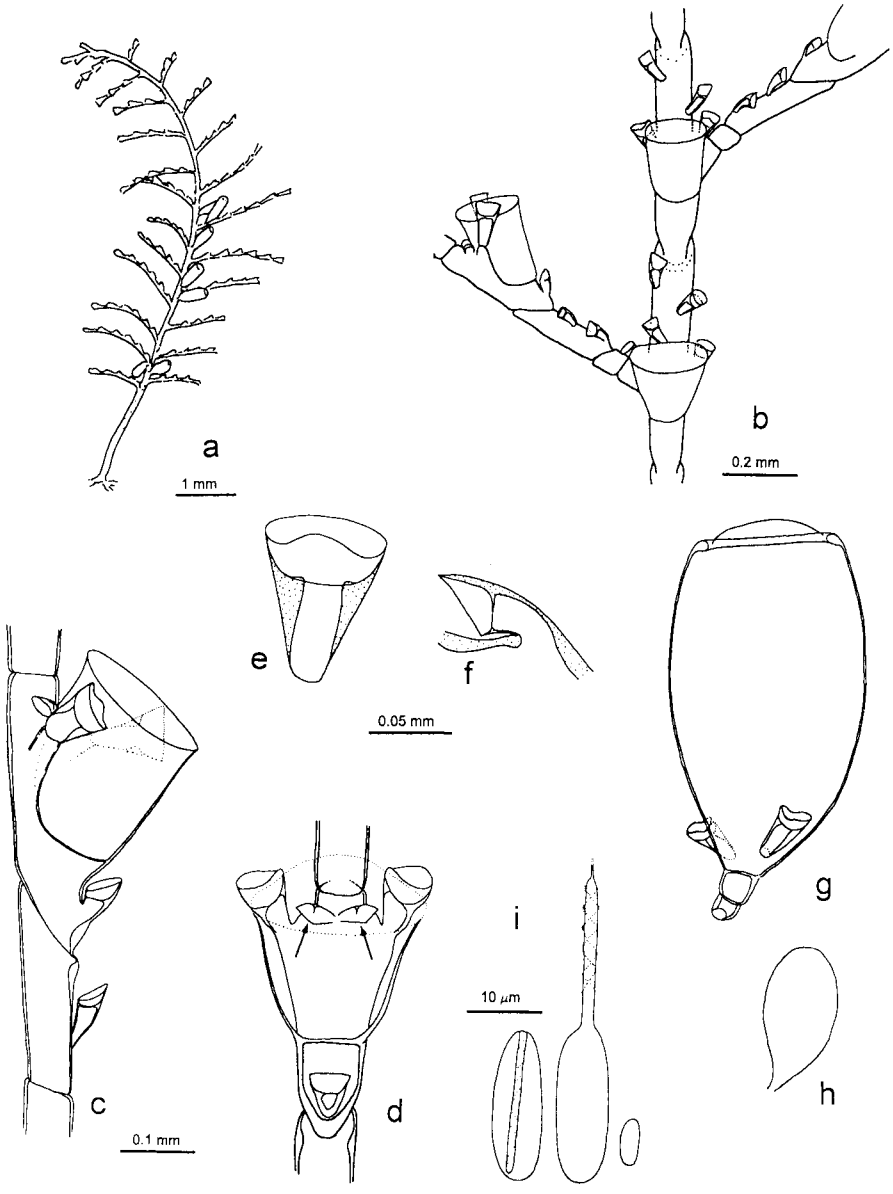

Fig. 24. *Halopteris liechtensternii* (Marktanner-Turneretscher, 1890) after material from Île de Bendor, France; a, single fertile plume; b, part of caulus with two hydrocladia; c, part of hydrocladium; d, frontal view of hydrotheca showing pair of reduced nematothecae behind hydrotheca (arrows); e, lateral nematotheca. f, median inferior nematotheca; g, female gonotheca, same scale as b; h, male gonotheca, same scale as b; i, nematocysts: undischarged and discharged microbasic mastigophore, smaller capsule from tentacles.

axillar ones, and two (up to five possible) superior ones. In the distal region of the stem, the superior nematothecae can be placed on a separate intersegment if a transverse node is present.

Hydrocladia inserted on small stem apophysis. First segment short, quadrangular, without nematothecae, second segment longer, with two nematothecae only, remaining part heteromerously segmented by alternating oblique and transverse nodes, up to six main segments per cladium. Each main segment with one hydrotheca and normally five nematothecae: one median inferior, one on each side of hydrotheca, and one pair of smaller ones in the upper axil of the hydrotheca. Intersegment with one or two median nematothecae.

Hydrothecae cup-shaped in lateral view, with straight walls, slightly widening towards margin, more or less conical in frontal view, adnate for about half the length and with free part of adcauline wall overlapping subsequent transverse node if present, opening forming an angle of 40 to 50° with axis of hydrocladium.

Nematothecae of stem and hydrocladia all two chambered. Median inferior nematotheca seated below hydrotheca and reaching approximately to level of its base; distal chamber scoop-shaped, without adcauline wall. Lateral nematothecae seated on pedicel slightly shorter than nematotheca itself, reaching level of hydrothecal rim, conical, walls straight, basal chamber longer than distal one, margin of distal chamber even or with one or two shallow emarginations on adcauline side. Paired nematothecae behind hydrotheca reduced, directed sideways, indistinctly two-chambered, scoop-shaped. Nematothecae of intersegments similar to median inferior ones, but longer.

Gonothecae of both sexes on same plume. Female gonotheca up to 1 mm long, developing on stem and hydrocladia below hydrothecae, sitting on pedicel composed of two segments, not curved, ovate with truncated distal end with thickened ring of perisarc and rounded lid; base with two nematothecae. Male gonotheca inserted on hydrocladia, smaller than female, sac-shaped, without nematothecae.

Nematocysts: a) microbasic mastigophore in nematophores, (19-20.5) × (5.5-7.0) μm, s = 0.8-1.1. b) small capsule in tentacles, (6-6.5) × (2-2.5) μm.

Colour.— Living colonies are yellow.

Variation.— Some hydrocladia are occasionally branched and may, together with *Antennella*-like form, occur in some colonies with otherwise normal plumes (Motz-Kossowska, 1908).

Type locality.— Rovigno, Adriatic Sea, Mediterranean.

Ecology.— Often present in shallow water. This is one of the few hydroids that also occur in well lighted zones.

Distribution.— Endemic to the Mediterranean; records from the Kyklades, Adriatic Sea, European coast of the western Mediterranean, Baleares, Morocco, depths from 0 to 40 m.

Remarks.— Contrary to most other descriptions, there is not a single nematotheca, but a pair behind the hydrotheca. Also the original material described by Marktanner-Turneretscher (1890) has such a pair of nematothecae. This pair is always present, but they can be reduced to a varied degree and are quite difficult to observe. They are best seen in a frontal view of material lacking soft tissue. In side view, one of the nematothecae will always hide the other and therefore give the false impression of only one nematotheca being present. Marktanner-Turneretscher (1890) used

Table 17. Variation of *Halopteris liechtensternii*, in µm if not stated otherwise.

sample no.	1	2	3	4
caulus height [mm]	17	20	16	20
max number of cladia per side	14	14	14	9
main segments	300-370	300-350	290-310	290-330
intersegments	250-300	170-220	230-260	210-280
abcauline side of hydrotheca	200-210	232-272	224-240	208-224
free adcauline side of hydrotheca	110-120	120-136	120-144	112-144
diameter of hydrotheca	190-200	190-200	180-220	180-200
max. number of hydrotheca per cladium	5	6	4	5
tentacle number	12-14	14	14	-
stolon diameter	120	170	150	140

the spelling *liechtensternii*, which is used here too. Most authors incorrectly used *liechtensterni*.

Halopteris liechtensternii resembles closely *H. polymorpha*, the more so since in the latter paired axillar nematothecae sporadically occur. *Halopteris liechtensternii* was kept separate because it has always paired axillar nematothecae and not only occasionally so as does *H. polymorpha*.

Halopteris liechtensternii has not frequently been recorded from the Mediterranean, though the author found it to be one of the most frequent shallow water thecate hydroids. The reason may be that it has often been confused with *H. diaphana*. (e.g. Gili, 1982; Riedl, 1959; Riedl, 1966). The species are superficially resembling in colony structure, but the pair of nematothecae behind the hydrotheca immediately distinguishes *H. liechtensternii* from *H. diaphana*. In the field, *H. liechtensternii* is easily distinguished from *H. diaphana* by its yellow colour, larger size, and more robust appearance. Both species often occur together.

Marktanner-Turneretscher (1890) did not designate a type specimen. As he apparently had only one specimen at his disposal, which specimen is now kept in the Natural History Museum of Vienna, this microslide is herewith designated the lectotype.

Halopteris tuba (Kirchenpauer, 1876)
(fig. 25, table 18)

Plumularia tuba Kirchenpauer, 1876: 44, pl. 1 fig. 2, pl. 4 figs 2-2d; Leloup, 1939: 12, fig. 8.
Acladia africana Marktanner-Turneretscher, 1890: 261, figs 11-11a.
Heteroplon Jäderholmi Stechow, 1912: 366, figs F-G.
Thecocaulus tuba; Bedot, 1921b: 9.
Acladia africana; Stechow, 1925b: 491.
Plumularia (Heteroplon) africana; Stechow, 1925b: 500, figs 44-45.
Halopteris tuba; Millard, 1962: 286, fig. 5; 1968: 277; 1975: 359, fig. 115A- G; 1978: 193.

Material examined.— T. Mortensen expedition station 31, described by Millard (1968), 29°54'25"S 31°09'45"E, ZMC, as *Halopteris tuba*, depth 124 m, many plumes up to 18 cm high, with female gonothecae.

Description (after examined material and Millard, 1962).— Colonies forming plumes that reach 22 cm in height.

Hydrocaulus monosiphonic, unbranched. Basal part of stem without hydrothecae or hydrocladia, with a few irregular, transverse nodes and a double row of movable nematothecae on anterior face. Basal parts end usually in one to two oblique hinge-joints. Where two hinge-joints occur segment in between bears a single median hydrotheca on anterior surface and a pair of hydrocladia arising one on each side of it, also one median inferior nematotheca and four to eight movable nematothecae irregularly arranged above hydrotheca. Remainder of stem bearing hydrothecae and hydrocladia on anterior surface, unsegmented except for extreme distal end, where regular, slightly oblique nodes may occur. First hydrotheca medially, a pair of hydrocladia arising from same level, one on each side. Thereafter hydrothecae are displaced alternately to right and left of mid-line and hydrocladia arising singly, alternately from right and left sides of hydrothecae (from right side of hydrotheca displaced towards right and vice versa). Hydrothecae and hydrocladia thus originating form two longitudinal rows on anterior surface of stem. Rarely a pair of hydrocladia arises from same level. Corresponding to each hydrotheca are five cauline nematothecae: one inferior, two laterals and two minute axillar ones. Inferior nematotheca is not situated immediately below its hydrotheca, but displaced towards opposite side of stem.

Hydrocladia up to 8 mm long with up to 20 hydrothecae. Hydrocladia inserted on short stem apophyses arising next to cauline hydrotheca, hydrothecae thus appear to be seated on apophysis. Apophyses without nematotheca, first segment of hydrocladium short, without hydrotheca, with one nematotheca. Remainder of hydrocladium homomerously segmented by oblique nodes. Only rarely intersegment without nematotheca can be delimited in distal region of hydrocladium. Each segment with one hydrotheca in about middle of segment and three nematothecae: one median inferior and two laterals. Naked nematophore in upper axil of hydrotheca; no superior nematothecae.

Hydrothecae cup-shaped, shallow, with diameter mostly exceeding depth and with smooth rim, almost cylindrical in lateral view, adnate for $^1/_3$ to $^1/_2$ of adcauline length. Hydrothecal opening at an angle of c. 50 to 60° with hydrocladium. Cauline hydrothecae with abcauline walls thickened and margin eroded, particularly on lateral and adcauline sides, so that no free part remains. Hydropore very small.

Nematothecae two-chambered with exception of cauline axillar ones which are one-chambered, spherical, and minute. Median inferior nematotheca hook-shaped, far below hydrotheca, immovable, adcauline wall of upper chamber lacking. Lateral nematothecae of hydrocladia seated on short, rounded pedicel, nematotheca long and conical, projecting beyond hydrothecal rim, with lower chamber much longer than upper one, walls straight, rim of upper chamber only slightly lowered on inner side. Lateral nematotheca of stem large, not seated on pedicel, one in axil of hydrocladium, the other separated and lateral to hydrotheca but often missing.

Gonothecae of both sexes borne on same plume or even same hydrocladium with male gonotheca being more distal than the female ones, developing below hydrothecae. Female gonotheca 2.8 to 3.6 mm long, oval, strongly flattened, with terminal aperture, with three large nematothecae near base. Pedicel of female gonotheca com-

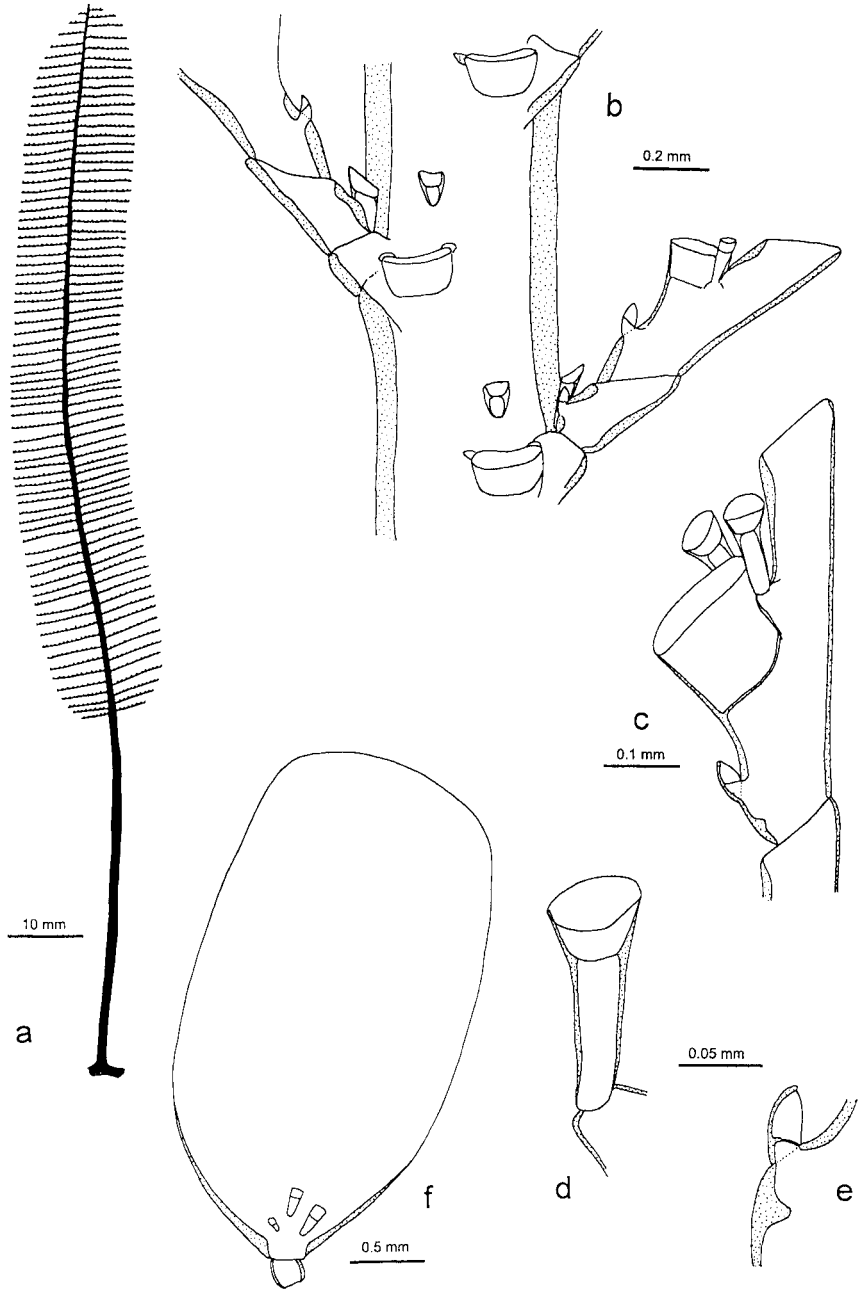

Fig. 25. *Halopteris tuba* (Kirchenpauer, 1876), after material examined; a, single plume; b, part of caulus in frontal view, note that lateral nematothecae opposite hydrocladia are absent; c, part of caulus from more distal region, lateral nematothecae (large) are still present; d, segment of hydrocladium, e, median inferior nematotheca; f, lateral nematotheca, same scale as e; g, female gonotheca.

Table 18. Dimensions *Halopteris tuba*, in µm if not stated otherwise.

sample no.	Station 31	Millard 1962
hydrocladial segments	570-580	430-640*
abcauline side of hydrotheca	90-130	120-200
free adcauline side of hydrotheca	50-70	-
diameter of hydrotheca	180-200	200-250
length of female gonotheca [mm]	3.4	2.8-3.6
nematothecae on female gonotheca	3	3
* length of posterior surface		

posed of one segment only. Only one embryo will develop per female gonotheca. Male gonotheca 0.36 to 0.44 mm long, elongated oval, with abcauline side more convex than adcauline and with distal aperture.

Type locality.— Algoa Bay, South Africa.

Distribution.— Endemic to South Africa.

Remarks.— The type material of this species has been re-examined by Leloup (1939) and the synonymy was treated by Stechow (1925b) and Millard (1962) who are followed here. *Halopteris tuba* is a characteristic species that forms the largest plumes within the genus. The cauline hydrothecae placed in a double row make it rather distinct, although *H. peculiaris* too can have the proximal cauline hydrothecae arranged in a slightly double row, but by no means as distinct as in *H. tuba*. *Halopteris tuba* is also distinguishable from *H. peculiaris* by its paired axillar nematothecae above the cauline hydrothecae. However, these are often exceedingly difficult to see with the normal, compound microscope because of the thickness of the stem. They can be seen with a good dissecting microscope though care must be taken not to confuse them with the lateral nematothecae. One of the conspicuous lateral nematothecae is displaced towards the axil of the hydrocladium, the other can be found on the other side at some distance from the hydrotheca; this nematotheca, however, is often missing. Because also the cicatrices are absent, the nematothecae must have been lost in the living colony and not through the collection procedures.

Halopteris crassa (Billard, 1911)
(figs 26-28, table 19)

Plumularia crassa Billard, 1911: 67, fig. 9; 1913: 26, fig. 17, pl. 1 fig. 18; Bedot, 1923: 220, fig. 13.
Thecocaulus heterogona Bale, 1924: 255, fig. 13 (syn. nov.); Trebilcock, 1928: 25.
Halopteris heterogona; Totton, 1930: 217, fig. 56a-d; Ralph, 1961: 45, fig. 6h-i; Rees and Vervoort, 1987: 123, 25c-d.

Material examined:

- 1) Lectotype, ZMA Coel. 4066, Siboga station 273 (Jedan Island, Aru Islands, Indonesia), depth 13 m, material described by Billard (1911, 1913) as *Plumularia crassa*, designated here the lectotype. Contains several fertile plumes and also fragments of plumes.
- 2) Syntypes of *Thecocaulus heterogona*, series of 5 slides from collection Bale, MVM F58220, all from Cape Maria van Diemen, probably all from the same colony, therefore schizosyntypes, depth 92 m.
- 3) Three Kings Islands, NW of New Zealand, NZOI station E848 (33.98°S 171.67°E), as *H. heterogona*, depth 250 m, large plume with gonothecae.

Description (after type material of *P. crassa* and *H. heterogona*).— Colony forming 4 to 6 cm, maximally 15 cm, high plumes.

Hydrocaulus robust, monosiphonic, unbranched, with basal part free of hydrocladia and with segments formed by transverse nodes. Basal part ends in two oblique hinge-joints. Above hinge-joints without segmentation in proximal part, homomerously segmented by very oblique nodes in more distal part, each segment with one hydrotheca and one hydrocladium. Hydrocladia originating on alternate sides of hydrothecae, except most proximal pair which may be opposite. Each hydrotheca associated with six to eight nematothecae: one median inferior, one pair of laterals, one small, scale-shaped axillar nematotheca, and two to six superior ones in a double row, two being the typical number. Lateral nematothecae unequally developed, with one in axil of hydrocladium being smaller. Both laterals frequently absent. Hydrothecae of stem cylindrical and inserted on conspicuous processes.

Hydrocladia inserted on short stem apophyses, developing lateral to cauline hydrothecae and displacing lateral nematotheca. First segment of hydrocladium short, without nematothecae. Second segment elongated, with one median nematotheca on upper face. Remaining part homomerously segmented by oblique nodes, up to 12 segments per hydrocladium, rarely a transverse node can delimit distally an intersegment without nematotheca. Segments with four nematothecae: one median inferior, one pair of laterals and a reduced, scale-shaped nematotheca in upper axil of hydrotheca, occasionally much reduced or present as naked nematophore with nematocysts.

Hydrotheca cup-shaped, rim not reaching beyond node, abcauline and adcauline walls straight in lateral view, converging proximally. Hydrotheca adnate for $^2/_3$ of adcauline length, angle of opening with hydrocladial axis 40 to 50°.

Nematothecae of stem and hydrocladia all two-chambered, except axillar ones. Median inferior nematothecae not reaching hydrotheca; adcauline wall of upper chamber lacking. Lateral nematothecae on pedicels of similar height as nematotheca itself, reaching to or beyond rim of hydrotheca, mobile, shape conical, wall of upper chamber only slightly rolled inwardly or straight, upper chamber deep, as long as lower one, margin of upper chamber on inner side with broad notch that may reach bottom of chamber.

Gonothecae of both sexes on same plumes. Female gonotheca inserted singly below side of cauline hydrothecae. Male gonothecae develop on hydrocladia in corresponding position as female ones. Female gonothecae with pedicel composed of two segments, 2 to 2.5 mm long, flattened, with tapering base and truncated end, base with two to five large nematothecae. Male gonothecae small, sac-shaped, with small, distal aperture, 0.3 to 0. 5 mm long, with indistinct one- segmented pedicel with or without a nematotheca.

Variation.— The small nematotheca in the upper axil of the hydrotheca can be reduced to a varied degree, often only a naked nematophore is present. In the material from Three Kings Islands the lateral nematothecae are very short and immovable, the hydrocladia lack segmentation.

Type locality.— Jedan Island, Aru Islands, Indonesia

Distribution.— Indonesia, North Cape of New Zealand.

Remarks.— After examination of type material of the nominal species *Plumularia*

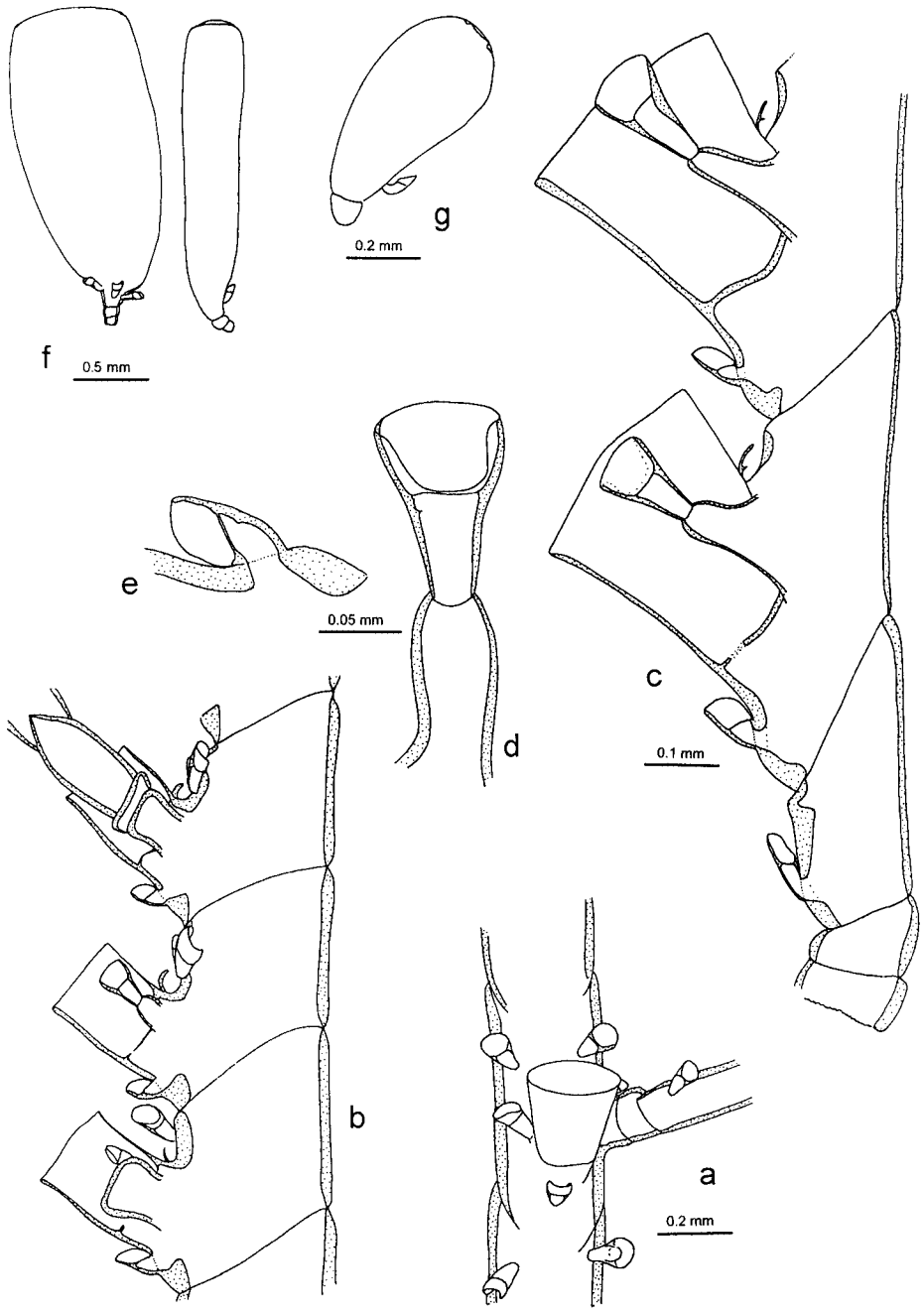

Fig. 26. *Halopteris crassa* (Billard, 1911); after type material of *P. crassa* Billard, 1911; a, anterior view of stem with base of one hydrocladium; b, lateral view of stem, hydrocladia only partially shown; c, proximal part of hydrocladium; d, lateral nematotheca; e, median inferior nematotheca; f, female gonotheca in frontal view (left) and lateral view (right); g, male gonotheca, note different scale in f.

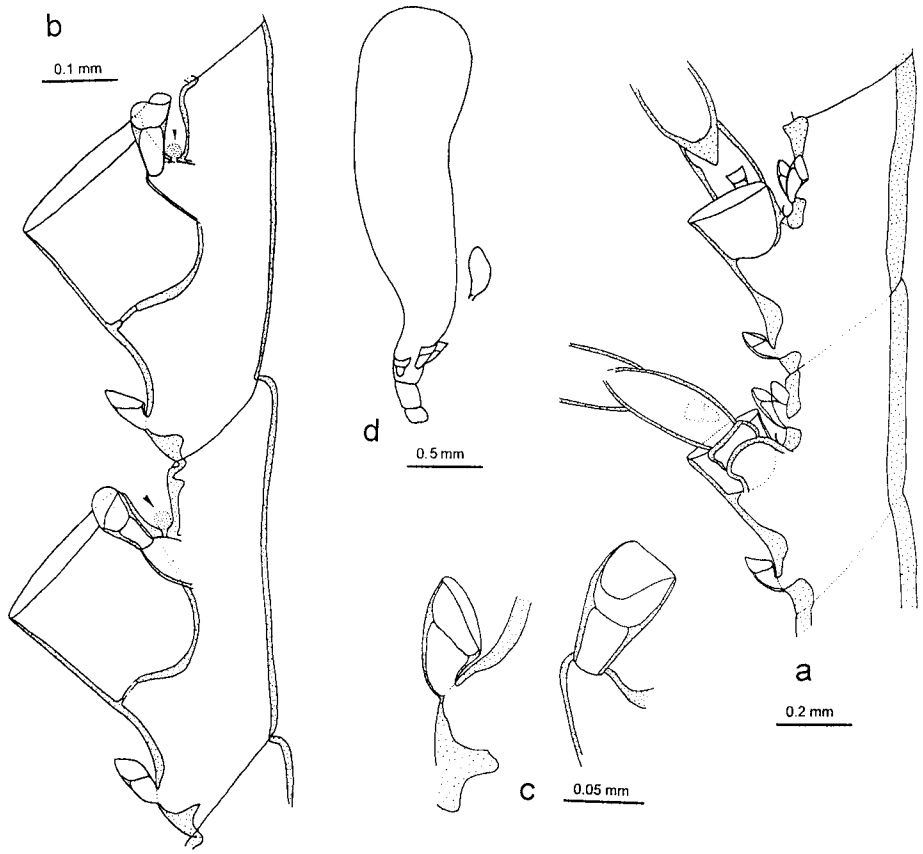

Fig. 27. *Halopteris crassa* (Billard, 1911); after type material of *Thecocaulus heterogona* Bale, 1924; a, segmented part of stem with proximal parts of two hydrocladia, note absence of lateral nematothecae; b, part of hydrocladium, arrowheads point towards naked nematophore in upper axil of hydrotheca; c, median inferior and lateral nematothecae of hydrocladial segments; d female (left) and male gonotheca (right).

crassa Billard, 1911 and *Thecocaulus heterogona* Bale, 1924, it became evident that both are identical (figs 26 & 27). The only noticiable difference was the absence of lateral nematothecae of the cauline hydrothecae in the type material of *T. heterogona*. These lateral nematothecae, however, have been observed by Totton (1930) and he pointed out that they are frequently absent in more proximal parts of the stem. Also in the type material of *H. crassa*, these lateral nematothecae are often missing. In the type material of *H. heterogona*, no axillar nematotheca is visible above the hydrothecae of the hydrocladia. However, there is a distinct nematophore. Because Totton (1930) observed an axillar nematotheca in material originating from close to the type locality of *T. heterogona* (see also figure 25d in Rees & Vervoort, 1987), the presence of such a nematotheca must be variable, as is also the presence of nematothecae lateral to the cauline hydrothecae. No nematothecae could be found on the male gonothecae in the type material of *T. heterogona*. This need not to be a real difference as they might have been lost. The female gonothecae had rather crumpled walls, which indicates that

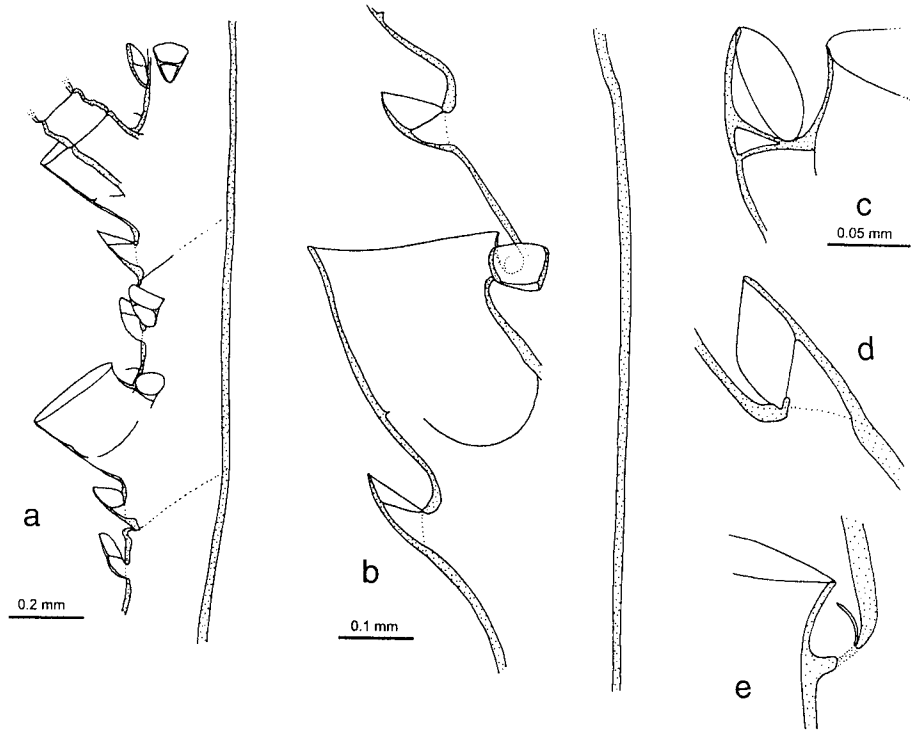

Fig. 28. *Halopteris crassa* (Billard, 1911); after material from Three Kings Islands; a, lateral view of caulus with proximal parts of two hydrocladia; b, part of hydrocladium; c, lateral nematotheca; d, median inferior nematotheca; e, upper axil of hydrotheca with scale-shaped axillar nematotheca.

their wall is thinner than in the type material of *H. crassa*. The hydrothecae of *P. crassa* are larger than those of *T. heterogona*, which is, however, of little significance for separating the species (see also table 19).

The type material of *H. crassa* and of *T. heterogona* presents unique characters and is easily separable from most other species, except perhaps *H. peculiaris*. The homomerous segmentation of the hydrocladia and the lack of a superior nematotheca make it quite distinct. Only quite rarely the type material of *T. heterogona* has an intersegment intercalated between two main segments. No nematothecae could be observed on such intersegments.

Halopteris crassa is only separable from *H. peculiaris* by the complete absence of nematothecae above the cladial hydrothecae. This character is rather variable in *H. peculiaris* and it could well be that *H. crassa* represents only an extreme form of *H. peculiaris*. For further discussions see under the latter. *Halopteris tuba* also resembles *H. crassa*, but the former is characterised by cauline hydrothecae in a double row and two axillar nematothecae above the cauline hydrothecae (see also table 14).

The material from near the Three Kings Islands (fig. 28) differs markedly from the other material, though it was taken in the vicinity of the type locality of *H. heterogona*, however, in much deeper waters. Its hydrocladia lack any segmentation and the lateral nematothecae are very short, the lower chamber being almost absent (fig.

Table 19. Dimensions *Halopteris crassa*, in µm if not stated otherwise.

sample no.	1	2	Ralph, 1961
caulus segments	610-680	640-760	600-750
hydrocladial segments	600-640	550-620	450-600
abcauline side of hydrotheca	260-290	160-170	160
free adcauline side of hydrotheca	130-150	50-70	80
diameter of hydrotheca	220-260	210-230	125
length of female gonotheca [mm]	2.0	2.5	2.2-2.5
nematothecae on female gonotheca	2-5	2-3	3-5
nematothecae on male gonotheca	1	0	0

28c). The nematothecae seem to be immovable. Its female gonotheca has a length of about 2.2 mm and bears five nematothecae.

Halopteris peculiaris (Billard, 1913)
(figs 29-30, table 20)

Plumularia buski var. *peculiaris* Billard, 1913: 23, fig. 12, pl. 1 fig. 17.
Plumularia alternata; Jarvis, 1922: 345, pl. 25 fig. 16 (in part, after Millard, 1962).
Halopteris glutinosa; Millard, 1958: 200, fig. 10A-D; 1962: 285, fig. 4K; 1968: 276; 1975: 352, fig. 113A-F; 1978: 193 [not *Halopteris glutinosa* (Lamouroux, 1816)].
Not *Halopteris glutinosa*; Schmidt, 1971: 38 [= *H. platygonotheca*].
Plumularia buski var. *peculiaris*; ?Redier, 1966: 90, pl. 2 figs 2 & 4; Rees & Vervoort, 1987: 123.
Halopteris buskii; Rees & Vervoort, 1987: 119, fig. 24, tab. 23 (in part, only material from station 111).

Material examined:
- 1) Lectotype, ZMA Coel. 4072, as *Plumularia buskii* var. *peculiaris* Billard, 1913; Siboga station 99 (6°7.5'N 120°26'E, Borneo, Indonesia), depth 16-23 meters, *Lithothamnion* substrate, one large colony with several plumes up to 7 cm high, with male and female gonothecae, designated here lectotype of *Halopteris peculiaris*.
- 2) Siboga station 99 (6°7.5'N 120°26'E, Borneo, Indonesia), ZMA Coel. 5242, as *Plumularia buskii* var. *peculiaris* Billard, 1913, one plume.
- 3) Lizard Island, N. point, Australia, RMNH Coel 12043, as *Halopteris buskii*, depth 5 m, coll. A. Svoboda, 6.viii.1976, colony with numerous plumes reaching 4.5 cm, male and female gonothecae present.
- 4) South Africa (32°50'S 28°18.5'E), SAM H-278, depth 86 m, described by Millard (1962) as *Halopteris glutinosa*, slide and alcohol material, many plumes up to 18 cm high, with female gonothecae.

Description (based on lectotype material).— Colony forming 7 cm high plumes arising from tubular stolons.

Hydrocaulus thick (up to 0.4 mm), monosiphonic, occasionally branched, with basal part free of hydrocladia and with many segments formed by transverse nodes. Basal part ends in oblique hinge-joint. Hydrocaulus above basal part not segmented over major part, only distally with homomerous segmentation by oblique nodes. Hydrocladia inserted on alternate sides of hydrothecae, except most proximal pair which can be opposite, with up to 60 rather tightly packed hydrocladia per side. Hydrothecae may form a double row in lower parts of stem. Each hydrotheca with six to seven nematothecae: one median inferior, one pair of laterals, one small axillar

nematothecae and two or three superior ones in a double row; lateral nematothecae comparatively small. Hydrothecae of stem cylindrical, some eroded.

Hydrocladia placed on short apophyses developing lateral of cauline hydrothecae. Hydrocladia up to 4 mm long with up to eight hydrothecae. First segment short, without nematothecae. Second segment elongated, with one median nematotheca. Remaining part of hydrocladia subdivided by oblique nodes and irregular transverse nodes. Intersegments often present, but often also fused to main segment without indication of a node. Each hydrotheca with at least four nematothecae: one median inferior, one pair of laterals and a reduced, scale-shaped axillar nematotheca. Intersegments, or their homologue if fused to main segment, only in c. 30% of all cases with a nematotheca.

Hydrotheca cup-shaped, abcauline and adcauline walls straight in lateral view and converging proximally, rim even. Hydrotheca adnate for half of adcauline length, angle of opening with hydrocladium 40 to 50°.

Nematothecae of stem and hydrocladia all two-chambered, except those in upper axil of hydrotheca. Median inferior nematothecae do not reach hydrotheca, adcauline wall of upper chamber lacking. Lateral nematothecae on pedicels of similar height as nematotheca itself, reaching to or beyond rim of hydrotheca, movable, conical, upper chamber as deep as lower one, wall of upper chamber slightly rolled inwardly or straight, inner side of upper chamber with broad emargination, outer side with shallow emargination or even.

Gonothecae of both sexes on same plume. Female gonothecae arise singly below side of stem hydrothecae; male gonothecae develop on hydrocladia below hydrothecae. Female gonotheca with pedicel composed of two segments, 2 mm long, flattened, with tapering base and truncated end with lid, and with two or three large nematothecae near base. Male gonotheca 0.4 mm long, oblong, with small distal aperture, one nematotheca near base, and with one-segmented pedicel.

Variation.— In the South African material the height of the stem ranges between 1.5 and 18 cm, the female gonothecae reach a length of 3.8 mm, zero to six superior nematothecae occur above the cauline hydrothecae, the lateral nematothecae have walls more strongly rolled inwardly (see fig. 30), the size of the hydrothecae can be much larger, and the percentage of presence of superior nematothecae on the hydrocladia is extremely variable. The female gonotheca may bear two to five nematothecae (after sample no. 4 and Millard, 1975).

Type locality.— 6°7.5'N 120°26'E (near Borneo, Indonesia), depth 16 to 23 meters, on *Lithothamnion* grounds.

Distribution.— Borneo, Lizard Island, South Africa from Still Bay to Mozambique, littoral to 411 m.

Remarks.— The material described by Billard (1913) as *Plumularia buski* var. *peculiaris* was conceived as distinct from *H. polymorpha* (which includes Billard's *P. buskii*) and described here as a separate species. *Halopteris peculiaris* differs distinctly from *H. polymorpha* by having thicker and taller plumes (up to 7 cm in the type material, cf. figs 21a and 29a). The height of the plumes is c. three times that of *H. polymorpha*, although the latter can exceptionally also reach that size. More importantly, the female gonotheca is much larger (2 mm compared to 0.7 mm in *H. polymorpha*). The intersegments of the hydrocladia, or their homologues if fused to the main segments, often lack a nematotheca, otherwise there is only a single one (see also table 14).

Halopteris peculiaris, however, agrees in many details with *H. crassa*, especially in the characters of the caulus (size, segmentation, nematothecae) and the female gonothecae (see figs 27-30). Also the hydrocladia agree to some extent, however, the superior nematothecae are present in one-third of all hydrothecae inspected, frequently even placed on a separate intersegment. Besides this difference, Billard (1913) kept var. *peculiaris* separate from *P. crassa* on account of the smaller size of the

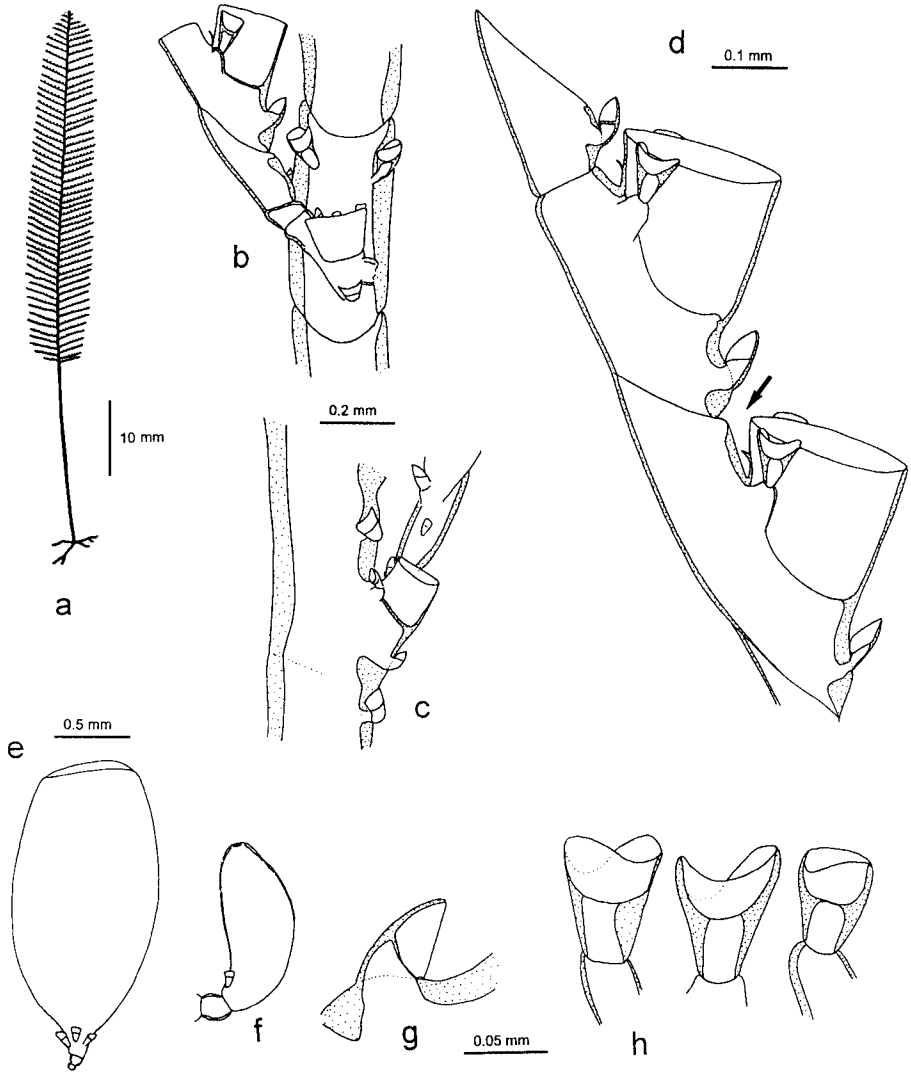

Fig. 29. *Halopteris peculiaris* (Billard, 1913); after lectotype; a, single plume; b, part of caulus in frontal view with one hydrocladium; c, part of caulus in lateral view, segmentation is almost completely reduced, same scale as b; d, part of hydrocladium, note absence (arrow) or presence of nematothe ca or intersegment; e, female gonotheca in frontal view; f, male gonotheca, same scale as b, note that e is drawn at a different scale; g, median inferior nematotheca; h, several lateral nematothecae that show extent of shape variation, same scale as g.

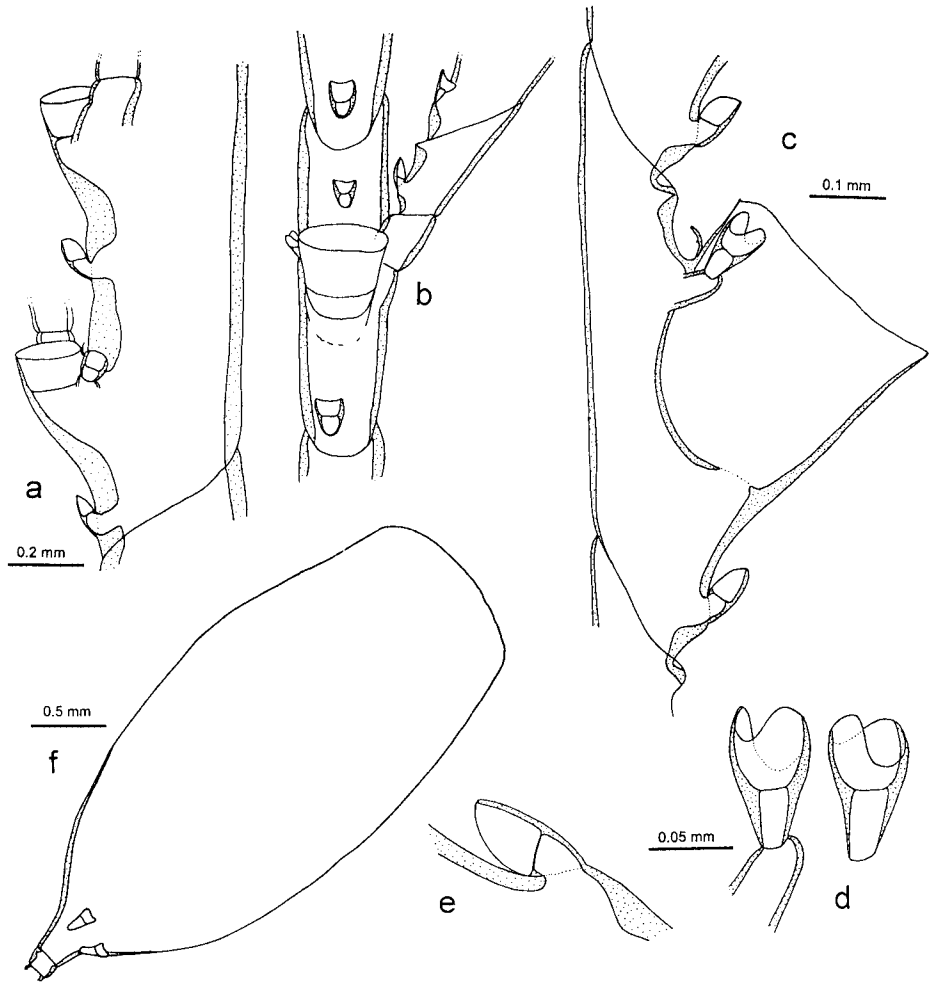

Fig. 30. *Halopteris peculiaris* (Billard, 1913); after material from South Africa (sample no. 4); a, part of caulus in lateral view, segmentation is much reduced; b, hydrocaulus in frontal view in more distal part; c, segment of hydrocladium, note absence of intersegments and superior nematotheca (besides axillar one); d, two lateral nematothecae; e, median inferior nematotheca, same scale as d; f, female gonotheca, note large size.

hydrothecae and the more reduced superior nematothecae. With the inclusion of the material from New Zealand (formerly recorded as *H. heterogona*), the last argument becomes invalid, as the axillar nematotheca can be reduced to a varied degree. The size of the hydrothecae also varies considerably in most species of *Halopteris*, including *H. crassa*, and is generally not accepted for species discrimination. Thus, *H. peculiaris* is kept separate from *H. crassa* only on account of the variable presence of intersegments and superior nematothecae. In *Halopteris crassa* superior nematothecae are always absent.

The material described by Millard (1958, 1962, 1975) as *Halopteris glutinosa* resembles closely *H. peculiaris* and is here assigned to that species. For this study, one of

Table 20. Dimensions *Halopteris peculiaris*, in µm if not stated otherwise.

sample no.	1	4	Millard, 1958	Rees & Vervoort, 1987*
max. caulus height [mm]	70	180	17	30
caulus diameter [mm]	0.4	-	0.13-0.26	0.27-0.32
hydrocladial main segments	320-360	610-830	210-540	495-580
hydrocladial intersegments	230-250	fused	60-330	included above
abcauline side of hydrotheca	200	290-300	150-260	175-200
free adcauline side of hydrotheca	89-90	80-110	80-135	-
diameter of hydrotheca	200-210	300-320	185-290	220-235
max. length female gonotheca [mm]	1.9	3.8	-	-

* only material from station 111

Millard's samples (SAM H-278) could be re-examined (fig. 30). The material consists of large plumes (18 cm) and their hydrocladia mostly lack either intersegments or superior nematothecae (besides the axillar one). Only rarely a small superior nematotheca is present. It thus appears to be almost identical with *H. crassa*, only differing in the lack of the pair of cauline, superior nematothecae. Millard (1962) accurately figured the variability of this species and found absence or presence of intersegments and arrangement of nematothecae highly variable within and between colonies. Millard (1975) considered the shape of the lateral nematothecae as characteristic for her material. A comparison with the Pacific material nevertheless shows that they are within the acceptable range of shape variation (cf. figs 29h and 30d)

The colony from Lizard Island (Great Barrier Reef, sample no. 3) deviated most. It had fewer hydrocladia and the intersegments or superior nematothecae were often lacking, but the majority of main segments was either followed by an intersegment with a nematotheca or had a superior nematotheca if a transverse node was absent. The female gonotheca was also smaller (1.5 mm) than in the other material, but it had three nematothecae and a pedicel composed of two segments. It thus comes quite close to *H. polymorpha*.

The account of variability in presence or absence of a superior nematotheca or intersegments given here makes it clear that the type material of *H. crassa* and also the material of *H. heterogona* are probably only extreme forms of a variable species that can lack superior nematothecae and intersegments to a varied degree. This variability makes this species also difficult to separate from *H. polymorpha*, if they are separate species at all. Both species are here separated on account of the regular presence of superior nematothecae in *H. polymorpha*, the generally larger and thicker stems of *H. peculiaris*, and the size of the female gonotheca, which in *H. peculiaris* is much larger (table 14). These are arguably unreliable characters and other systematist might chose to combine either *H. peculiaris* with *H. polymorpha* as Billard (1913) and Rees and Vervoort (1987) did, or combine all in one taxon. However, it is argued that the separation used here is the best interim solution until more material, and hopefully also population genetic studies, provide further and more reliable arguments.

Halopteris glutinosa (Lamouroux, 1816) (fig. 31)

Aglaophenia Glutinosa Lamouroux, 1816: 171; Van Praët, 1979: 908, fig. 94.
Plumularia glutinosa; Billard, 1909: 327; 1910: 36, fig. 16.
Not *Plumularia (Heteroplon) glutinosa;* Stechow, 1925b: 502.
Not *Halopteris glutinosa;* Millard, 1962: 285, fig. 4K; 1968: 276; Schmidt, 1971: 38; Millard, 1975: 352, fig. 113A-F; 1978: 193 [all *H. peculiaris*].
Not *Halopteris glutinosa;* García-Corrales et al., 1978: 40, fig. 17.

Material examined.— Schizoholotype of *Aglaophenia glutinosa*, MNHN slide L1249, slide prepared by Billard (1909, 1910) from part of dried plume of Lamouroux' collection.

Description (after Lamouroux, 1816 and type material).— Colonies forming plumes 6 to 8 cm high, original colour intensively red.

Stems homomerously segmented, nodes oblique. Each segment with a hydrotheca, hydrocladium, and six nematothecae: one median inferior, a pair of laterals, one axillar, and two superior ones in lateral positions.

Hydrocladia alternate, inserted on apophyses lateral to stem hydrothecae, first segment elongated, with median nematotheca, remainder of hydrocladium mostly homomerously segmented, all repeats of similar length, nodes oblique, occasionally a transverse node delimits an intersegment from a main segment. Each hydrotheca surrounded by up to five nematothecae: one median inferior, a pair of laterals, possibly an axillar one, and at least sometimes a median superior one.

Nematothecae two-chambered, median inferior immovable, curved, adaxial side missing. Lateral nematothecae placed on pedicel, conical, walls mostly straight, with deep emargination on inner side.

Gonothecae unknown.

Type locality.— 'Mers des Indes et de l'Australasie', collected by Péron & Lesueur (Lamouroux, 1816).

Remarks.— The only type material left of Lamouroux' *Aglaophenia glutinosa* is a slide made by Billard (Van Praët, 1979). This slide was made from the original type specimen, later destroyed by fire during World War II. Because the original material was a dried herbarium specimen, the quality of the slide is poor and does not allow detailed observations. The preparation is much crumpled and tangled. Therefore, it is not entirely clear whether or not a superior nematotheca occurs above the cladial hydrothecae. Billard (1913) stated that there are no such axillar nematothecae. Although it is nearly impossible to make reliable observations on the material, in some cases putative axillar nematothecae could be seen. However, the presence of an axillar nematotheca above the cauline hydrothecae is quite certain. With our present knowledge, *H. glutinosa* could either be conspecific with *H. polymorpha*, *H. peculiaris*, or *H. buskii*. The rather uniform length of the hydrocladial segments argues against *H. peculiaris*, and the size of the plume makes *H. buskii* the most likely guess. After Lamouroux (1816), his material of *H. glutinosa* was provided by Péron & Lesueur, being predominantly dredged (!) material from southern Australia (Wallace, 1984). Also the red colour of the plumes (Lamouroux, 1816) strongly argues in favour of this interpretation. However, because insufficient reliable information is available, notably on the female gonotheca, the species is here kept separate. If the origin of the

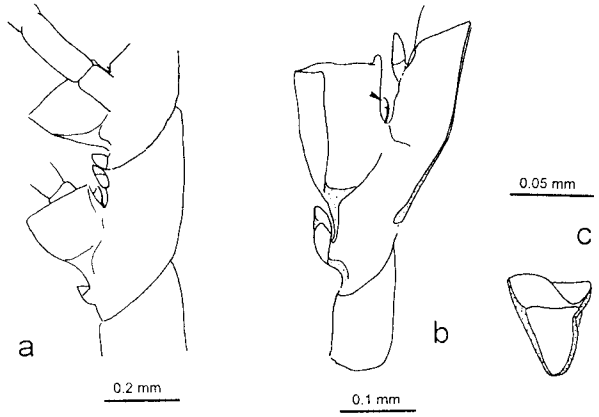

Fig. 31. *Halopteris glutinosa* (Lamouroux, 1816) after schizoholotype material; a, part of stem in lateral view; b, part of hydrocladium, hydrotheca folded, note putative axillar nematotheca (arrowhead); c, lateral nematotheca.

type material can reliably be traced down to southern Australia, *H. buskii* could possibly be synonymised with *H. glutinosa*.

Billard (1909, 1910) synonymised *Halopteris glutinosa* with *Heteroplon pluma* Allman, 1883, which is here considered to be conspecific with *H. buskii*. Billard (1913) stated that both *H. glutinosa* and *H. pluma* lack axillar nematotheca. However, in the type material of *H. pluma* Allman, 1883 available for this study (fig. 19), such axillar nematothecae are present and the material is indistinguishable from the type material of *H. buskii*. *Heteroplon pluma* Allman, 1877, therefore, is referred to *H. buskii* (see also discussion under *H. buskii*, p. 62-64).

Stechow (1925b) applied the name *Plumularia glutinosa* to some material from South Africa and Millard (1958, 1962, 1968, 1975) later followed him in using that name. However, the South African material is here referred to *H. peculiaris* (see discussion p. 87).

Halopteris minuta group

Remarks.— This possibly natural assemblage contains *H. minuta, H. everta, and H. pseudoconstricta*. The characters used to distinguish these species are given in table 21.

Table 21. Distinguishing characters of the *Halopteris minuta* group.

species	*Halopteris minuta*	*Halopteris everta*	*Halopteris pseudoconstricta*
superior nematotheca on cauline main segments	often present, not axillar	always present axillar	always present, not axillar
hydrothecae with abcauline ridge	no	yes	no
curvature of abcauline side of hydrotheca	moderate	strong	moderate, often with internal cusp
stolons with internal pegs	yes	yes	no
shape of female gonotheca	s-shaped	unknown	semi-circular

Halopteris minuta (Trebilcock, 1928)
(fig. 32, table 22)

Thecocaulus minutus Trebilcock, 1928: 25, pl. 7 figs 6-6a.
Halopteris constricta Totton, 1930: 217, fig. 56a (syn. nov.); Ralph, 1961: 43, fig. 6a-e.
Halopteris minuta; Ralph, 1961: 45, fig. 6f.
Not *Halopteris constricta;* Millard, 1957: 227, fig. 14a [= *H. pseudoconstricta*].
Not *Halopteris constricta;* Vervoort & Vasseur, 1977: 68, figs 29, 30a-b.
Not *Halopteris constricta;* Park, 1990: 83 fig. 5 [= *H. diaphana* (Heller, 1868)].

Material examined.
- 1) Syntype material of *Thecocaulus minutus* (see Stranks, 1993), MVM F57899, two slides from Trebilcock's collection, from St. Clair (Dunedin, New Zealand), Apr.-May 1923.
- 2) Wellington, Barretts Reef, New Zealand, several fertile plumes collected 14.xii.1994 by author, depth 10 m, slide in collection of author.
- 3) Moorea Atoll, RMNH Coel. 11608 and 11609 (described by Vervoort & Vasseur, 1977), labelled *Halopteris constricta.*

Description.— Colony forming up to 9 mm high plumes arising from creeping, ramified stolons. Stolons flattened strap-like, bearing tubular nematothecae and strengthened internally by chitinous pegs (after Ralph 1961).

Stem monosiphonic, unbranched, with basal part ($^1/_6$) devoid of hydrothecae and hydrocladia and longer distal part bearing hydrothecae and hydrocladia. Basal part divided into segments by two or three straight nodes, last node ending in oblique hinge-joint, segments with one nematotheca. Stem above basal part heteromerously segmented by alternating, oblique and transverse nodes, all nodes distinct. Main segments of stem bear one hydrocladium on alternate sides. Main segments with hydrotheca and three or four nematothecae: one median inferior, one pair of laterals, and sometimes one behind adcauline wall of hydrotheca, but distal to axil. Intersegments with one or two nematothecae.

Hydrocladia inserted on well-formed apophyses lateral of cauline hydrothecae. Apophysis without nematotheca. First segment of hydrocladium mostly elongate, longer than wide, often with indicated partition into two parts of equal size, without nematotheca. Second segment up to two times as long as first, with one median nematotheca on upper side. Remaining part of hydrocladia organised as in caulus with up to three hydrothecae. Thickness of perisarc variable, but no internal ridges or septae present in individual segments. Main segments with three nematothecae: one median inferior and a pair of laterals. Nematotheca behind hydrothecae absent. Intersegments occasionally divided into two segments with the more proximal lacking a nematotheca.

Hydrotheca cup-shaped, rim in many cases not reaching beyond distal end of segment, occasionally slightly flared, abcauline wall almost straight, adcauline wall often with slight concavity in upper half. Hydrotheca adnate for half of adcauline length, angle of aperture with hydrocladium 40 to 50°.

Nematothecae of stem and hydrocladia all two-chambered. Median inferior nematotheca mostly not reaching hydrotheca, with short adcauline wall partly fused to hydrocladium. Lateral nematothecae on pedicels which are slightly shorter than nematotheca itself, reaching almost to rim of hydrotheca, mobile, conical, walls straight,

lower chamber slightly longer than upper one, margin of upper chamber lowered on inner side for about half its height. Nematothecae of intersegments and occasional superior ones on caulus similar to basalmost median inferior ones, but with longer free adcauline wall and mobile.

Female gonotheca inserted singly or in opposite pairs below hydrothecae of stems or occasionally singly in similar position on hydrocladia, pedicel composed of two quadrangular segments. Gonotheca up to 0.8 mm long, ovate, axis s-shaped, aperture facing away of stem. Gonothecal base with an intragonothecal septum and thickened lateral walls, below septum two conical nematothecae. Male gonothecae unknown.

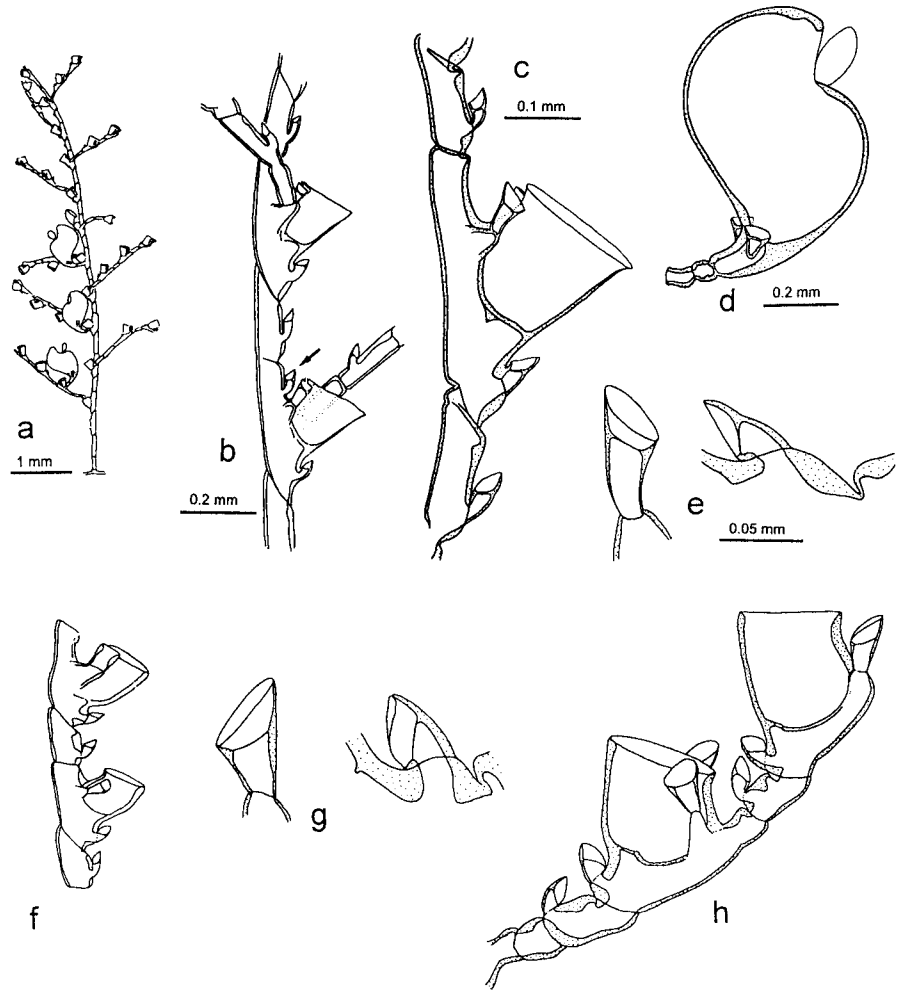

Fig. 32. *Halopteris minuta* (Trebilcock, 1928); a-e material from Wellington, f-h from syntype material of *T. minutus*; a, whole plume with gonothecae; b, part of stem with proximal parts of hydrocladia, arrow points to nematotheca on distal part of main segment; c; part of hydrocladium; d, gonotheca, note characteristic shape; e, lateral and median inferior nematothecae; f, part of hydrocaulus, same scale as b; g, lateral and median inferior nematothecae; h, whole hydrocladium, same scale as c.

Variation.— The first pair of hydrocladia may be opposite (Ralph 1961). The walls of the hydrothecae may be thickened to a varied degree.

Type locality.— St. Clair, Dunedin, New Zealand.

Distribution.— New Zealand (Ralph, 1961); ? Moorea, Tahiti (Vervoort & Vasseur, 1977).

Remarks.— When establishing *Halopteris constricta*, Totton (1930) did not discuss its relationship with *Thecocaulus minutus* Trebilcock, 1928, although he cites Trebilcock's study. Ralph (1961) admitted the strong similarity of *H. constricta* and *H. minuta* (= *T. minutus*) and thought that they might prove to be conspecific. However, she kept both species separate on account of the following differences: *H. minuta* has i) shorter intersegments, ii) thickened walls of the hydrothecae, and iii) a lower length/diameter ratio of the hydrothecae. The last argument was found to be invalid after the examination of the material of the present study. Thickened walls of the hydrotheca seem also to be present in some specimens referable to *H. constricta*, namely in the type material (see Totton 1930: fig. 56a; Vervoort & Vasseur, 1977: fig. 30b). Ralph's (1961) figures also do not depict such a difference. The only character left would be the shorter intersegments. However, intersegment length can vary considerably in other species (cf. e.g. *A. quadriaurita* in Millard, 1977). Therefore, *Halopteris constricta* is seen here as a slightly larger and more elongate form of *H. minuta*. *Halopteris constricta* thus becomes a junior synonym of *H. minuta*. Another fact arguing for this interpretation is the special hydrorhiza that was described by Ralph (1961) as being identical in both nominal species. Ralph (1961) describes and figures the stolons as strap-like structures with many internal pegs and provided with nematothecae.

Only a few, mostly infertile samples of *Halopteris constricta* have been described so far. Gonothecae are not known for material assigned earlier to *H. minuta*. The new sample from Wellington used in this study had many female gonothecae and agrees in most aspects with the description of *H. constricta* as given by Ralph (1961). The only difference is the absence of a nematotheca on the apophysis of the stem. Such a nematotheca, however, is also absent in the type material of *H. constricta* (Vervoort & Vasseur 1977). Contrary to the observations of Vervoort and Vasseur (1977), there may occasionally be a nematotheca behind the stem hydrothecae. This, however, is variable even within one colony, and the nematotheca is not situated in the axil of the hydrotheca (fig. 32b, arrow). Such a nematotheca is also figured by Vervoort & Vasseur (1977: fig. 30b, holotype material of *H. constricta*).

Millard (1957, 1962, 1966) referred samples from South Africa to *H. constricta*. Because the South African material has differently shaped gonotheca, Millard later (1975) assigned this material to the new species *H. pseudoconstricta*. African records of this *H. constricta* are therefore not included here. Already Millard (1975) noted that *H. constricta* and *H. pseudoconstricta* are hardly identifiable without knowing the female gonotheca. This also holds true for several other species, e.g. in the *H. diaphana* group. Therefore, all records of sterile material for these species should be treated as doubtful. The material assigned to *Halopteris constricta* by Vervoort & Vasseur (1967) from French Polynesia was re-examined for this study. It is all infertile and therefore not correctly identifiable. Moreover it differs from *H. constricta* by the horizontal nodes that are below and not above the level of the hydrothecal rim, the segments

Table 22. Variation and dimensions of *Halopteris minuta*, in µm if not stated otherwise.

sample no.	1	2
caulus height [mm]	6	8
max. number of cladia per side	4	5
hydrocladial main segments	230-240	290-380
hydrocladial intersegment	80-110	130-250
first cladial segment	50-110	70-100
second cladial segment	110-150	150-200
abcauline side of hydrotheca	130-150	150-160
free adcauline side of hydrotheca	50-70	70-90
diameter of hydrotheca	140-150	150
max. number of hydrothecae per cladium	2	3
tentacle number	-	12-14

are shorter, the caulus is almost homomerously segmented, and the stolons are tubular. Therefore this sample is probably a different species and the record of *H. constricta* for Moorea is considered dubious here.

The record of *H. constricta* from Korea by Park (1990) is based on a misidentification and the material is here tentatively assigned to *H. diaphana*.

Halopteris everta (Mulder & Trebilcock, 1909) (fig. 33, table 23)

Plumularia everta Mulder & Trebilcock, 1909: 31, pl. 1 fig. 5.

Material examined.

- 1) Two syntype slides MVM F57965, ex. collection Trebilcock no. 26 (see Stranks, 1993), labelled as types on original labels, includes also hydrorhiza.
- 2) MVM slide F57983, labelled *Plumularia campanulaformis* var. *dubia*, type, contains also one plume of *H. everta*, ex. collection Trebilcock, original label indicates presence of *P. everta* no. 26, locality ?

Description.— Colony forming up to 6 mm high plumes arising from creeping, ramified stolons. Stolons flattened and strengthened internally by regular chitinous pegs, with conical nematothecae.

Stem monosiphonic, unbranched, with basal part (1/4) devoid of hydrothecae and hydrocladia and longer distal part bearing hydrothecae and hydrocladia. Basal part divided into segments by two or three straight nodes, last node ending in oblique hinge-joint. Stem above basal part heteromerously segmented by alternating oblique and transverse nodes. Transverse nodes sometimes indistinct in proximal region of plume. Main segments with one hydrocladium on alternate sides, one hydrotheca, and four nematothecae: one median inferior, one on each side of hydrotheca and invariably one in axil of hydrotheca. Intersegments with one nematotheca.

Hydrocladia inserted on well-formed stem apophysis, developed laterally of hydrotheca. Apophysis without nematotheca. First segment quadrangular to elongate, often with indicated partition into two parts of equal size, without nematotheca. Second segment up to two times as long as first, with one median nematotheca

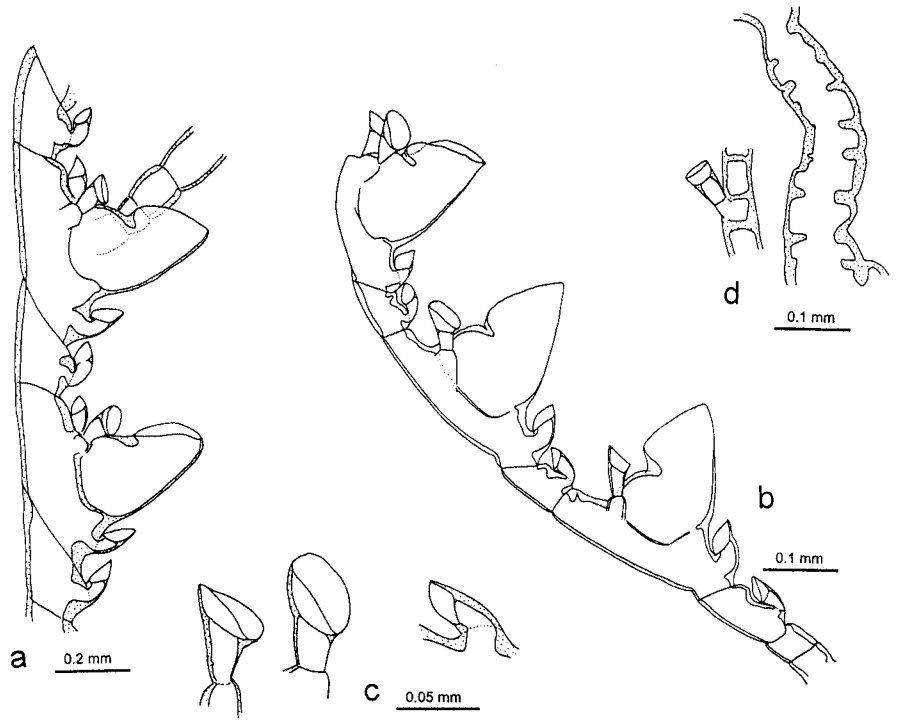

Fig. 33. *Halopteris everta* (Mulder & Trebilcock, 1909); after syntype material; a, part of stem with proximal part of one hydrocladium (upper repeat), note presence of single nematotheca above hydrothecae; b, hydrocladium; c, nematothecae, left: two lateral ones seen from adaxial, right: median inferior one; d, stolons showing characteristic internal thickenings and nematotheca, left stolon in lateral view, right one in frontal view.

on upper side. Remaining part of hydrocladia organised as in caulus with up to three repeats. Main segments with three nematothecae: one median inferior and a pair of laterals. No nematotheca present behind hydrothecae.

Hydrotheca curved, margin in many cases not reaching beyond distal end of segment, abcauline wall convex, adcauline wall with deep constriction in upper third, forming an intrathecal shelf and causing an everted margin. Hydrotheca adnate for half of adcauline length, angle of opening with hydrocladium zero to 50°.

Nematothecae of stem and hydrocladia all two-chambered. Median inferior nematothecae mostly not reaching hydrotheca, with short adcauline wall partly fused to wall of segment. Lateral nematothecae on pedicel shorter than nematotheca itself, mobile, conical, walls straight, lower chamber longer than upper one, margin of upper chamber lowered on inner side down to bottom. Nematothecae of intersegments and occasional superior ones on caulus similar to basalmost median inferior nematothecae, but with longer free adcauline wall and mobile.

Gonothecae unknown.

Type locality.— Torquay, Victoria, Australia.

Distribution.— Known from type locality only.

Remarks.— *Halopteris everta* has been found only once. The strong constriction in

the adcauline wall of all hydrothecae, giving the latter a folded appearance, makes this species very characteristic (fig. 33b). Besides this character, *H. everta* is similar to *H. minuta*, notably the stolons with the regular internal thickenings and the nematothecae. *H. everta* could very well represent an extreme form of *H. minuta*. Also *H. minuta* regularly has a concavity in the upper half of the abcauline hydrothecal wall, but by no means as strong as *H. everta* (the name of *Halopteris constricta* Totton, 1930, here seen as a synonym of *H. minuta*, possibly refers to that concavity too). A further difference between *H. everta* and *H. minuta* is the axillar nematotheca above the cauline hydrothecae in the former. *Halopteris minuta* has only occasionally a nematotheca behind the cauline hydrothecae and it is not axillar. This difference, however, could also be due to the special shape of the hydrothecae in *H. everta*. More material from Australia, including also gonothecae, is needed to consolidate the validity of the characters used to separate *Halopteris everta* from the remaining species in this group.

Table 23. Variation and dimensions *Haloperis everta*, in µm if not stated otherwise.

sample no.	1
caulus height [mm]	6
max number of cladia per side	6
hydrocladial main segments	240-260
hydrocladial intersegments	90-110
second cladial segment	120-150
abcauline side of hydrotheca	170-190
free adcauline side of hydrotheca	60-70
diameter of hydrotheca	~120
max. number of hydrothecae per cladium	3

Halopteris pseudoconstricta Millard, 1975
(fig 34, table 24)

Halopteris constricta; Millard, 1957: 227, fig 14A; 1962: 282, fig. 4G; 1966b: 493 [not *Halopteris constricta* Totton, 1930: 217, fig. 56a = *H. minuta*].
Halopteris pseudoconstricta Millard, 1975: 355, fig. 114D-G; 1978: 193.

Material examined.
- 1) Holotype SAM-H542 kept by SAM, intertidal region at Melkbosstrand, Table Bay, South Africa, coll. 17.xi.1967, several plumes in alcohol and one slide, fertile female colonies.
- 2) False Bay, South Africa, SAM-H132, 10.ix.1957, depth 3-5 m, rock bottom (see Millard, 1962), several plumes in alcohol and one slide, fertile female colonies.

Description.— Colony forming up to 9 mm high plumes or simple stems arising from creeping, ramified, tubular stolons. Nematothecae on stolons not observed in available material.

Hydrocaulus monosiphonic, unbranched, with basal part ($^1/_4$) devoid of hydrothecae and hydrocladia and a longer distal part bearing hydrothecae and hydrocladia. Basal part divided into segments by two or three straight nodes, last segment ending in oblique hinge-joint, segments with variable number of nematotheca. Stem above basal part heteromerously segmented by alternating oblique and transverse nodes. Main segments of stem with one hydrocladium on alternate sides (occasionally most proximal hydrocladia opposite), hydrotheca, and three to four nematothecae: one median inferior, one on each side of hydrotheca and often one on distal part of segment, but not in axil of hydrotheca. Intersegments with one, rarely two nematothecae. Main segments longer than intersegments.

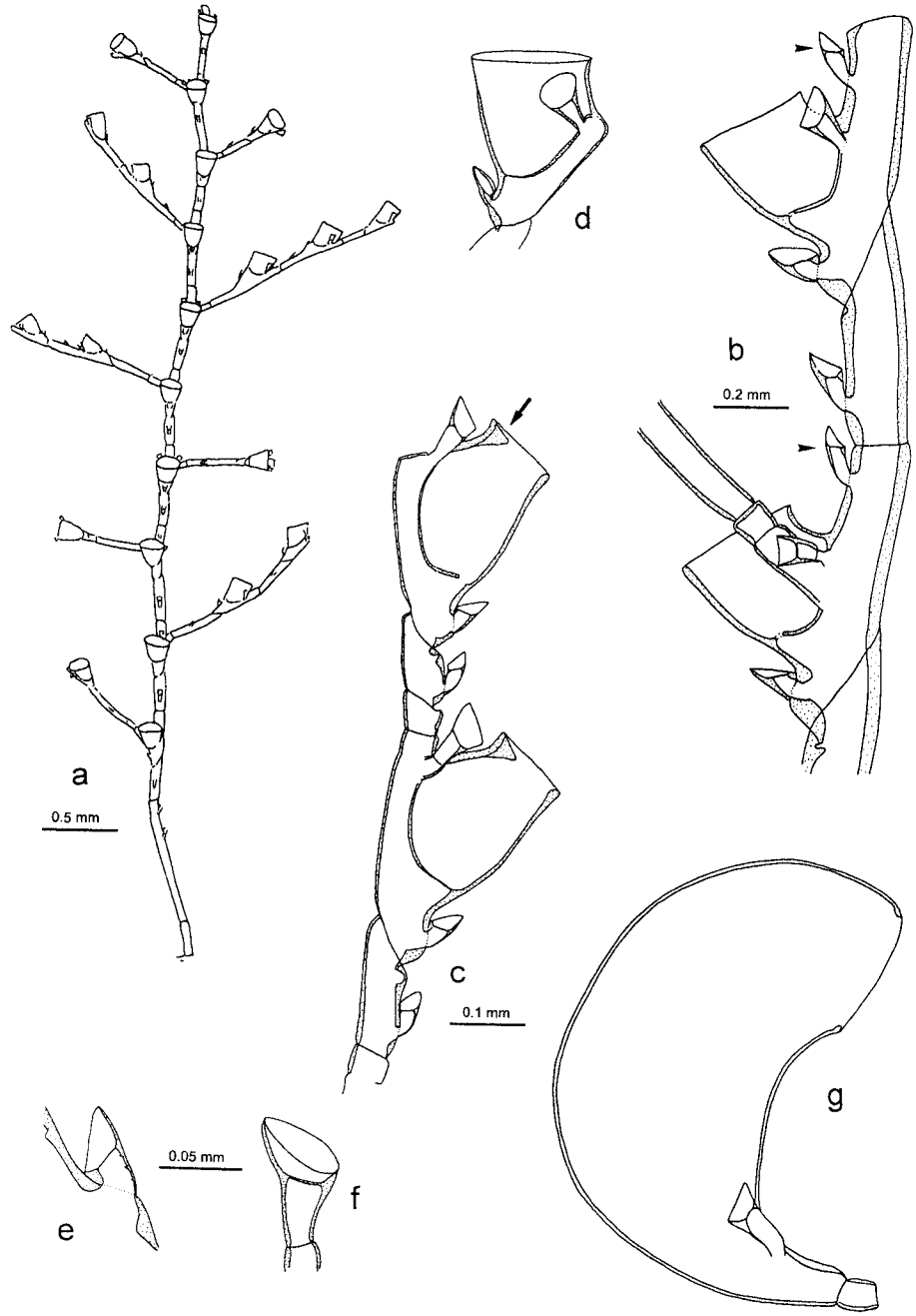

Fig. 34. *Halopteris pseudoconstricta* Millard, 1975; c, e, f, from holotype, others from sample 2; a, complete plume; b, part of caulus in lateral view with one proximal part of hydrocladium, note presence of superior nematothecae (arrowheads); c, hydrocladium, note internal cusp on adcauline wall of hydrotheca (arrow); d, terminal main segment from hydrocladium, note absence of internal cusp, same scale as c; e, median inferior nematotheca; f, lateral nematotheca, same scale as e; gonotheca, terminal opening points towards plume, same scale as b.

Hydrocladia inserted on well-formed apophyses lateral to cauline hydrothecae. Apophysis without nematotheca. First segment of hydrocladium quadrangular, without nematotheca, sometimes two such elements present. Second segment elongated, with one median nematotheca on upper side. Remaining part of hydrocladia organised as in caulus with up to six repeats. Main segments with three nematothecae: one median inferior and a pair of laterals. No nematotheca behind hydrothecae. Intersegments may occasionally be divided into two segments, more proximal one lacking a nematotheca.

Hydrotheca cup-shaped, rim not reaching beyond distal end of segment, abcauline wall almost straight, adcauline wall distinctively concave. Hydrotheca adnate for half of adcauline length, angle of opening with hydrocladium 40 to 50°. Adcauline internal cusp occasionally present near opening of hydrotheca.

Nematothecae of stem and hydrocladia all two-chambered. Median inferior nematothecae not reaching hydrothecal base, with short adcauline wall partly fused to wall of segment, probably immovable. Lateral nematothecae on short pedicels, conical to funnel-shaped, mobile, lower chamber longer than upper one, rim of upper chamber lowered on adcauline side for about half of height. Nematothecae of intersegments and occasional superior ones on caulus similar to basalmost median inferior ones, but with longer free adcauline wall and mobile.

Female gonothecae inserted singly or in opposite pairs below hydrothecae of stems or occasionally singly in similar position on hydrocladia, up to 0.66 mm long and with a maximal diameter of 0.4 mm; each gonotheca placed on short, quadrangular segment. Entire axis of gonotheca strongly curved towards caulus, inner side straight or nearly so, outer wall evenly curved to form a semi-circle. Distal end truncated, with lid of smaller diameter than maximal width of gonotheca; two nematothecae at gonothecal base. Male gonotheca unknown.

Type locality.— Melkbosstrand, Table Bay, South Africa.

Variation.— The internal cusp (fig. 34) in the hydrotheca was only seen in the holotype material; it is absent in the other sample. Though typically the cormoid form is a plume, a colony may also have simple, *Antennella*-like stems. Some plumes have a reduced number of hydrocladia, while some hydrocladia can be branched (Millard, 1975).

Table 24. Variation and dimensions of *Halopteris pseudoconstricta*, in µm if not stated otherwise.

sample no.	1	2
caulus height [mm]	7	5
max. number of cladia per side	6	4
hydrocladial main segments	310-370	320-380
hydrocladial intersegments	130-170	200-220
second cladial segment	190-220	270-310
abcauline side of hydrotheca	160-180	150-160
free adcauline side of hydrotheca	60-90	60-70
diameter of hydrotheca	110-160	140-160
tentacle number	~10-12	~10-12
stolon diameter	90	90

Distribution.— South Africa; Angola; Vema Seamount (South Atlantic).

Remarks.— Millard (1957, 1962) originally assigned her *H. pseudoconstricta* material to *H. constricta* Totton, 1930 (here = *H. minuta*). After Ralph's (1961) description of the female gonotheca of the latter it became evident that the South African material must belong to another species and Millard (1975) established the new species *H. pseudoconstricta* for her South African material. The s-shaped axis of the gonotheca of *H. minuta* readily distinguishes it from *H. pseudoconstricta*. The proposal of Park (1990) to unite both species is therefore not accepted here. Furthermore, *H. minuta* has stolons with regular internal pegs and nematothecae. Such stolons were not observed in *H. pseudoconstricta*. The internal cusp in the hydrotheca is also rather characteristic for *H. pseudoconstricta*, however, it is not present in all colonies. Millard (1975) did not mention this cusp. The trophosomes of both species are otherwise indistinguishable.

Halopteris campanula group

Remarks.— This group contains only *Halopteris campanula* and *H. simplex*. Both are quite similar; for their distinction see under *H. simplex*.

Halopteris campanula (Busk, 1852)
(fig. 35, table 25)

Plumularia campanula Busk, 1852: 401; Bale, 1884: 124, pl. 10 fig. 5; 1887: 22; 1888: 776, pl. 20 figs 1-6; Marktanner-Turneretscher, 1890: 255; Billard, 1908: 759; Mulder & Trebilcock, 1909: 32; Billard, 1910: 31; Bale, 1913: 133; Billard, 1913: 17, pl. 1 figs 11-13; Bale, 1915: 295; Jäderholm, 1919: 22, pl. 5 fig. 4; Hodgson, 1950: 40, fig. 69.

Plumularia indivisa Bale, 1882: 39, 46, pl. 15 fig. 1.

Plumularia laxa Allman, 1883: 19, pl. 1 figs 5-6; Billard, 1910: 31.

Plumularia rubra Von Lendenfeld, 1884: 476, pl. 13 figs 11-12, pl. 14 fig. 15; Bale, 1888: 778, pl. 20 figs 1-6.

Plumularia torresia Von Lendenfeld, 1884: 477, pl. 13 figs 13-14, pl. 14 fig. 16.

Plumularia campanula var. *geelongensis* Mulder & Trebilcock, 1916: 76, pl. 11 figs 2-2c.

Halopteris campanula var. *zelandica* Totton, 1930: 219, fig. 57a-b; Ralph, 1961: 46, fig. 6g; Rees & Vervoort, 1987: 129.

Halopteris campanula; Leloup, 1938: 20, fig. 14; Pennycuik, 1959: 156, 177; Rees & Vervoort, 1987: 124, fig. 26.

Halopteris campanula var. *campanula* Ralph, 1961: 47; Watson, 1973: 184; 1975: 170.

Material examined.

- 1) Wellington, Barretts Reef, New Zealand, several colonies collected 14.xii.1994 by author from 10 m depth, fertile, *Corhiza*-form, alcohol material deposited as RMNH Coel. 27610.
- 2) Port Jackson, Australia, NHMV no. 1120, as *Plumularia rubra*, pinnate form, described by Marktanner-Turneretscher (1890), collected by Von Lendenfeld.
- 3) Torres Strait, Australia, MVM slide F59277, *Plumularia torresia*, from collection Bale (Stranks, 1993), labelled as: Von Lendenfeld's type by Bale, from Torres Strait, 1886.

Description.— Colonies forming varied and irregularly branched stems, either plumose cormoids arising directly from creeping tubular hydrorhiza (*Halopteris*-form), or irregular, plumose cormoids and hydrocladia that arise from a short polysi-

phonic stem formed by stolon-like tubes. In peripheral parts of colony simple, unbranched hydrocladia bearing gonothecae may develop directly from creeping stolons (*Antennella*-form, fig. 35a, right). Hydrocladia of erect forms occasionally branched. Colony up to 10 cm high but usually less than 5 cm high; single plumes up to 2 cm high.

Hydrocaulus with hydrothecae, except for basal part of varied length having some nematothecae and with a hinge-joint. Main axis above hinge-joint mostly homomerously segmented by oblique nodes. Intersegments only delimited in extreme distal parts of stem by weak, transverse nodes. Not all segments bear hydrocladia, these alternately on left and right sides. Each segment with median, frontal hydrotheca and four nematothecae: one median inferior, one pair of laterals, and a superior one that may be placed on separate intersegment in distal region of caulus.

Hydrocladia inserted on short, often indistinct apophyses lateral to cauline hydrothecae; apophysis devoid of nematotheca. First segment of hydrocladium elongate, with proximal transverse and distal oblique node, without hydrotheca but with one nematotheca. Rest of hydrocladium segmented homomerously by oblique nodes, in distal part heteromeroulsy by alternating oblique and transverser nodes. Up to ten hydrothecae per hydrocladium present. Segments without internal ridges.

Hydrothecae cup-shaped, rim reaching far beyond transverse node if present, abcauline and adcauline walls straight in lateral view, converging proximally. Rim can be slightly flaring, opening at an angle of 40 to 50° with hydrocladial axis. Abcauline wall sometimes slightly thickened; half to two- thirds of adcauline wall adnate.

Nematothecae of stem and hydrocladia all two-chambered. Median inferior nematothecae do not reach hydrotheca, short, abcauline wall thick, wall of upper chamber missing on adcauline side and slightly emarginated on abcauline side. Other median nematothecae similar. Lateral nematothecae short and robust, placed on triangular pedicel shorter than nematotheca itself, lower chamber shorter or just as long as upper one, sometimes almost missing. Upper chamber with walls rolled inwardly; inner wall missing and outer wall with distinct emargination over half its height (spanner-type).

Gonothecae of both sexes arising on same plumes, females occurring either distal or proximal to male ones. Female gonotheca up to 0.9 mm long, pear-shaped, strongly flattened ($^1/_2$) in one direction, with oval terminal thickening and lid. At base two nematothecae, both on adcauline side. Female gonotheca placed on pedicel formed by two quadrangular segments. Male gonotheca only half the size of female ones, oblong, rounded, not flattened, base with one adcauline nematotheca. Male gonotheca placed on pedicel of one or sometimes two segments, in which case second segment indistinct.

Nematocysts (sample no. 1): a) microbasic mastigophore, sometimes like eurytele, with many strong spines, in nematophores, (19-22) × (6-8) µm, s = 0.8; b) rounded capsule, (4-5) × (3-4) µm; c) elongate capsule from tentacles, (5-6) × (2-2.5) µm.

Colour.— Living colonies deep orange (New Zealand material) or brick-red to yellow (Von Lendenfeld, 1884; Watson, 1973, Australian material).

Variation.— Young, infertile colonies resemble a species of *Antennella*. Stolons may bear nematothecae (Leloup 1938).

Type locality.— Bass Strait, Australia.

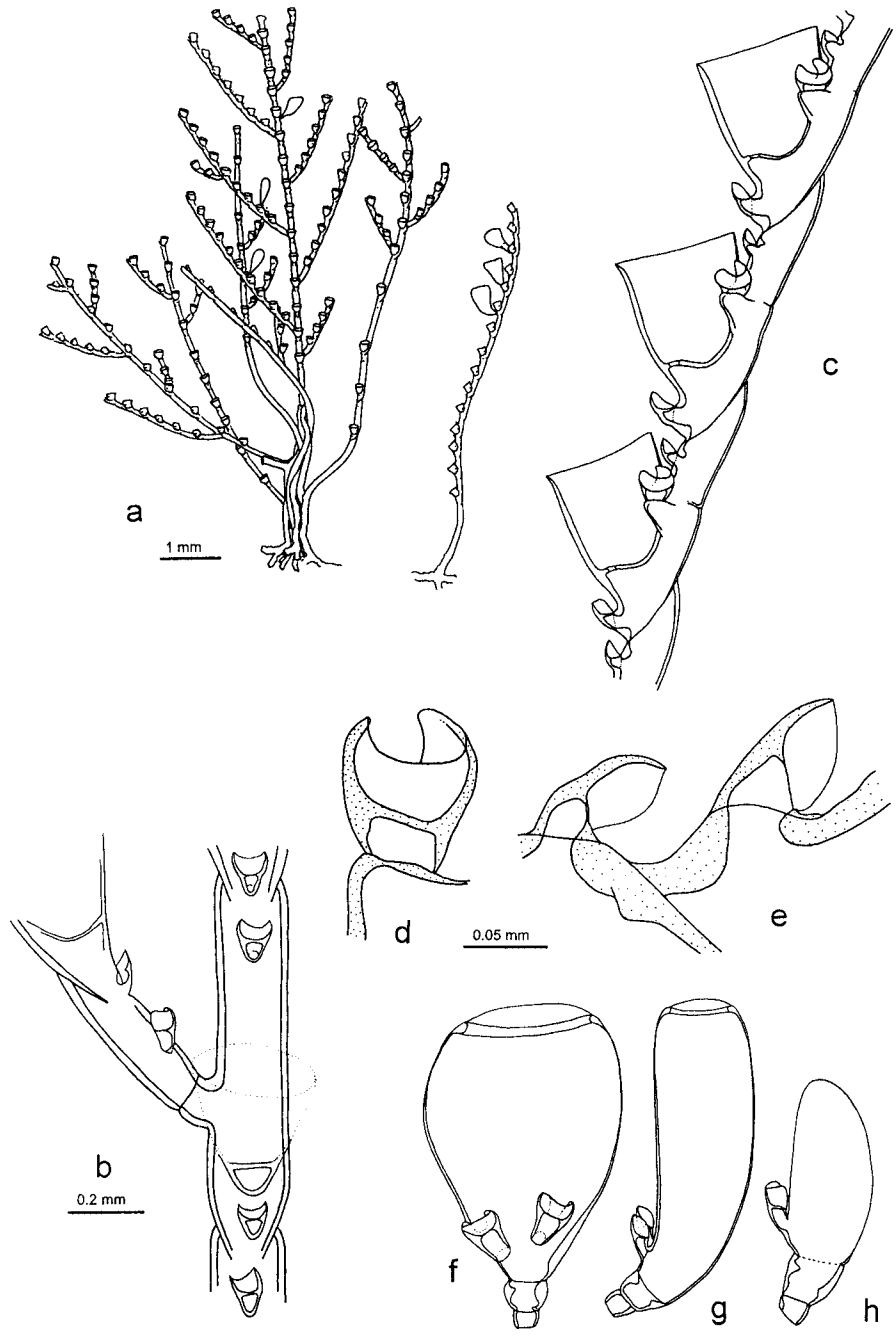

Fig. 35. *Halopteris campanula* (Busk, 1852), all after sample 1; a, part of colony, at right polysiphonic form, at left simple *Antennella*-like form; b, part of caulus with one hydrocladium; c, part of hydrocladium; d, lateral nematotheca with its pedicel; e, median nematotheca; f, female gonotheca in adcauline view; g, female gonotheca in lateral view; h, male gonotheca in lateral view.

Table 25. Variation and dimensions of *Halopteris campanula*, in µm if not stated otherwise.

sample no.	1	2
max. number of cladia per sid	5	5
length of apophysis	60-90	60-90
length of 1st cladial segment	350-460	390-410
cladial segments (main+inter)	770-800	720-880
abcauline side of hydrotheca	260-280	200-230
free adcauline side of hydrotheca	130-160	100-120
diameter of hydrotheca	270-300	210-220
max. number of hydrothecae per cladium	11	10
tentacle number	20-24	18-20

Distribution.— New Zealand; Australia; Japan; Malay Archipelago; Gulf of Suez; Gulf of Aden; Red Sea (Rees & Vervoort 1987).

Remarks.— *Halopteris campanula*, as understood at present, can occur in very different growth forms, often even occurring within the same colony. It can either grow in the plumose form typical for *Halopteris*, arising directly from the hydrorhiza, or the cormoids (pinnate or simple) can grow from an erect, polysiphonic stem formed by stolon-like tubes (*Corhiza*-form), or, finally, it can grow as simple hydrocladia developing directly from creeping stolons (*Antennella*-form). The hydrocladia can also be branched. All these forms were initially described as separate species (*Plumularia campanula, P. laxa,* and *P. torresia* as the polysiphonic form, *P. rubra* as the *Halopteris*-form, and *P. indivisa* as the *Antennella*-form). Colonies showing only the *Antennella*-form are presumably not mature and have no gonothecae. Otherwise they would be difficult to distinguish from *Antennella campanulaformis*. The occurrence of all four forms within one colony shows that the present generic separations of the Halopteridídae is problematic. At least it can be assumed that the various modes of growth now used for generic separations can evolve easily and therefore the genera as delimited at present are most probably polyphyletic. However, population genetic methods should be applied first to demonstrate that the various growth forms actually belong to one and the same species (cf. Thorpe et al., 1992). Pennycuik (1959) considered at least some of the simple *Antennella*-forms as a distinct *A. indivisa* species, but without giving arguments.

The complex synonymy of this species has been treated by a number of authors (see Bale, 1884; 1887; Marktanner-Turneretscher, 1890; Billard, 1908; 1910). The distinction of the variety *H. campanula* var. *geelongensis* (Mulder & Trebilcock, 1916) is not apparent and is here seen as unnecessary. Totton (1930) created the variety *zelandica*, which was based on otherwise variable characters of the hydrotheca and nematotheca. Following the arguments of Rees & Vervoort (1987) such a subdivision is also not recognised here, nor is it desirable.

Antennella campanulaformis (Mulder & Trebilcock 1909) closely resembles *H. campanula* in its structure, the main differences being that *A. campanulaformis* has more cylindrical hydrothecae and its female gonothecae are rounded and do not taper in their proximal half. *A. campanulaformis* is only known in the simple, unbranched form.

Halopteris simplex (Warren, 1914)

Schizotricha simplex Warren, 1914: 83, figs 1-4, pl. 6; Millard, 1962: 292; 1975: 369, fig. 118A-C; 1978: 197 [not *Antennella simplex* Bedot, 1914 = *A. siliquosa*].

Type locality.— Near mouth of St. John's River, South Africa.

Distribution.— South Africa.

Remarks.— *Halopteris simplex* was removed from *Schizotricha* for reasons discussed under that genus (see p. 133 and also Totton, 1930). *Halopteris simplex* is a small species (14 mm high maximally) with monosiphonic stem, and it has only its proximal hydrocladia branched, the more distal ones are usually unbranched. The hydrocladia and branches are rather short and have only two or three hydrothecae. For further details see Millard (1975). *Halopteris simplex* closely resembles *H. campanula* in most details, but apparently differs in lacking superior nematothecae on the hydrocaulus.

Halopteris diaphragmata group

Remarks.— This group contains *Halopteris diaphragmata* and *H. jedani*. Both species possess hydrothecae with a large, abcauline diaphragm. They resemble each other closely. For their distinction see under *H. jedani*.

Halopteris diaphragmata (Billard, 1911)
(fig. 36, table 26)

Plumularia diaphragmata Billard, 1911: 68, fig. 10; 1913: 40, fig. 31A-B, pl. 3 fig. 28.
Thecocaulus diaphragmatus; Bedot, 1921b: 8.

Material examined.

- 1) Syntypes, ZMA Coel. 4061, as *Plumularia diaphragmata*, Siboga station 164 (1°42.5'S 130°47.5'E, near New Guinea), depth 32 m, on small pebbles and shells, two plumes maximally 25 mm high, one plume stained, infertile, type designation by Billard (1913).
- 2) Siboga station 99 (6°7.5'N 120°26'E, Sulu Archipelago), ZMA Coel. 4061 and 5240, as *Plumularia diaphragmata*, depth 16-23 m, on *Lithothammnion*, 4 and 1 plumes, 20 to 45 mm, with gonothecae, sample designated cotypes by Billard (1913).
- 3) Siboga station 80 (2°25'S 117°43'E, Borneo), ZMA Coel. 4061, as *Plumularia diaphragmata*, depth 40-50 m, on coralline sand, several fragments of plumes, infertile.

Description.— Colonies forming plumes that arise directly from creeping hydrorhiza, stolons tubular, ramified.

Hydrocaulus up to 4.5 cm high, monosiphonic, unbranched, with basal part (up to $^1/_4$ to $^1/_3$ of total length) devoid of hydrothecae and hydrocladia, with transverse nodes and numerous nematothecae in a double row. Basal part ends in two deeply cut oblique hinge-joints that frame first hydrotheca and first hydrocladium. Distal part with alternate hydrocladia, up to 40 per side. Distal part with indistinct homomerous segmentation by oblique nodes, or segmentation absent. Each hydrotheca associated with seven to nine nematothecae: one median inferior, a pair of laterals, a pair of axillar ones, and two to four superior ones in two rows.

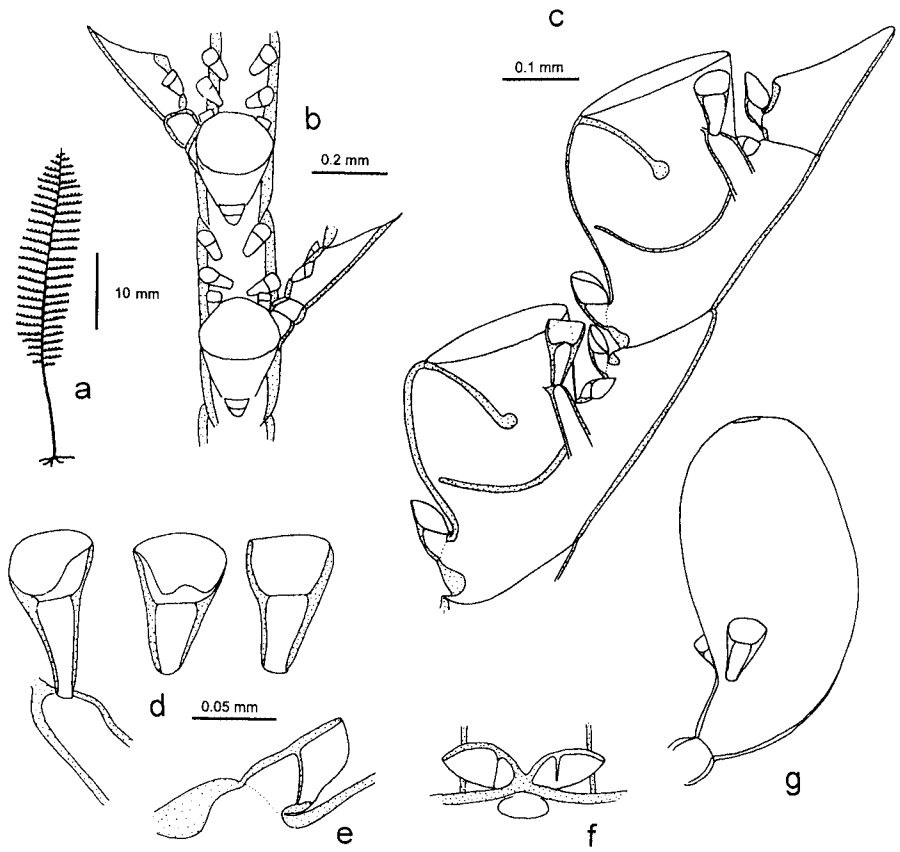

Fig. 36. *Halopteris diaphragmata* (Billard, 1911); after sample no. 2; a, single plume; b, part of hydrocaulus with bases of hydrocladia; c, part of hydrocladium, note varied presence of transverse nodes; d, three lateral nematothecae seen from inner side and showing range of variability; e, median inferior nematotheca, same scale as d; f, axillar pair of nematothecae in frontal view, same scale as d; g, presumed male gonotheca, same scale as c.

Hydrocladia only rarely branched, inserted on well formed apophyses lateral to each cauline hydrotheca, first segment quadrangular with transverse ends, without nematothecae, second segment elongated, with two to three nematothecae, distal node oblique, remainder of hydrocladium with up to eight repeats ending in oblique nodes, occasionally repeat subdivided by transverse node into main- and intersegment. Each repeat with a hydrotheca and six nematothecae: one median inferior, a pair of laterals, a pair of axillar ones, and a superior one (rarely two) that is located on intersegment if transverse node is present.

Hydrotheca cylindrical, abcauline side bulging slightly, with large internal septum originating from abcauline side of hydrothecal rim, septum spans about $^2/_3$ of hydrothecal depth and often ends in thickening; opening of hydrotheca at an angle of 20 to 40° with axis of hydrocladium; hydropore close to abcauline wall. Polyp is curved S-like due to presence of septum.

Nematothecae all two-chambered. Median inferior movable, conical, straight, adaxial side shortened but present, with lowered adaxial wall of upper chamber. Lateral nematotheca on pedicel of similar length as nematotheca itself, conical, movable, lower chamber deeper than upper one; walls of upper chamber straight or slightly rolled inwardly, inner side much lowered or not, if lowered sometimes with additional short adaxial cusp. Axillar nematothecae scale-shaped but with septum, presumably not movable, one side missing, placed in upper axil of hydrotheca and facing in opposite directions. Other nematothecae similar to median inferior ones, but adaxial side longer.

Presumed male gonotheca c. 0.4 mm long, pear-shaped, with slightly curved base; distal end rounded and with small aperture, base with two nematothecae, pedicel composed of one segment.

Type locality.— 1°2.5'S 130°47.5'E, Indonesia, depth 32 m.

Distribution.— Indonesia.

Remarks.— With its large abcauline septum in the hydrothecae, *Halopteris diaphragmata* is a characteristic species that can only confused be with *H. jedani*. The differences between these two are discussed under the latter. *Halopteris diaphragmata* is a rarely recorded species and seems to be a restricted in its distribution to the Indonesian region.

Halopteris jedani (Billard, 1913)
(fig. 37, table 26)

Plumularia jedani Billard, 1913: 41, figs 37-39.
Thecocaulus jedani; Bedot, 1921b: 8.

Material examined.— Syntypes, ZMA Coel. 4053, as *Plumularia jedani*, Siboga station 273 (Jedan Island, Aru Islands, Indonesia), depth 13 m, 5 plumes, up to 1 cm high, damaged, this material formed the basis for Billard's (1913) first description and therefore syntypes by inference, very likely they represent only one colony.

Diagnosis.— *Halopteris* species strongly resembling *H. diaphragmata*, hydrocaulus up to 1.5 cm high, homomerously segmented by oblique nodes, cauline hydrotheca with pair of axillar nematothecae, hydrocladia alternate, heteromerously segmented, intersegments with one to two nematothecae, cladial hydrothecae either without or with single axillar nematotheca, lateral nematothecae with emarginations on sides (bivalved). Female gonotheca 0.7 mm long, pear-shaped, end truncated and with large lid, base with two nematothecae, pedicel composed of one segment.

Type locality.— Island of Jedan, Aru Islands, Indonesia; depth 13 m.

Distribution.— Known from type locality only.

Remarks.— *Halopteris jedani* is so similar to *H. diaphragmata*, that only a shortened diagnosis is provided here that outlines the more important points. *Halopteris jedani* is distinguishable from *H. diaphragmata* only by the possession of a single axillar nematotheca above the cladial hydrothecae, the regular presence of transverse nodes in the hydrocladia, and the occasional presence of two nematothecae on the intersegments. The presence or absence of transverse nodes is varied in *H. diaphragmata* and cannot be used as reliable character to separate the two species. Thus, only the single

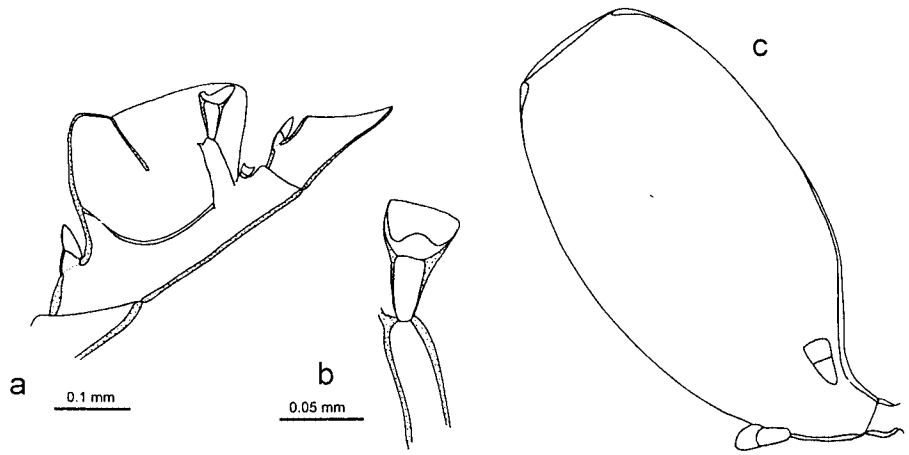

Fig. 37. *Halopteris jedani* (Billard, 1913), after syntype material; a, part of hydrocladium; b, lateral nematotheca seen from inside; c, female gonotheca, same scale as a.

versus paired axillar nematothecae remain as separating characters. Because also this character can be variable in some species (see *H. polymorpha*), it is conceivable that *H. jedani* is only a form of *H. diaphragmata*. However, because only few samples of both species are known and the extent of variation of each nominal species can only be examined in newly collected material, both species are here kept separate.

Some dimensions of *H. jedani* are given in table 26 together with those of *H. diaphragmata*, to allow an easier comparison.

Table 26. Dimensions of *Halopteris diaphragmata* (columns one and two), and *H. jedani* (last column), in µm.

species, sample no.	*H. diaphragmata* sample 2	*H. diaphragmata* sample 3	*H. jedani* syntypes
hydrocladial repeats	510-530	600-650	440-530
abcauline side hydrotheca	140-170	120-160	140-150
free adcauline side hydrotheca	110-140	120-130	100-110
diameter hydrotheca	180-200	180-200	160-210

Halopteris group with opposite hydrocladia

Remarks.— This group contains the following species: *Halopteris catharina, H. gemellipara, H. geminata, H. gracilis, H. opposita, H. plagiocampa,* and *H. zygocladia.* They are all characterised by hydrocladia that are nearly always arranged in opposite pairs. Although they are formally rather well separable, it remains uncertain how reliable the character "opposite hydrocladia" is and to what extent it is either an apomorphy, or only a variant of the alternate state. Table 27 gives the characters used to distinguish the species.

Table 27. Distinguishing characters for *Halopteris* group with opposite hydrocladia.

species / character	*Halopteris catharina*	*Halopteris gemellipara*	*Halopteris gracilis*	*Halopteris geminata*	*Halopteris opposita*	*Halopteris plagiocampa*	*Halopteris zygocladia*
caulus branched	no	no	no	dichotomous	no	no	no
caulus segmentation	hetero-merous	homo-merous	hetero-merous	hetero-merous	homo-merous	hetero-merous	homo-merous
pairs of lateral nematothecae	2	1	1	1	1	1	1
chambers lateral nematothecae	2	1	2	2	2	2	2
inrolled lateral nematotheca	no variable	no	yes,	no	no	no	yes
hydrotheca with internal ridge	no	no	no	no	yes	no	no
axillar nematotheca of cauline hydrothecae	none	none	2	unknown	1	none	none
axillar nematotheca of cladial hydrothecae	none	none	1	1	1	none	none
shape of female gonotheca	flattened cylinder	unknown	pear-shaped	unknown	unknown	cornucopia	pear-shaped

Halopteris catharina (Johnston, 1833)
(fig. 38, table 28)

Plumularia catharina Johnston, 1833: 497, figs 61-62; Kirchenpauer, 1876: 27, pl. 1 fig. 12, pl. 3 figs 12-13; Marktanner-Turneretscher, 1890: 253; Nutting, 1900: 60, pl. 3 figs 1-2; Hartlaub, 1905: 681; Jäderholm, 1909: 107, pl. 12 fig. 7; Ritchie, 1913: 1, figs 1-3; Bedot, 1914: 94, pl. 5 figs 17-19; Broch, 1918: 56-58, figs 25-26; Stechow, 1919: 114.

Thecocaulus catharina; Bale, 1915: 294.

Schizotricha catharina; Bedot, 1921b: 12; 1925b: 349; Stechow, 1925b: 497.

Halopteris catharina; Totton, 1930: 217; Vervoort, 1972: 236; Stepanjants, 1979: 124, pl. 23 fig. 3; Gili et al, 1989: 83, fig. 12; Cornelius & Ryland, 1990: 152, fig. 4.23; Ramil & Vervoort, 1992a: 145, fig 37e-g; Cornelius, 1995: 126, fig. 29.

Material examined.

- 1) Roscoff, France, Atlantic Ocean, MHNG 292, as *Schizotricha catharina*, collection Bedot, fertile, branched hydrocladia, polysiphonic stem.
- 2) Great Britain, NHMV 1122, as *Plumularia catharina*, described by Marktanner-Turneretscher (1890).
- 3) Cornwall, Palperro, English Channel, Great Britain, ROMIZ B1035, as *Halopteris catharina*, depth unknown, coll. and det. D. Calder, 5.vii.1989, fertile, branched hydrocladia.

Description.— Colony forming up to 4 cm high plumes arising from ramified, tubular stolons.

Hydrocaulus typically monosiphonic, unbranched, with basal part ($^1/_4$) devoid of hydrothecae and hydrocladia, and a longer distal part bearing hydrothecae and hydrocladia. Basal part divided into segments by means of transverse nodes, last node oblique, each segment with variable number of up to 11 frontal nematothecae in two longitudinal rows. Stem above basal part heteromerously segmented by well

formed, alternating oblique and transverse nodes. Main segments of stem with opposite pair of hydrocladia, only occasionally in more distal region there may be only one hydrocladium and consequently then in alternate arrangement. Main segments with frontal hydrotheca and five nematothecae: one medial proximal, and two pairs of laterals. Axillar nematotheca never present. Intersegments with one to four nematothecae.

Hydrocladia insert below hydrothecae on long stem apophyses without nematothecae. First hydrocladial segment long, with two nematothecae on upper surface. Remaining part of hydrocladium segmented as described for hydrocaulus. Main segments similar to those of stem, intersegments with one to two nematothecae.

Hydrotheca cup-shaped, placed in middle of segment, rim reaching distal end of segment, abcauline and adcauline walls straight in side view, converging proximally. Hydrotheca adnate for about half its length or slightly more. Rim of hydrotheca smooth, flat, at an angle of c. 35 to 45° with hydrocladium.

Nematothecae of stem and hydrocladia all two-chambered and movable. Median inferior nematotheca of main segments conical, adcauline wall of upper chamber much lowered. Lateral nematotheca in pairs, larger one on pedicel about as long as nematotheca itself, shorter nematotheca at base of pedicel, both nematothecae conical with lowered adcauline wall of upper chamber, abcauline wall straight. Larger lateral nematothecae reaching hydrothecal rim or slightly beyond it. Nematothecae of intersegments and others similar to median inferior nematothecae.

Gonothecae of both sexes on the same plume, developing on main segments below hydrotheca of stem and hydrocladia. Female gonotheca up to 1 mm long, forming a slightly flattened cylinder, tapering near base, only slightly curved in basal region and there with two nematothecae; terminal region truncated, with annular thickening and lid. Gonothecal pedicel composed of two quadrangular segments. Male gonotheca smaller and slender, largest diameter in middle, tapering towards both ends, basally with two (?) nematothecae, pedicel one-segmented, occasionally second, indistinct segment present.

Type locality.— Great Britain.

Variation.— Parts of the colony or younger stages may occur in the simple *Antennella*-like form. Such infertile stems can be mistaken for *Antennella quadriaurita*. The hydrocladia of *H. catharina* may be branched. The main axis can also be as in *Corhiza*. In the *Corhiza*-form, the main stem is polysiphonic, formed by erect stolon-like tubes that branch off hydrocauli or hydrocladia. The second lateral pair of nematothecae can be much smaller than those on the pedicel and can be mistaken for a single, reduced axial nematotheca.

Distribution.— The species is widely distributed in the temperate and southern-boreal regions of the Atlantic including the Mediterranean, occurring on both the western and eastern sides of the Atlantic, reaching as far south as the Straits of Magellan, depth range down to 412 m (Gili et al., 1989; Ramil & Vervoort, 1992a).

Remarks.— *Halopteris catharina* is a rather distinct species that is easy to recognise. Problems only arise with the forms differing from the typical plumose stems, especially the forms with polysiphonic stems and the *Schizotricha*-like form. Population genetic methods should be applied to test whether they are really the same species (see Thorpe et al., 1992).

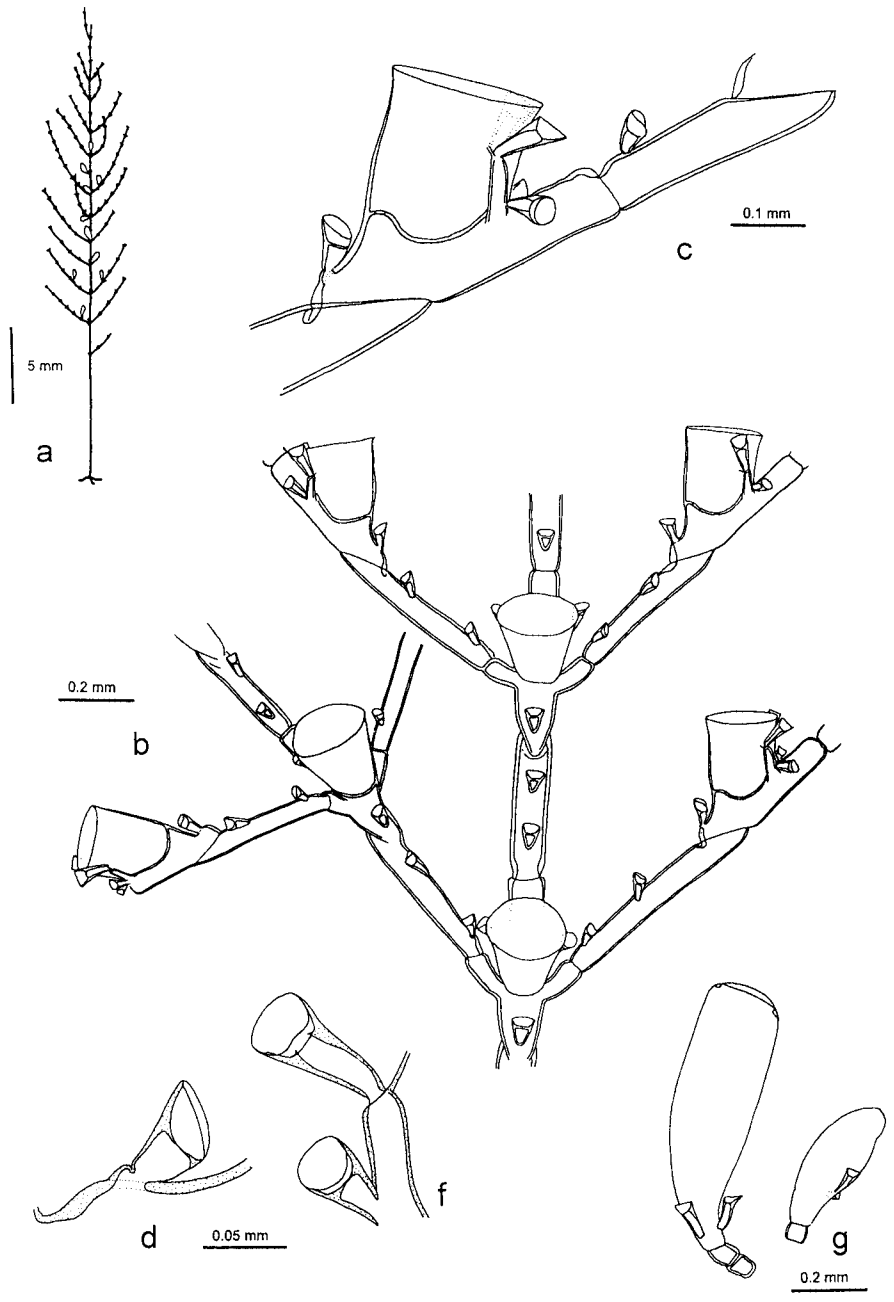

Fig. 38. *Halopteris catharina* (Johnston, 1833); a, normal plumose colony, sample no. 2; b, part of caulus with opposite, branched hydrocladia, sample no. 1; c, part of hydrocladium with main segment and intersegment, sample no. 1; d, median inferior nematotheca, sample no. 1; f, pair of lateral nematothecae seen from inner side, sample no. 1; g, gonothecae, left female, right male, both sample no. 1.

Table 28. Measurements and variation of *Halopteris catharina*, in µm if not stated otherwise.

sample no.	1	2	3
hydrocaulus height [mm]	30	-	40
max number of cladia per side	8	-	11
length of apophysis	80-120	90-120	90-130
length of 1st cladial segment	390-570	625-688	480-800
cladial main segments	360-430	520-580	480-530
cladial intersegments	270-400	450-490	450-540
abcauline side of hydrotheca	180-210	220-240	200-220
free adcauline side of hydrotheca	110-130	120-130	120-130
diameter of hydrotheca	180-200	200-220	220-240
max. number of hydrothecae per cladium	8	6	-
pedicel of lateral nematothecae	80-90	60-80	70-80
tentacle number	12-14	-	-
stolon diameter	90	-	-

Billard (1904) described a species of *Antennella* as *Plumularia catharina* var. *articulata* that most probably bears no relationship to *H. catharina* at all. Billard's sample is inadequately described and re-investigation of the type material is needed (see Van Praët, 1979; however, the material could not be found in MNHN, pers. com. M. J. d'Hondt). Any relationship to *H. catharina* is unlikely because in Billard's fig. 3 there is only one pair of lateral nematothecae and not two pairs (cf. fig. 38f).

Halopteris gemellipara Millard, 1962

Halopteris gemellipara Millard, 1962: 283, fig. 4A-F; 1975: 351, fig. 112C-F; 1978: 193.

Type locality.— Agulhas Bank, South Africa, depth 120 m.

Distribution.— Endemic to South Africa.

Remarks.— *Halopteris gemellipara* is rather well documented and Millard (1962, 1975) should be consulted for accurate description. It is a rather unique *Halopteris* species as it has one-chambered lateral nematothecae. It superficially resembles a sample of *H. crassa* taken in the Three Kings Islands region (fig. 28), but *H. gemellipara* is readily distinguished from it by its opposite hydrocladia, the one-chambered lateral nematothecae, and the lack of axillar nematothecae.

Halopteris gracilis (Clarke, 1879)
(fig. 39, table 29)

Plumularia gracilis Clarke, 1879: 246, pl. 5 [not *Antennella gracilis* Allman, 1877].
Plumularia clarkei; Nutting, 1900: 61, pl. 3 figs 5; Stechow, 1923b: 224.
Thecocaulus clarkei; Bedot, 1921b: 8.
Antennella diaphana diaphana; Van Gemerden-Hoogeveen, 1965: 51 (in part).

Material examined.

- 1) Holotype of *Plumularia gracilis* Clarke, 1879, MCZH 2238, from off Havana (Cuba), few fragments only.

- 2) Tortugas, Florida, U.S.A., RMNH Coel. 1620 (2 slides), (station 210 in Van Gemerden-Hoogeveen, 1965, as *Antennella diaphana diaphana*), coll. 10.vi.1925, depth 49 m, fertile.
- 3) Florida, Tortugas, U.S.A, RMNH Coel. 1621 (1 slide), as *Antennella diaphana diaphana*, (described by Van Gemerden-Hoogeveen, 1965; station 219), collected 2.vi.1925, depth 46 m.
- 4) Florida, off St. Lucie Island, U.S A., ROMIZ B1096, *Halopteris clarkei*, coll. 4.x.1976, id. D. Calder, infertile plumes up to 3 cm.

Description.— Colony forming 2 to 5 cm high plumes with mostly opposite hydrocladia that are placed at an angle of 150 to 180° when viewed from above. Plumes arise from ramified, tubular stolons.

Hydrocaulus monosiphonic, unbranched, with basal part ($^1/_5$) devoid of hydrothecae and hydrocladia and a longer distal part. Basal part divided into segments by transverse nodes, last node oblique, each segment with variable number of nematothecae. Stem above basal part heteromerously segmented by alternating oblique and transverse nodes, transverse nodes can be more or less reduced in proximal part of stem, up to 15 hydrothecae on hydrocaulus. Main segments with opposite pair of hydrocladia, one hydrotheca and five nematothecae: one median inferior, one pair of laterals, and an axillar pair. Intersegments bear four to eight nematothecae in two rows.

Hydrocladia inserted on short apophyses lateral to cauline hydrothecae. Apophysis followed by short, quadrangular segment; both lack nematothecae. Next segment long, with two nematothecae on upper surface. Remaining part of hydrocladium heteromerously segmented as described for stem, with up to 15 hydrothecae. Intersegments with one or rarely two nematothecae. Main segments as described for caulus but with single axillar nematotheca.

Hydrotheca cup-shaped, placed in middle of main segment, rim reaching beyond distal end of segment, adaxial and abaxial wall quite straight and parallel in lateral aspect. Hydrotheca adnate for about half its length, rim smooth and flat, opening at an angle of c. 45 to 65° to main axis.

Nematothecae of stem and hydrocladia all two-chambered. Median inferior nematotheca of main segments conical, adcauline wall of upper chamber much lowered. Lateral nematothecae on rounded pedicel shorter than nematotheca itself, reaching rim of hydrotheca, conical and with distal end variably rolled inwardly, both chambers of comparable size, inner and outer sides of upper chamber with broad emargination (half height of wall), inner notch often sinuated. Nematothecae of intersegments and others similar to median inferior but with longer lower chamber. Axillar nematothecae smaller, also two-chambered, adcauline wall of upper chamber lacking.

Female gonothecae inserted below cladial hydrothecae, up to 0.6 mm long and 0.3 mm in diameter, pear-shaped, only proximal part slightly curved, with two nematothecae near base, terminal region truncated, with rounded lid. Pedicel formed by two segments. One egg per gonotheca. Male gonotheca unknown.

Nematotcysts: a) telotrichous microbasic mastigophores, with shaft 2.0 times longer than capsule, undischarged capsule, (20-23.5) × (5.5-6.5)µm, found in nematophores; b) smaller capsules in tentacles, (5-6) × (1.5-2.0)µm.

Variation.— Some hydrocladia may be branched.

Type locality.— Off Havana, Cuba.

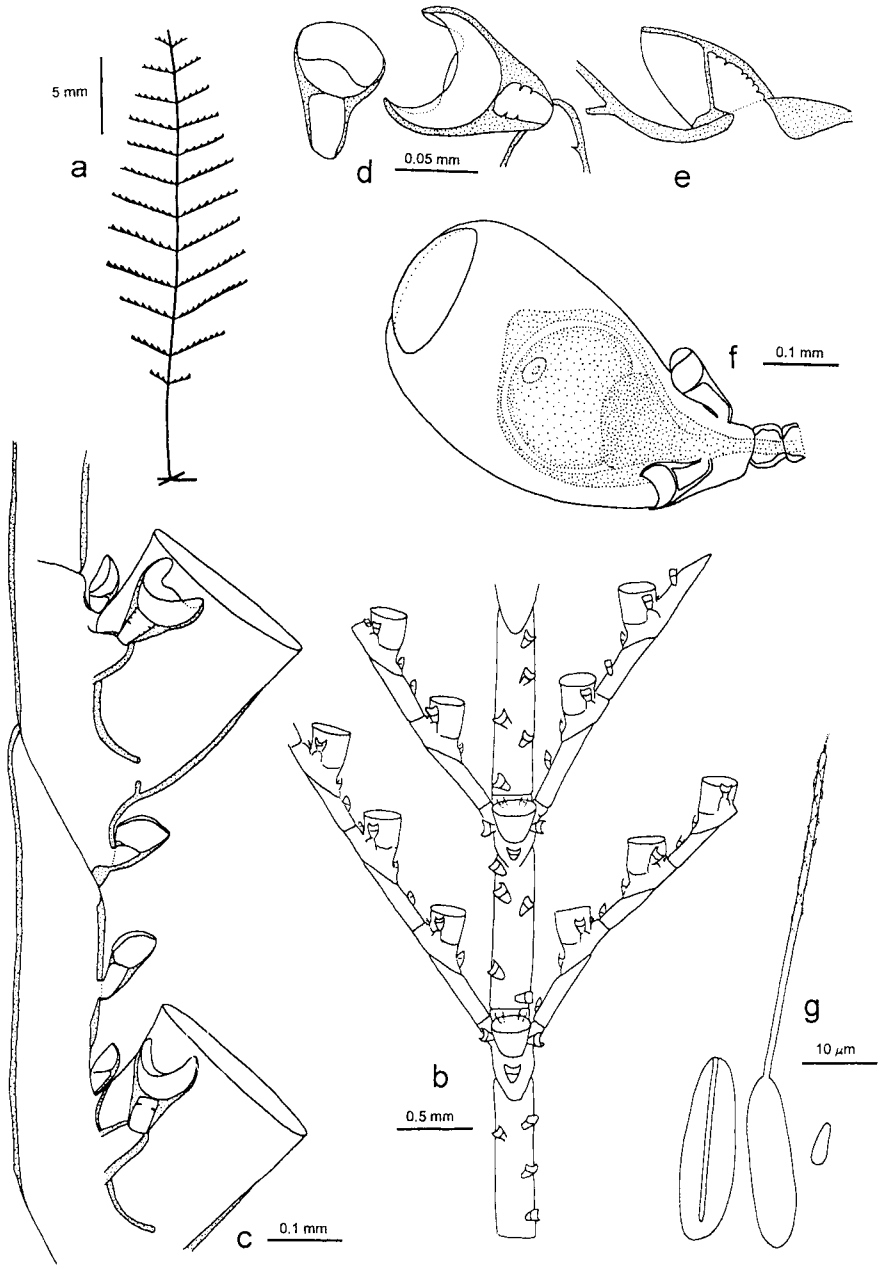

Fig. 39. *Halopteris gracilis* (Clark, 1879); all after sample no. 4, except left nematotheca in d which is from holotype material, and f which is from sample no. 2; a, whole plume, note opposite hydrocladia; b, part of stem with proximal parts of hydrocladia; c, part of hydrocladium, note presence of single nematotheca in upper axil of hydrotheca; d, nematothecae, from left to right, lateral nematotheca from holotype, lateral nematotheca with pedicel; e, median inferior nematotheca, same scale as e; f, female gonotheca and gonophore with one egg; g, nematocysts: large microbasic mastigophore, same discharged, small capsule from tentacles.

Distribution.— Cuba to Florida.

Remarks.— The type material of *Halopteris gracilis* consists of a few damaged stem fragments only. However, some important characters as the opposite hydrocladia and the nematothecae in the upper axil of the hydrothecae could be observed. The identification of the other samples as *H. gracilis* is therefore quite reliable. Some material of *H. gracilis* has been incorrectly identified as *Antennella diaphana* by Van Gemerden-Hoogeveen (1965). Otherwise this species has been found only rarely. *Halopteris geminata* (Allman, 1877) closely resembles *H. gracilis*, as has already been noted by Nutting (1900). The differences between these species are discussed under *H. geminata*.

Bedot (1914) considered *H. gracilis* to be synonymous with *H. catharina*. However, this is improbable because *H. gracilis* has only one pair of lateral nematothecae and *H. catharina* lacks axillar nematothecae. Also the dimensions of both species are rather different.

Halopteris geminata (Allman, 1877)
(fig. 40, table 29)

Plumularia geminata Allman, 1877: 32, pl. 20 figs 1-4; Nutting, 1900: 61, pl. 3 figs 3-4.

Material examined.— MCZH collection as *Plumularia geminata* Allman, 1877, without collection number, probably type material as Allman's material of the Gulf Stream Survey was deposited in MCZH, but type status uncertain; label similar to that in other samples collected during Pourtalès's Gulf Stream Exploration (A. B. Johnston, pers. com); with male gonotheca, contains also a polysiphonic species of *Eudendrium*.

Description (after Nutting 1900 and MCZH material).— Colonies forming up to 2.5 cm high plumes with dichotomously branched caulus. Plumes with opposite hydrocladia.

Table 29. Variation and measurements of *Halopteris gracilis* (sample 1 and 2) and *Halopteris geminata* (*H. gem*), in [µm] if not stated otherwise.

material	1	2	*H. gem*
caulus height [mm]	30	25	-
max. number of cladia per side	15	>15	-
cauline main segments	480-650	410-520	480-510
cauline intersegments	900-1300	1000-1200	810-1160
diameter caulus	230-280	220-240	160-180
nematothecae/cauline intersegment	4-8	4-6	4-9
length of apophysis	80-140	50-60	60
length of 2nd cladial segment	600-740	530-580	510-580
cladial main segments	400-460	350-420	450-510
cladial intersegments	380-500	410-500	490-620
abcauline side of hydrotheca	280-300	220-250	260-270
free adcauline side of hydrotheca	120-150	120-130	150-160
diameter of hydrotheca	220-250	210-230	250-280
pedicel of lateral nematothecae	30-40	30-40	-
tentacle number	appr. 14	-	-

Hydrocaulus homomerously segmented, in distal part of stem often heteromerously segmented. Segments of stem with nematothecae arranged as in hydrocladia, only axillar nematothecae seem to be paired, and with up to six nematothecae on homologues of intersegments.

Hydrocladia heteromerously segmented by alternating oblique and transverse nodes, but transverse nodes often reduced. Each hydrotheca associated with four nematothecae: one median inferior, one pair of laterals, and a small axillar one. Intersegments, or their equivalents if no transverse node present, with two to three nematotheca.

Hydrotheca cup-shaped, rim reaching beyond transverse node if present, slightly flared, abcauline and adcauline walls straight and only slightly converging proximally. Hydrotheca adnate for half of adcauline length, angle of opening with hydrocladial axis 50 to 60°.

Nematothecae of stem and hydrocladia all two-chambered. Median inferior nematothecae do not reach hydrotheca, movable, adcauline wall of upper chamber lacking. Lateral nematothecae on pedicels of similar height as nematotheca itself, reaching almost to rim of hydrotheca, mobile, shape conical and wall of upper chamber straight, lower chamber longer than upper one, rim of upper chamber on inner side lowered to bottom of upper chamber. Nematothecae of intersegments similar to median inferior ones.

Male gonotheca elongated, pear-shaped, with one nematotheca at its base.

Type locality.— Sand Key, Florida, U.S.A.

Distribution.— Florida, Barbados

Remarks.— The material examined, possibly the type of Allman's species, consists of fragments only. The hydrocauli show the characteristic opposite hydrocladia, but no portion of the branched stem was found. The minute structure was found to resemble closely *Halopteris gracilis* (Clarke, 1879). Only the lateral nematothecae have a straight wall and there are two or three nematothecae on the cladial intersegments instead of one only. Measurements for *H. geminata* are given in the table 29, together with those of *H. gracilis* to allow an easier comparison. Following Nutting (1900), both species are also kept separate on account of the dichotomously branched caulus in

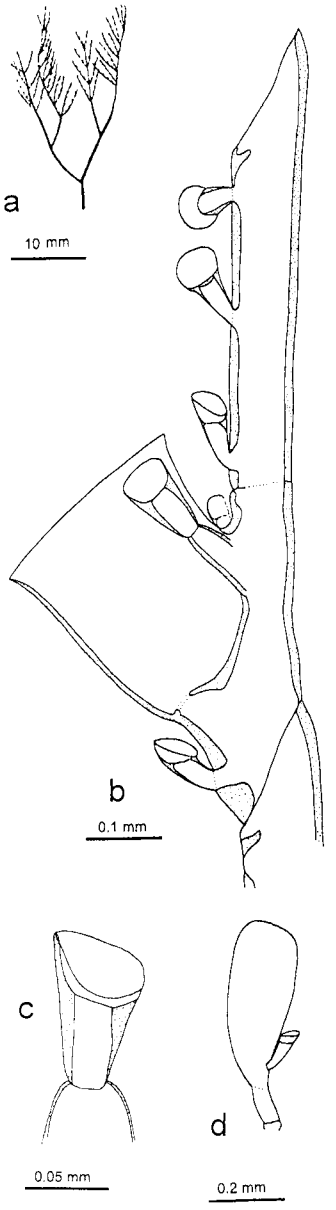

Fig. 40. *Halopteris geminata* (Allman, 1877); a after Allman, 1877, b-d after probable type material; a, colony; b, hydrocladial repeat, note presence of small nematotheca in upper axil of hydrotheca; c, lateral nematotheca, adaxial view; d, male gonotheca.

H. geminata. More material of this species is needed to clarify its relationship to *H. gracilis*, with which it is probably conspecific.

Halopteris opposita (Mulder & Trebilcock, 1911) (fig. 41, table 30)

Plumularia opposita Mulder & Trebilcock, 1911: 120, pl. 2 fig. 5; Billard, 1913: 23; Stechow, 1923b: 223.
Thecocaulus oppositus; Bedot, 1921b: 9; Blackburn 1938: 316, fig. 2.
Plumularia opposita Var. (a) Mulder & Trebilcock, 1911: 121, pl. 2 fig. 5a.
Thecocaulus oxyrhynchus Stechow, 1923b: 223.
Halopteris opposita; Watson, 1973: 184, fig. 47.

Material examined.
- 1) Holotype, slide F57990 from MVM, ex collection Trebilcock (Stranks, 1993), labelled: 28 *Plumularia opposita*, Type; thus holotype by original designation.
- 2) Pearson Island, South Australia, MVM slide F42023, ex. collection Watson (Watson, 1973), 8.i.1969, depth 30 m.

Description.— Colony forming up to 9 mm high plumes arising from tubular, ramified stolons.

Hydrocaulus monosiphonic, unbranched, with basal part (1/4) devoid of hydrothecae and hydrocladia and longer distal part bearing hydrothecae and hydrocladia. Basal part divided into segments by two or three straight nodes, last node ending in oblique hinge-joint, segments with one nematotheca. Stem above basal part segmented heteromerously by alternating oblique and transverse nodes. Sometimes second intersegment without nematotheca is delimited from distal end of main segment. Main segments of stem with two hydrocladia on opposite sides, a hydrotheca, and four nematothecae: one median inferior, one pair of laterals, and an axillar one. Intersegments with one or two nematothecae. Majority of nodes deeply constricted.

Hydrocladia inserted on well-formed stem apophysis, placed lateral to hydrothecae. Apophysis without nematotheca. First segment of hydrocladium short, without nematotheca. Second segment elongate, with one median nematotheca on upper side. Remaining part of hydrocladia organised as in caulus with up to three repeats. Thickness of perisarc variable. Main segments with four nematothecae: one median inferior, a lateral pair, and a smaller one in upper axil of hydrothecae. Intersegments with one nematotheca. Sometimes second intersegment without nematotheca is delimited from distal end of main segment.

Hydrotheca cup-shaped, abcauline wall slightly concave with internal, semicircular, transverse ridge in lower part, adcauline wall straight, adnate for half its length, angle of opening with hydrocladial axis 40°.

Nematothecae of stem and hydrocladia all two-chambered. Median inferior nematothecae mostly reaching hydrotheca, with short adcauline wall, partly fused to hydrocladium, presumably immovable. Lateral nematothecae on pedicels longer than nematotheca itself, nematotheca reaching beyond rim of hydrotheca, conical, movable, lower chamber slightly longer than upper one, rim of upper chamber missing on inner side. Nematothecae of intersegments similar to basalmost median inferior ones, but with longer free adcauline wall and movable.

Gonothecae unknown.

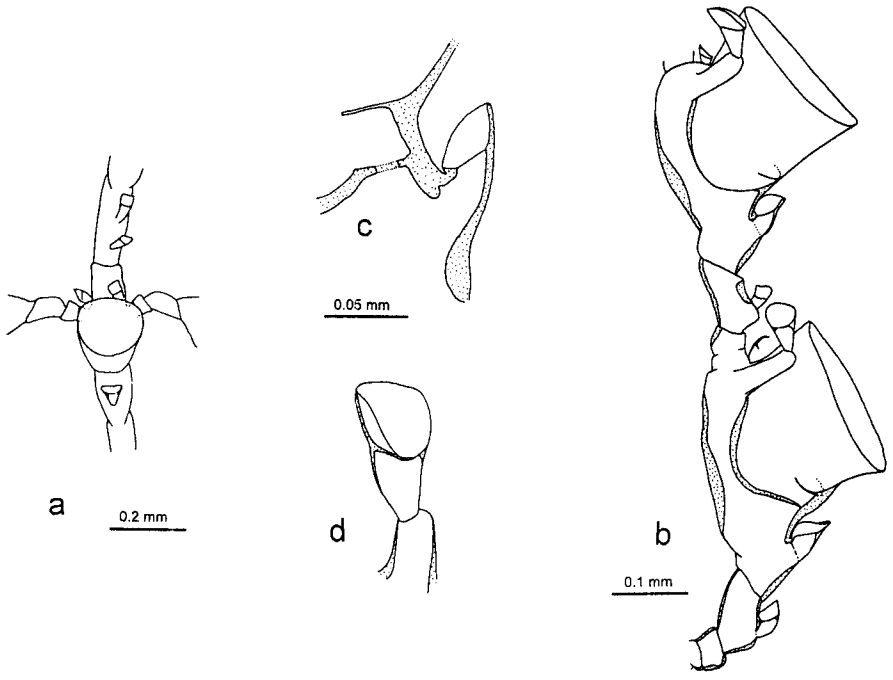

Fig. 41. *Halopteris opposita* (Mulder & Trebilcock, 1911); a, part of caulus with bases of opposite hydrocladia; b, proximal part of hydrocladium; c, median inferior nematotheca and basal part of hydrotheca with intrathecal ridge; d, lateral nematotheca seen from inner side.

Type locality.— Torquay, Victoria, Australia.

Distribution.— South Australia, Victoria, Sir Joseph Banks Islands, Australia.

Remarks.— Although its gonothecae are unknown, *Halopteris opposita* is a rather distinct species. Its opposite hydrocladia and the abcauline, intrathecal ridge make it readily identifiable. The only species of *Halopteris* with opposite hydrocladia and a nematotheca in the upper axil of the hydrothecae is *H. gracilis* from the Caribbean. However, the size and number of nematothecae readily distinguish *H. gracilis* from *H. opposita* (see also table 27).

Table 30. Dimensions of *Halopteris opposita*, in µm if not stated otherwise.

sample no.	1	2
cauline main segments	390-470	430-460
cauline intersegments	200-320	320-350
nematothecae/cauline intersegment	1-2	1-2
cladial main segments	280-320	320-340
cladial intersegments	100-110	90-150
abcauline side of hydrotheca	120-140	120-170
free adcauline side of hydrotheca	50-70	80-100
diameter of hydrotheca	-	180-230

Stechow (1923b) created a new species, *Thecocaulus oxyrhynchus*, for Mulder & Trebilcock's (1911) var. a of *Plumularia opposita*, because it is supposed to have a differently shaped hydrotheca. No material of this variety was available and the figure of Mulder & Trebilcock (1911, fig. 5a) does not show a significant difference with the typical form. Following Blackburn (1938), *Thecocaulus oxyrhynchus* is here treated as a synonym of *Halopteris opposita*. Billard (1913) thinks that *P. opposita* is synonymous with his *H. buskii* (= *H. nuttingi*), which seems improbable.

Halopteris plagiocampa (Pictet, 1893)
(fig. 42, table 31)

Plumularia plagiocampa Pictet, 1893: 56, pl. 3 fig. 50; Billard, 1913: 31, fig. 23; Jäderholm, 1919: 21.
Thecocaulus plagiocampus; Bedot, 1921b: 9.

Material examined.
- 1) Siboga station 77 (3°27'S 117°36'E, Indonesia), ZMA Coel. 4043, as *Plumularia plagiocampa*, depth 59 m, fragment of a plume in bad condition.
- 2) Siboga station 164 (1°4.5'S 130°47.5'E, Indonesia), ZMA Coel. 5289, as *Plumularia plagiocampa*, depth 32 m, two plumes 10 and 11 mm, with female gonothecae.
- 3) Siboga station 164, ZMA Coel. 4043, as *Plumularia plagiocampa*, depth 32 m, 6 plumes, max. 25 mm, some with female gonothecae.
- 4) Siboga station 258 (Kei Island, Indonesia), ZMA Coel. 4043, as *Plumularia plagiocampa*, depth 22 m, 3 plumes, up to 8 mm, with male gonothecae.

Description.— Colony forming up to 25 mm high plumes with opposite hydrocladia. Plumes arise from ramified, tubular stolons. *Antennella*-like stems not observed. Stolons with frequent nematothecae.

Hydrocaulus monosiphonic, unbranched, with basal part devoid of hydrothecae and hydrocladia and a longer distal part. Distal part heteromerously segmented by alternating oblique and transverse nodes. Transverse nodes subdividing repeats may be weak or absent in lower part of stem. Intersegments longer than main segments, with two to four median nematothecae. Main segments with opposite hydrocladia, a hydrotheca in middle, and three nematothecae: one median inferior and a pair of laterals.

Hydrocladia arise on short apophysis lateral to cauline hydrothecae, up to eight hydrocladia per side. Apophysis followed by short, quadrangular segment, both lacking a nematotheca. Next segment long, with one nematothecae on upper surface. Remaining part of hydrocladium heteromerously segmentred by alternating oblique and transverse nodes, often with quadrangular segment without nematothecae intercalating between main- and intersegments. Intersegments with single median nematotheca. Main segments with three nematothecae: one median inferior and a pair of laterals.

Hydrotheca cup-shaped, placed in middle of main segment, rim reaching distal end of segment, adaxial and abaxial walls quite straight and parallel in side view. Hydrotheca adnate for about half its length, rim smooth and flat, opening at an angle of about 40 to 50° with hydrocladial axis.

Nematothecae of stem and hydrocladia all two-chambered and movable. Median inferior nematotheca of main segments conical, adcauline wall of upper chamber

lowered. Lateral nematothecae on short, rounded pedicel, conical, walls straight, rim even or only slightly emarginated on inner side, lower chamber longer than upper one. Nematothecae of intersegments and others similar to median inferior ones but with longer lower chamber.

Gonothecae of two sexes only known from separate colonies, arising from stems. Female gonotheca up to 0.73 mm long, placed on pedicel of two quadrangular segments. Outer surface of female gonotheca evenly curved for its entire length and thus forming a semi-circle, inner side only curved near base, then straight, end truncated with large lid, base with three nematothecae. Male gonothecae up to 0.65 mm long, on a pedicel of one or two segments, sausage-shaped, only slightly curved, with two nematothecae near base, terminal lid small and inconspicuous.

Nematotcysts: a) microbasic euryteles, often with lower half of shaft swollen and thus resembling pseudostenoteles, found in nematophores only, (17-18) × (8.5-9) µm, s = 0.7 to 1.4; b) smaller capsule in tentacles, almond-shaped, (4-5) × (1) µm.

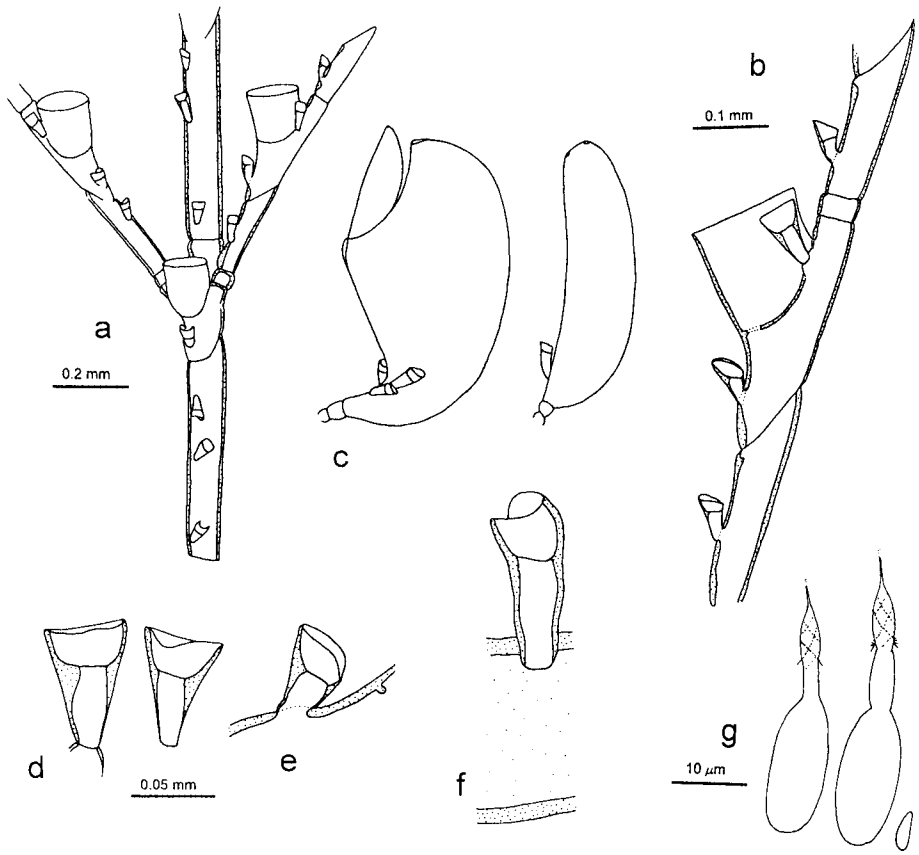

Fig. 42. *Halopteris plagiocampa* (Pictet, 1893); a and female gonotheca in c from sample no. 1, all others from sample no. 4; a, part of stem showing opposite hydrocladia; b, part of hydrocladium; c, female (left) and male gonotheca (right), same scale as a; d, lateral nematothecae showing degree of variation in shape; e, median inferior nematotheca, same scale as d; f, stolon in lateral view with nematotheca, same scale as d; g, nematocysts: two microbasic euryteles and small capsule from tentacles.

Type locality.— Bay of Amboina.

Distribution.— Indonesia, Japan (Billard, 1913; Jäderholm, 1919).

Remarks.— No type material of *H. plagiocampa* seems to be available anymore. Pictet's material collected in Amboina is kept by the Museum of Natural History of Geneva, but no material of this species could be located by the present author. Pictet's (1893) figures and description, however, are detailed enough to recognise this species and it is quite certain that the other samples attributed to *H. plagiocampa* also belong to here.

Table 31. Dimensions of *Halopteris plagiocampa*, measurements in µm.

sample no.	4
cladial main segments	300-340
cladial intersegments	240-290
abcauline side hydrotheca	120-140
free adcauline side hydrotheca	70-80
diameter hydrotheca	140-150

Halopteris plagiocampa is identical with *H. diaphana* in almost all details, except for the arrangement of the hydrocladia. Especially notable is the similarity of the gonothecae (cf. figs 15f and 42c). The nematocysts differ slightly as *H. plagiocampa* has somewhat unusual euryteles, however, similarly shaped euryteles can also be found in *H. diaphana* and it is not clear whether their condition might not be an artifact of fixation. Because the possession of opposite hydrocladia is otherwise considered a good distinguishing character, *H. plagiocampa* is here kept separate. Also biogeographical arguments favour their specific distinction.

Halopteris zygocladia (Bale, 1914)
(fig. 43, table 32)

Plumularia zygocladia Bale, 1914: 171, pl. 26 fig. 2.
Schizotricha zygocladia; Bedot, 1921b: 13.

Material examined.— Syntype material, 3 slides MVM F58339, collection Bale (Stranks, 1993), original labels: *Plumularia zygocladia* Bale, North East of North Reef 'Endeavour' 1913.

Description.— Colony forming up to 4 cm high plumes. Hydrocladia in opposite pairs.

Hydrocaulus robust, monosiphonic, unbranched, homomerously segmented by oblique nodes. Each segment with one hydrotheca and up to eight nematothecae: one median inferior, one pair of laterals, and two to five median ones on distal part of segment. Cauline hydrothecae near proximal end of segment.

Hydrocladia inserted on short apophyses lateral to cauline hydrothecae. Apophysis without nematotheca. First segment of hydrocladium elongated, with one median nematotheca on upper side. Remaining part of hydrocladia organised in homomerous repeats with oblique nodes, up to ten repeats per hydrocladium. Rarely a transverse node delimits distal intersegment from main segment. Segments with four nematothecae: one median inferior, one lateral pair and one (rarely two) nematotheca on distal part of segments.

Hydrotheca cup-shaped, abcauline and adcauline walls straight in lateral view, converging proximally, rim often slightly flared. Hydrotheca adnate for half of its adcauline length, angle of opening with hydrocladial axis 40 to 50°.

Nematothecae of stem and hydrocladia all two-chambered. Median inferior nema-

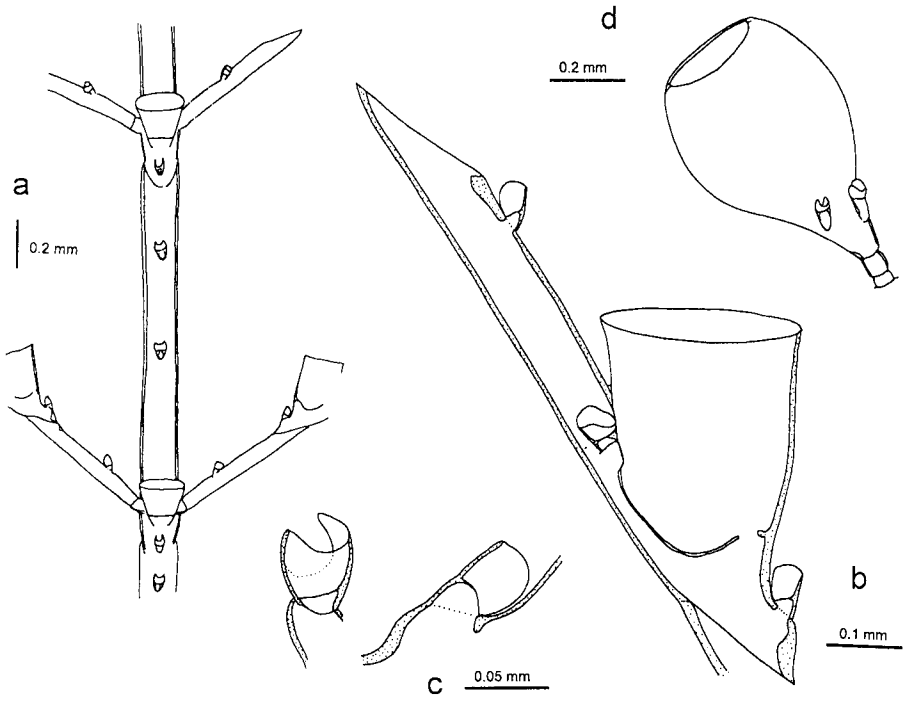

Fig. 43. *Halopteris zygocladia* (Bale, 1914); after type material; a, part of stem showing opposite hydrocladia, note segment length; b, segment of hydrocladium; c, lateral (left) and median inferior (right) nematotheca; d, female gonotheca.

totheca not reaching hydrotheca, probably not movable, adcauline wall of upper chamber absent, abcauline wall emarginated. Lateral nematothecae on short pedicels, mobile, wall of upper chamber rolled inwardly, lower chamber short. Upper chamber with deep emargination on inner side and a less deep one on outer side (spanner-type of nematotheca).

Female gonothecae inserted singly below side of hydrothecae of stem and hydrocladia. Male gonothecae not seen. Female gonotheca placed on pedicel composed of two segments, body of gonotheca up to 0.7 mm long, rounded, with tapering base and truncated end, with distal lid, and with two nematothecae near base.

Additional information.— Bale (1914) describes the colour as whitish.

Type locality.— 38 miles north-east of North Reef Lighthouse, Capricorn Group, Queensland, Australia, depth 135 m.

Distribution.— Only known from type locality.

Remarks.— Female gonotheca, hydrothecae and nematothecae of *Halopteris zygocladia* are indistinguishable from those of *H. campanula*. *Halopteris zygocladia* only differs from *H. campanula* by its opposite hydrocladia and the much longer cauline

Table 32. Dimensions of *Halopteris zygocladia*, measurements in µm.

material	type
cauline segments	1900-2840
cladial segments	800-1000
abcauline side hydrotheca	260-270
adcauline side hydrotheca	110-130

segments that also bear more nematothecae. Although *H. campanula* is a highly variable species, opposite or alternate hydrocladia is a reliable character to separate species and as a consequence *H. zygocladia* is here recognised as a valid species.

Halopteris group of various species

Remarks.— This left-over assemblage contains the following species: *H. carinata*, *H. concava*, *H. infundibulum*, and *H. regressa*, the majority being rather distinct species.

Halopteris concava (Billard, 1911)

Plumularia concava Billard, 1911: 65; 1913: 19, figs 9-10, pl. 1 fig. 14.
Thecocaulus concavus; Bedot, 1921b: 8.

Diagnosis (after Billard, 1913).— Plumes 6 cm high, monosiphonic, with alternate hydrocladia, five to six pairs of nematothecae above cauline hydrotheca. Hydrocladia: only distally some intersegments demarcated, two to four median nematothecae above hydrotheca, one lateral nematotheca on each side, those deeply emarginated on inner and outer side, axillar nematothecae absent. Hydrotheca with deeply concave adcauline side, free for about half its length. Gonotheca pyriform, with two nematothecae.

Type locality.— Duroa Strait, Kei Islands, Indonesia, 52 m

Distribution.— Known from type locality only.

Remarks.— *Halopteris concava* is characterised by hydrothecae with a concave adaxial wall and the numerous cauline nematothecae. The species has been found once only and it could not be re-examined for this study. Billard (1913) provides good description and figures for this species.

Halopteris infundibulum Vervoort, 1966
(fig. 44)

Halopteris infundibulum Vervoort, 1966: 133, fig. 36.

Material examined.— Schizoholotype, RMNH Coel. 3757, Galathea station 626, 42°10′ S 170°10′E, depth 610 m, slide, part of plume, with eroded gonothecae.

Description (after schizoholotype and Vervoort, 1966).— Colony forming up to 3.5 cm high plumes with alternate hydrocladia.

Hydrocaulus monosiphonic or polysiphonic, unbranched, with basal part free of hydrocladia, hydrothecae, and nematothecae. Basal part ends in two hinge-joints framing a segment with nematothecae. Hydrocaulus above hinge-joints segmented by transverse nodes that can be weak or absent. Each cauline segment with a hydrocladium and hydrotheca. Lateral to each cauline hydrotheca two pairs of nematothecae. Between two successive hydrothecae two median nematothecae.

Hydrocladia placed on well formed apophyses lateral to cauline hydrothecae and displacing lateral nematotheca. First segment short, with proximal transverse node and distal oblique node, without nematotheca. Remainder of hydrocladium

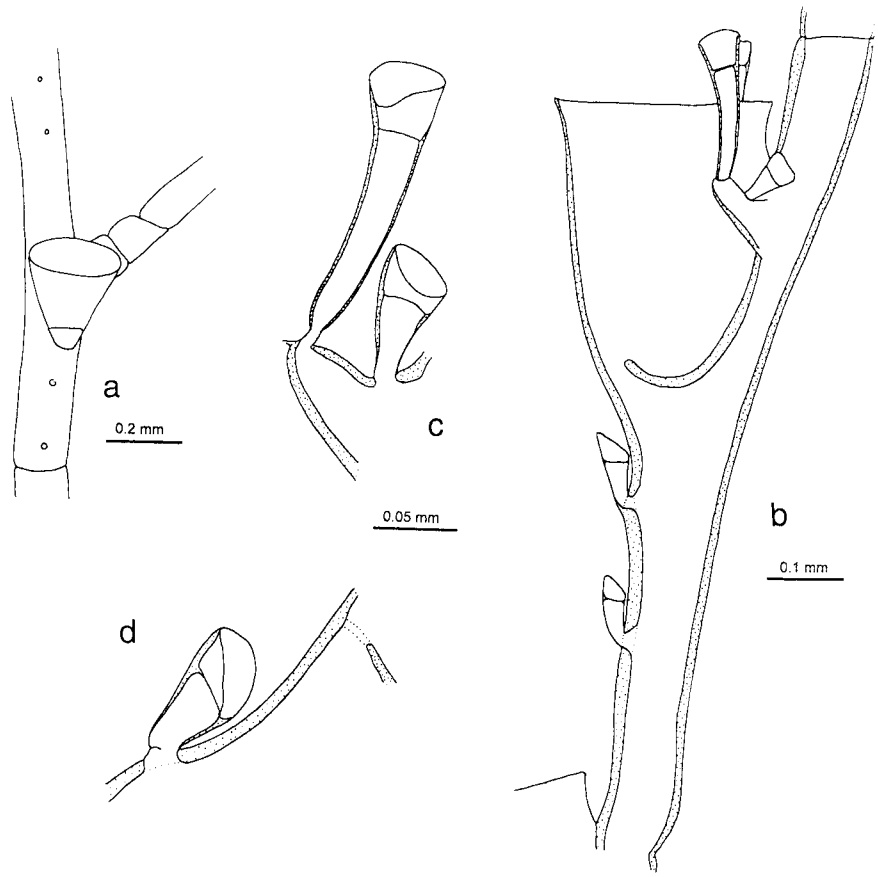

Fig. 44. *Halopteris infundibulum* Vervoort, 1966; after schizoholotype; a, part of hydrocaulus and hydrocladium, nematothecae are lost; b, part of hydrocladium; c, lateral nematothecae; d, median inferior nematotheca, same scale as c.

mostly unsegmented, only occasionally a transverse node above hydrotheca can be found. Hydrocladia bear 8 to 12 hydrothecae. Each hydrotheca with two pairs of lateral nematothecae. Between two successive hydrothecae two median nematothecae.

Hydrotheca almost cylindrical, fairly deep, with slightly flared rim, adcauline wall adnate for $^3/_4$ of its length, angle of opening with hydrocladial axis c. 80°.

Nematothecae all two-chambered and movable. Median nematothecae conical, walls mostly straight, lower chamber deeper than upper one, adaxial side of upper chamber lowered. First lateral nematotheca on long pedicel, nematotheca long, reaching beyond hydrothecal margin, conical, slightly curved, lower chamber much longer than upper one, walls of upper chamber straight and emarginated on inner side to half height of wall. Second pair of laterals seated on lower, distal half of pedicel of first pair, shorter than first one, otherwise similar.

Gonothecae only known in immature state, cone-shaped, with two nematothecae, and placced on long pedicel.

Type locality.— East of Cape Foulwind, South Island, New Zealand, depth 610 m.

Distribution.— Known from type locality only.

Remarks.— *Halopteris infundibulum* is easily separable from all other congeners. Two pairs of lateral nematothecae are also found in *H. catharina* and *H. carinata*. However, the opposite hydrocladia of *H. catharina* and the toothed margin of *H. carinata* readily distinguish those species from *H. infundibulum*. Other obvious characters such as segmentation, lateral nematothecae, etc. make it quite distinct.

Vervoort (1966) noted that the extreme basal part of the only specimen of *H. infundibulum* so far found has accessory tubules forming a polysiphonic stem. It may thus be that older colonies have a fully polysiphonic stem.

Halopteris carinata Allman, 1877
(fig. 45, table 33)

Halopteris carinata Allman, 1877: 33, pl. 19 figs 3-7; Bale, 1887: 80; Nutting, 1900: 86, pl. 17 figs 7-9; Bedot, 1923: 216, fig. 3; Stechow 1926: 106; Vervoort, 1968: 54, fig. 26; Calder, 1996.

Material examined.— Florida, off Palm Beach (26°48.4'N 79°58.6'W), U.S.A., ROMIZ B1084, as *H. carinata*, depth 37 m, 16.ix.1975, infertile colony up to 9 cm high, one branched hydrocaulus present.

Description (after Vervoort, 1968 and examined material).— Colonies forming up to 13 cm high plumes that arise from tangled mass of stolons. Plumes slender, hydrocladia relatively short, hydrocladia alternate, up to 40 hydrocladia per side.

Stems monosiphonic, either unbranched or branched once, with basal part devoid of hydrothecae and hydrocladia and divided into segments by transverse nodes, segments with up to ten nematothecae. Basal part separated from distal part by oblique hinge-joint. Distal part homomerously segmented by only slightly oblique nodes. Each segment of caulus with hydrocladium, hydrotheca, and seven nematothecae: one median inferior, a pair of laterals, and four superior ones distributed rather irregularly or in two rows on distal part of segment.

Hydrocladia placed on apophyses lateral to hydrothecae; first segment quadrangular, second segment elongated with distal, oblique node and one median nematotheca. Remainder of hydrocladium composed of either alternating main- and intersegments or fused main- and intersegments. Main segments with hydrotheca surrounded by five nematothecae: one median inferior and two pairs of laterals. Intersegments, or their equivalents if fused to main segment, with one nematotheca.

Hydrotheca more or less cup-shaped, abcauline wall slightly bulging, adcauline wall straight, adnate for about $^3/_4$ of its length. Rim of hydrotheca with distinct cusp on abcauline side, continuing down abcauline side as frontal ridge (carina). Plane of hydrothecal opening at an angle of 60-70° to hydrocladial axis.

Nematothecae all two-chambered except second lateral pair. Median inferior scoop-shaped, not movable, adcauline side short, inner side of upper chamber missing. First pair of lateral nematothecae on long pedicels fused to hydrotheca, nematotheca cylindrical, apparently fixed to pedicel and forming a wide angle with it, composed of two chambers of equal depth, rim smooth and even, overtopping hydrothecal rim. Second pair of lateral nematothecae scale-shaped and placed in upper axil of lateral pedicel. Remaining nematothecae conical, movable, with inner side of upper chamber absent.

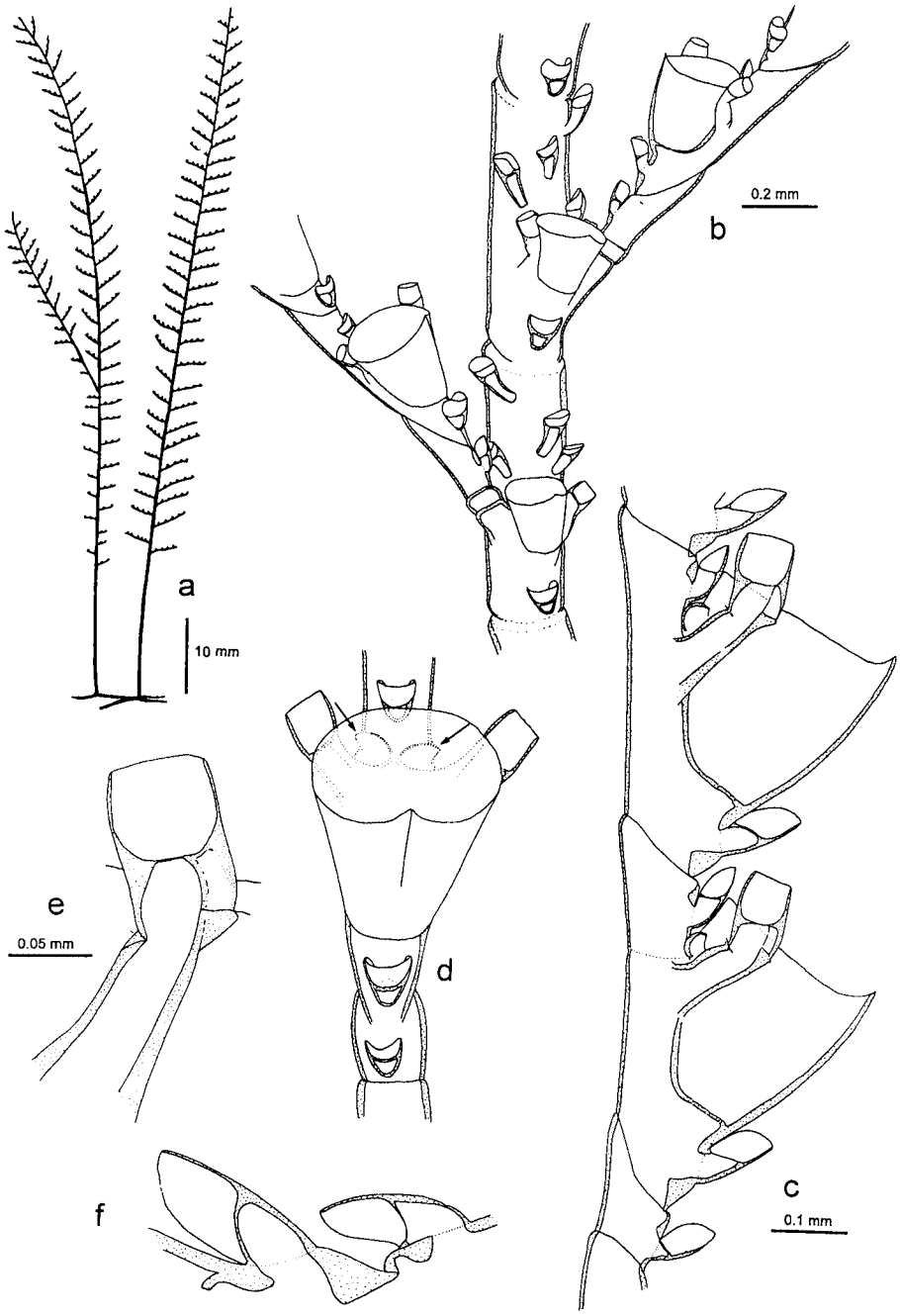

Fig. 45. *Halopteris carinata* Allman, 1877; after sample from ROMIZ; a, part of colony with two plumes, left one with branched hydrocaulus; b, part of hydrocaulus with bases of two hydrocladia; c, part of hydrocladium, note presence or absence of transverse nodes; d, hydrotheca in frontal view, note abaxial cusp and carina, arrows point towards scale-shaped second lateral pair of nematothecae, same scale as c; e, first lateral nematotheca; f, median inferior (left) and superior (right) nematotheca, same scale as e.

Only male gonothecae known, sac-shaped, c. 0.5 mm long, without visible aperture or nematothecae.

Type locality.— Florida, off Carysfort Reef, depth 64 m (Allman, 1877).

Distribution.— Florida, Bermuda, Caribbean, Brazil, shallow waters to 161 m (Calder, in press).

Table 33. Dimensions of *Halopteris carinata*, in µm if not stated otherwise.

material	Palm Beach
caulus diameter	220-400
cladial main segments	340-480
cladial intersegments	140-200
abcauline side hydrotheca	230-290
free adcauline side hydrotheca	100-140
diameter	220-250
number of tentacles	~14

Remarks.— *Halopteris carinata* is readily distinguished from other species of *Halopteris* by its barrel-shaped lateral nematothecae on a long pedicel, by the small median abcauline tooth on the otherwise even hydrothecal rim, and the hydrothecal carina. In being morphologically distinct and the type species of a widely recognised genus, *H. carinata* has an uncomplicated taxonomic history (see also Vervoort, 1968; Calder, in press).

The first lateral nematothecae is special in its apparent immobility and shape, which is nearly cylindrical. As can be seen from fig. 45e, it is distinctly two-chambered, but its broad base is fused to the pedicel.

Halopteris regressa (Billard, 1918)

Plumularia regressa Billard, 1918: 24.

Type locality.— Indonesia, exact locality not given.

Remarks.— Billard (1918) described *H. regressa* from a 0.5 cm high, infertile fragment of one plume and he did not provide a figure. *Halopteris regressa* is at present not recognisable. Billard (1918) noted that it closely resembles material of *P. buskii* described by him in 1913, material which is here referred to *H. polymorpha*. According to Billard (1918), *H. regressa* differs only in the absence of axillar nematothecae, though an axillar nematophore could be present.

Halopteris rostrata Millard, 1975

Halopteris rostrata Millard, 1975: 357, fig. 114A-C; 1978: 193.

Type locality.— Off Natal, 29°11'S 32°02'E, depth 70 m.

Distribution.— South Africa.

Remarks.— *Halopteris rostrata* is well documented by Millard (1975). As *H. carinata* it has an abcauline cusp on the rim of the hydrotheca, but seems to lack a carina below it. *H. rostrata* has small (1 cm) plumes and its gonothecae are unknown. Perhaps it will prove to be the juvenile form of another species.

Genus *Monostaechas* Allman, 1877

Diagnosis.— Halopteridídae with or without erect stems. If present and polysiphonic, stem composed of intercommunicating tubes of equal diameter and impor-

tance, irregularly giving rise to hydrocladia. If absent, hydrocladia arise directly from hydrorhiza. Hydrocladia branched in one plane or forming a sympodium, successive branches arising from posterior surface of previous hydrocladium, typically all branches directed towards same side, or, rarely, alternating, or helicoid. Hydrotheca cup-shaped, margin without cusps.

Type species.— *Monostaechas dichotoma* Allman, 1877 [syn. *Plumularia quadridens* McCrady, 1858].

Remarks.— Species of *Monostaechas* are all characterised by the special branching pattern of their hydrocladia. Each successive hydrocladium originates from the posterior side of the basal, ahydrothecate segment of the previous hydrocladium. A stem can be either present or absent. In the last case, the hydrocladia directly develop from the creeping stolons. In some species, a stem can be present. In the most simple case this is a caulus-like structure that branches into sets of hydrocladia. In some cases the stem branches dichotomously or trichotomously several times and then gives off sets of hydrocladia. In some species the stem can be longer and give off sets of hydrocladia laterally (*M. fisheri*), or it can be a polysiphonic bundle of stolon-like tubes that give off sets of hydrocladia, corresponding to the situation in *Corhiza* (e.g. *M. faurei*).

The characteristic branching pattern could be good synapomorphy and thus the genus may prove to correspond to a clade. This has to be confirmed by a cladistic analysis including all members of the Plumularioidea. The affinities of *Monostaechas* with the other Halopteridídae are not very obvious because it is not entirely clear what the homologue of the caulus is, and whether it bears hydrothecae or not. Especially *M. fisheri*, that has a main axis lacking hydrothecae, and the appearance of *M. quadridens* with its dichotomously branched stems, illustrate the point. *Monostaechas* could thus also belong to the Plumulariidae.

Billard (1913) and Millard (1975) use the term 'helicoid sympodium' differently. In *Monostaechas*, the successive hydrocladia typically branch from the backside of the previous hydrocladium and are therefore in one plane and all on one the same side (Billard's 'scorpioid sympodium', the term 'scorpioid' probably relates to the resulting curved structure). When the successive hydrocladia are not all directed towards the same side, but in alternate direction, Billard (1913) speaks of a 'helicoid sympodium'.

Table 34. Important distinguishing characters of *Monostaechas* species.

character	*M. faurei*	*M. fisheri*	*M. natalensis*	*M. quadridens*	*M. sibogae*
stem	polysiphonic	present,-unbranched	polysiphonic or absent	present or not, can be branched	absent
cladial branching	one sided	one sided	one sided	one sided	two sided, or helicoid
hydrotheca	completely adnate	free for one half	free for one half	free for one half	free for one half
axillar nematotheca	absent	present	absent	present	absent?
cladia adnate for some distance	no	no	yes	no	no
lateral nematothecae	2 pairs	1 pair	2 pairs	1 pair	1 pair

This type of branching is so far only known from *M. sibogae*. Millard (1975) incorrectly used the term helicoid sympodium for a branching pattern that corresponds to Billard's scorpioid sympodium and contrasts it to a dichotomous branching pattern. If these terms are used at all, Billard's (1913) intentions should be followed as it has been done by Vervoort (1968). The characters used to distinguish the known species are given in table 34. The species are easy to separate, *M. fisheri* only is somewhat problematic.

Monostaechas faurei Millard, 1958

Monostaechas faurei Millard, 1958: 204, fig. 11; 1968: 277, fig. 5E; 1975: 362, fig. 116A-D; 1978: 195.

Type locality.— Off Natal, 28°41'S 32°22'E, 62 m.

Distribution.— South Africa.

Remarks.— This is a very distinct species and well described by Millard, 1975. It is characterised by its completely adnate hydrothecae and the hydrocladia that after branching are adnate for a short distance before bending away. At the distal end of the adnate part, both hydrocladia are connected and they communicate through a pore.

Monostaechas fisheri Nutting, 1905
(fig. 46, table 35)

Monostaechas fisheri Nutting, 1905: 952, pl. 5 fig. 3, pl. 12. fig. 8; Bedot, 1921b, fig. 6; Vervoort, 1968: 64; Calder, 1983: 17.

Material examined.— Syntype material, NMNH 22146, as *M. fisheri*, Albatross station 4072, NE coast of Maui Island, Hawaii, depth 102 m, material described by Nutting (1905), sample contains only a few fragments, gonothecae present.

Description (after Nutting, 1905 and examined material).— Cormoids develop from a straggling hydrorhiza, reach 2 cm in height and have a central axis (stem) that bears on opposite sides sets of hydrocladia branching in typical *Monostaechas* manner. Stem monosiphonic, straight, with distinct but irregular transverse nodes, with many nematothecae in a double longitudinal row on one side. Stem with apophyses bearing sets of hydrocladia. Hydrocladial sets born on both sides of stem, thus lying all in one plane and either alternately on left or right sides, or in opposite pairs.

Hydrocladia with basal segment with proximal transverse node and distal oblique node, bent for 90° near distal end, with apophysis for following hydrocladium on outer curvature, with three or four nematothecae on straight part and one nematotheca in axil of apophysis. Remainder of hydrocladium heteromerously segmented by alternating oblique and well formed transverse nodes, delimiting main- and intersegments. Main segments with large hydrotheca and four nematothecae: one median inferior, a pair of laterals, and a small axillar one. Intersegments with two median nematothecae. All of c. five hydrocladia of one set (sympodium) have identical structure; following hydrocladia inserted on apophysis on backside of basal segment of previous hydrocladium.

Hydrotheca cup-shaped, wall in lateral view nearly straight and only slightly

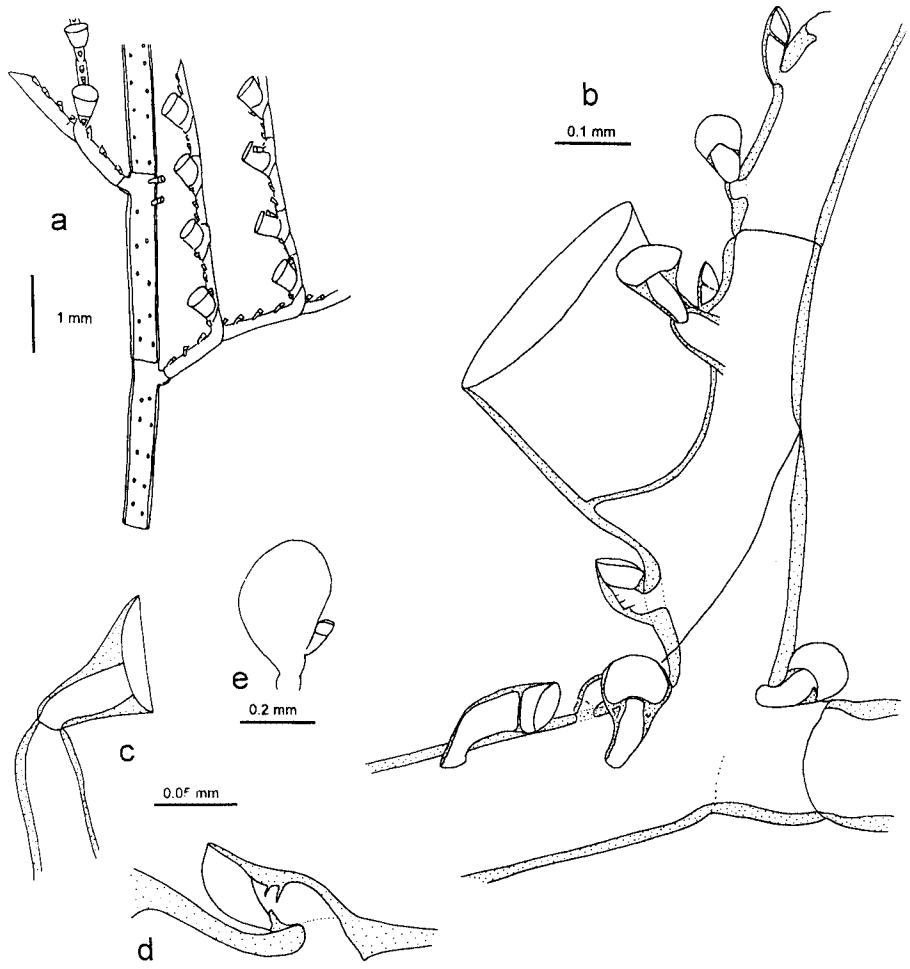

Fig. 46. *Monostaechas fisheri* Nutting, 1905; after sample from Albatross station 4072; a, part of cormoid with stem and parts of two hydrocladial sets, nematothecae of stem mostly lost and only pores left; b, part of hydrocladium showing curved end of basal segment and following main- and intersegment, as well as apophysis for next hydrocladium; c, lateral nematotheca on its pedicel, lateral view; d, median inferior nematotheca, same scale as c; e, male gonotheca.

converging towards base, abaxial wall thickened, rim smooth, even or slightly depressed laterally, adaxial wall free for about half its length, angle of opening with axis of segment about 40°.

Nematothecae all two-chambered and probably all movable. Median inferior well below hydrotheca, curved, adaxial side of upper chamber missing. Lateral nematothecae on pedicel of similar height as nematotheca itself, conical, walls straight, upper chamber shallow, inner side of upper chamber lowered to half height of outer side. Axillar nematotheca small, inner side reduced. Remaining nematotheca like median inferior, but with much longer lower chamber.

Male gonotheca spherical, with one nematotheca near base, and with indistinctly delimited pedicel of one segment.

Polyp coloured almost black by dark pigment granules.

Type locality.— No holotype material was designated, Nutting's material was all from Hawaiian Archipelago.

Distribution.— Hawaiian Archipelago, depth 100 to 283 meters.

Table 35. Dimensions of *Monostaechas fisheri*, in µm.

material	syntype
cladial main + intersegment	800-900
abcauline side hydrotheca	260-300
free adcauline side hydrotheca	150-200
diameter hydrotheca	320-360

Remarks.— When establishing *M. fisheri* Nutting (1905) did not discuss its differences with *M. quadridens*, which he had also found in the same region. The hydrocladia of *Monostaechas fisheri* are indistinguishable from those of *M. quadridens*. Only the stem of *M. fisheri* is different and characteristic: a long, straight main axis that gives off sets of hydrocladia laterally, branched in the typical *Monostaechas* fashion (scorpioid sympodium). *M. quadridens* can also have a stem, which, however, either branches dichotomously or ends after a short distance and passes into the scorpioid sympodium. If considering the variability of the stem of *M. quadridens*, *M. fisheri* can be conceived as a form of the former only. This was also the opinion of Bedot (1921b) and also Vervoort (1968) expressed doubts about the validity of *M. fisheri*. Calder (1983), however, kept them distinct without discussion. *Monostaechas fisheri* is here kept separate from *M. quadridens* on account of the long, unbranched stem. This stem could in fact be a hydrocaulus, which, however, lacks hydrothecae. More material of this interesting species should be examined, as the interpretation of the stem as a hydrocaulus will be decisive for the taxonomic position of the genus. At present, however, insufficient material is available for a comprehensive evaluation of the variability of the stem structure.

Nutting did not designate a holotype and therefore no precise type locality can be given. A lectotype was not selected here because not all of Nutting's samples could be examined; other colonies could be in better condition and more characteristic than the one seen here.

Monostaechas natalensis Millard, 1958

Monostaechas natalensis Millard, 1958: 206, fig. 12.; 1962: 291, fig. 2F; 1968: 277; 1975: 363, fig. 116E-G, 117A-C; 1978: 195.

Type locality.— Off Natal, 30°32'S 30°38.5'E, depth 46 m.

Distribution.— South Africa.

Remarks.— *Monostaechas natalensis* is well described by Millard (1958, 1975) and there is no need to repeat the description here. *Monostaechas natalensis* has a varied colony form and it can also produce simple stems and the sympodial form of growth typical for *Monostaechas* can be not so obvious. Thus, *M. natalensis* appears to be intermediate between the genera *Antennella*, *Corhiza*, and *Monostaechas*. If the typical branching pattern is less obvious, *Monostaechas natalensis* is similar to *Corhiza pannosa* and *Antennella sibogae*. *Corhiza pannosa* differs, however, in the structure of the lateral nematothecae, which are bivalved in *M. natalensis* and of the spanner type in *C. pannosa*. *Antennella sibogae* differs in having the opening of its hydrothecae perpendicular to the hydrocladia, the adaxial wall of the hydrotheca is parallel to the hydrocladium, and the superior nematothecae are in a double row.

Monostaechas quadridens (McCrady, 1859) (fig. 47, table 36)

Plumularia quadridens McCrady, 1859: 199.
Monostaechas dichotoma Allman, 1877: 37, pl. 22 figs 1-5.
Monostaechas quadridens; Nutting, 1900: 75, pl. 13 figs 1-4; 1905: 952; Ritchie, 1907a: 508, pl. 25 fig. 4; Stechow, 1909: 83; Jäderholm, 1919: 20; Stechow, 1925a: 252; Fraser, 1938a: 61; 1944: 334, fig. 343; 1948: 274; Pennycuik, 1959: 178, pl. 3 fig. 6; Mammen, 1965: 302, figs 98-99; Vervoort, 1968: 61, fig. 28; Millard & Bouillon, 1973: 85; 1974: 9; Millard, 1975: 365, fig. 11D-F; 1978: 195; Calder, 1983: 17, fig. 9.
Monostaechas fisheri var. *simplex* Billard, 1913: 16, fig. 7, pl. 1 fig. 10.
Monostaechas quadridens f. *stechowi* Leloup, 1935: 2, figs 2-3.
Antennella diaphana f. *typica*; Van Gemerden-Hoogeveen, 1965: p 49 (in part).

Material examined:
- 1) Cape Verde Islands, MHNG 336 as *M. fisheri*, coll. Bedot, without date, small cormoid, infertile.
- 2) South Carolina (32°30.0'N 79°42.3'W), U.S.A., ROMIZ B2105 as *Monostaechas* spec., depth 18 m, fertile, up to 35 mm high, with branched stem.
- 3) Florida, off St. Lucie inlet, U.S.A., ROMIZ B1102, depth 44 m, coll. J. Reed 21.vi.1977, fertile, up to 20 mm high.
- 4) New Providence, Bahamas, RMNH Coel. 1718 (2 slides), as *Antennella diaphana* f. *typica*, coll. no. 1149 described by Van Gemerden-Hoogeveen (1965), fertile, belongs to *M. quadridens*.
- 5) Seychelles, Mahé, Beau Vallon, MACT 2.862, as *M. quadridens*, described by Millard & Bouillon (1973), fertile, up to 2 cm.

Description.— Colonies forming erect structures arising from creeping, ramified stolons, 1 to 13 cm high, either composed of sets of branched hydrocladia (scorpioid sympodia) arising directly from stolons or sympodia mounted on hydrocaulus. Hydrocaulus varied and often irregular, either a simple stem that branches distally into hydrocladia, or hydrocaulus dichotomously branched once or repeatedly and then bearing hydrocladia. Secondary hydrocaulus-like stems can also branch from hydrocladia. Hydrocaulus segmented by transverse nodes into long segments with numerous nematothecae but without hydrothecae.

Hydrocladia occasionally simple, but mostly branched characteristically as a scorpioid sympodium by successive branching from posterior side of previous hydrocladium. Each hydrocladium with long ahydrothecate basal segment with proximal transverse node and distal oblique node, either curved near distal end or straight, with apophysis for following hydrocladium on backside of distal end, with several nematothecae on upper side, sometimes in a double row. Remainder of hydrocladium heteromerously segmented by alternating oblique and transverse nodes, delimiting main- and intersegments, transverse nodes indistinct or even absent in more proximal parts of hydrocladium. Main segments with large hydrotheca and four nematothecae: one median inferior, one pair of laterals, and a small axillar one. Intersegments bear two median nematothecae.

Hydrotheca cup-shaped, wall in lateral view nearly straight, slightly converging towards base, rim smooth, even, adaxial wall free for about half its length, angle of opening with axis of segment 40 to 50°.

Nematothecae all two-chambered; axillar nematotheca either one- or two cham-

bered. Median inferior nematotheca below hydrotheca movable, adaxial side of upper chamber missing. Lateral nematothecae on pedicel of similar height as nematotheca itself, conical, walls straight, upper chamber shallow, wall emarginated on sides (bivalved), or emargination on inner side. Axillar nematotheca small, inner side reduced. Remaining nematotheca like median inferior, but with much longer lower chamber.

Gonothecae of both sexes present in same colony. Female gonotheca 0.65 to 0.8

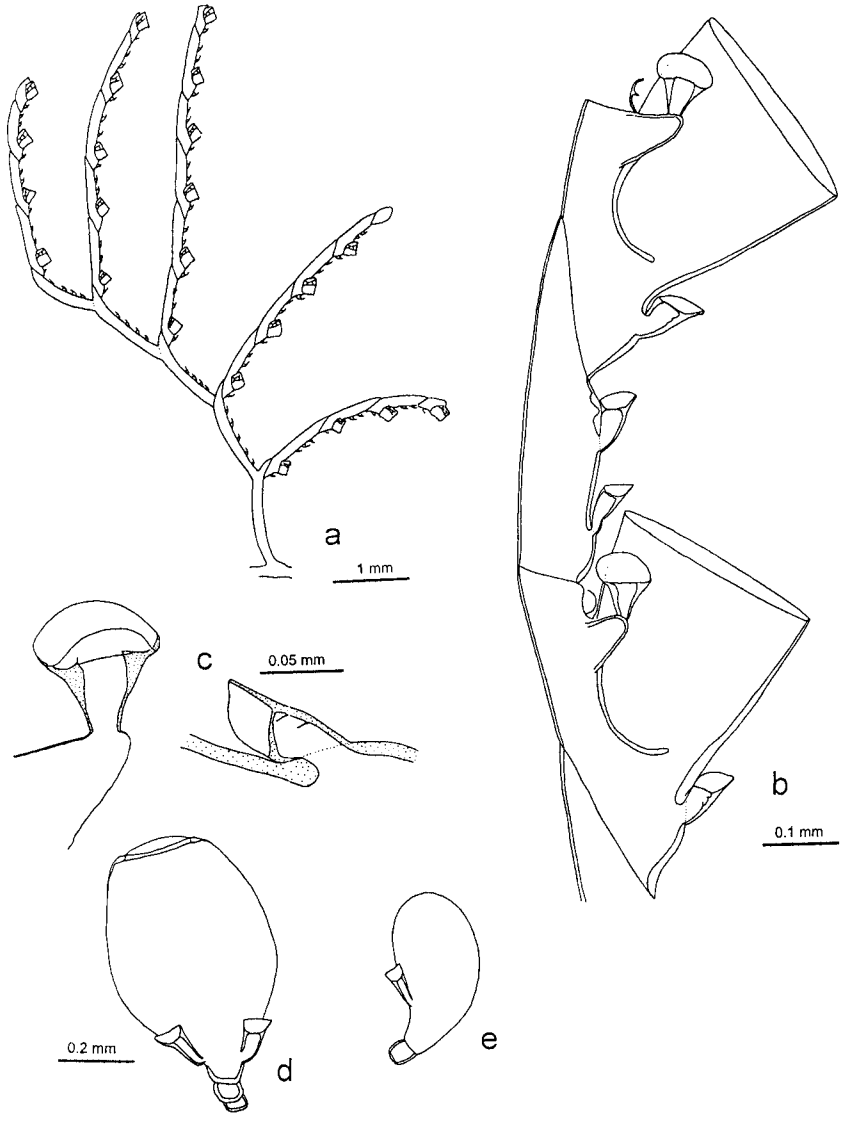

Fig. 47. *Monostaechas quadridens* (McCrady, 1859); a after material form Cape Verde Islands, b to e from Florida; a, one sympodium showing characteristic mode of branching; b, distal end of hydrocladium; c, lateral nematotheca (left) and median inferior nematotheca (right); d, female gonotheca; e, male gonotheca, same scale as d.

Table 36. Dimensions of *Monostaechas quadridens*, in µm.

sample no.	2	3	5
segment of main axis	2400	1240-1900	780
length main segment	360-460	420-530	340-450
length intersegment	320-450	420-480	380-540
abcauline side hydrotheca	220-250	220-250	190-230
free adcauline side hydrotheca	130-150	100-130	110-140
diameter hydrotheca	280-310	250-270	210-260

mm in length, pear-shaped, with truncated end and large lid, base with two nematothecae, pedicel composed of two segments. Male gonotheca 0.4 to 0.45 mm long, pear-shaped, with rounded end, indistinct aperture, base with one (rarely two) nematotheca, pedicel one-, rarely two-segmented.

Variation.— The intersegments typically bear two nematothecae, although occasionally one or three can be found. In branched stems, trichotomous branching may occur besides the more frequent dichotomous branching.

Type locality.— Charlston Harbour, U.S.A., material was floating in water.

Distribution.— California; Pacific Side of Mexico; Florida; Cape Verde Islands; Brazil; South Africa; Seychelles; India; Queensland, Australia; circumglobal in tropical and temperate waters.

Remarks.— *Monostaechas quadridens* is a widespread and frequently occurring species that has often been described; the synonymy has been discussed by various authors (e.g. Stechow, 1925a; Millard, 1975). Nutting (1900) and many other recent authors are here followed in considering *M. dichotoma* Allman, 1877 synonymous with *M. quadridens*. Also *Monostaechas fisheri* var. *simplex*: Billard, 1913 and *Monostaechas quadridens* f. *stechowi* Leloup, 1935 are here seen as coterminous with *M. quadridens*, following Vervoort (1968) and Calder (1983).

Part of the material described as *A. diaphana* by Van Gemerden-Hoogeveen (1965) proved to be typical *M. quadridens*. Although the author noted the differences of this material (1965: 53) she did not realise that it belonged actually to *M. quadridens* (see also under *Halopteris diaphana*, *H. gracilis*, and *H. alternata*).

The material examined agrees well with other descriptions. The stem is rather varied, even within the same colony. The largest colonies with much branched stems are usually reported from the south-east coast of the U.S.A. and the Caribbean. In other regions of the world the stem is mostly simple or absent (cf. Millard, 1975). The only material differing from the remaining samples are the Cape Verde Islands colonies (sample no. 1). It has lateral nematothecae of the spanner-type and not the bivalved type. The material is also rather damaged and axillar nematothecae could not be seen, although their absence could not be confirmed with certainty. All material examined has lateral nematothecae on a pedicel of comparable length. Vervoort (1968) described it as short to not present in material from the Caribbean. It seems therefore that this length can vary considerably.

Monostaechas sibogae Billard, 1913

Monostaechas sibogae Billard, 1913: 15, fig. 6.

Material examined.— Lectotype, ZMA Coel. 4166, Siboga station 77; corresponds to the material described by Billard (1913), therefore designated here as lectotype, one plume 9 mm high growing on Foraminiferan, damaged and flattened, no gonothecae left.

Type locality.— Borneo, Indonesia, 3°27'S 117°36'E, depth 34 m.

Distribution.— Known from type locality only.

Remarks.— The type material of this species was re-examined for this study. However, not much new information could be found that would supplement Billard's (1913) accurate description and figure. This species is unique by its branching pattern, characterised as a helicoid sympodium (see above under remarks for the genus). The hydrocladia are directed alternately to the right and to the left. The type material is quite damaged and flattened, probably due to examination under a coverslip. However, there are indications that the branches were originally not in one plane, but arranged like a helical whorl similar to a bottle-brush. In the type material there is no indication of an axillary nematotheca and Billard (1913) also does not mention such nematothecae. Therefore, *M. sibogae* does most probably has no axillar nematothecae, although the quality of the type material requires to be cautious on that matter. The lack of axillar nematothecae and the alternate direction of the hydrocladia set *M. sibogae* well apart from *M. quadridens*.

Genus *Schizotricha* Allman, 1883

Synonyms.— ?*Diplopteron* Nutting, 1900 (in part, not Allman, 1883).

Diagnosis.— Halopteridídae with a polysiphonic, erect stem, which may be branched or unbranched, with one main axial tube bearing pinnately arranged hydrocladia and hydrothecae. Hydrocladia alternate, the majority branched sympodially from anterior or lateral surface immediately below hydrothecae. Hydrothecae cup-shaped, with smooth rim. Lateral nematothecae movable and not fused to their pedicel or the hydrotheca.

Type species.— *Schizotricha unifurcata* Allman, 1883.

Remarks.— Allman's definition of *Schizotricha* simply relied on the branched hydrocladia and thus would have included also members now referred to the Plumulariidae and Kirchenpaueriidae. Millard (1975) used the narrower concept of Bedot (1921b) that includes in *Schizotricha* only species with cauline hydrothecae irrespective of the stem being either mono- or polysiphonic. However, basing a halopterid genus on branched hydrocladia alone, is problematic as branched hydrocladia occasionally also occur in various species of *Halopteris* that normally have unbranched hydrocladia (see Bedot, 1921b). Totton's (1930) more restricted scope of *Schizotricha* is therefore here preferred as it is based on a combination of characters. The above diagnosis thus excludes species with monosiphonic stems, or forms with a polysiphonic stem formed by tubes of equal importance. The former are retained in the genus *Halopteris*, the latter in the genus *Corhiza*.

The polysiphonic stem of *Schizotricha* is composed of stolon-like tubes accompanying the single, superficial hydrocaulus that can be branched and bears the hydrocladia. The accompanying tubes can bear nematothecae but neither do they have hydrothecae nor hydrocladia. Such as situation is also found in several other widely separate plumularid genera, e.g. *Polyplumaria*, *Cladocarpus* (cf. Millard, 1975) and

thus probably has evolved several times as a means of stabilising large cormoids. Although *Pseudoplumaria* and *Polyplumaria* are very similar to *Schizotricha*, they are here seen as belonging to a separate clade with reduced cauline hydrothecae. However, this has to be verified by a more comprehensive analysis.

Schizotricha as defined here includes the following species: *Schizotricha frutescens*; *S. unifurcata*; *S. profunda*, and *Schizotricha variabilis*. This list is most probably incomplete as for some plumulariids with branched hydrocladia the presence or absence of cauline hydrothecae is not known (e.g. *Schizotricha dichotoma* Nutting, 1900, *Diplopteron quadricorne* Nutting, 1900, *D. grande* Nutting, 1900, *D. longipinna* Nutting, 1900) and it is thus unclear whether they belong to *Polyplumaria* or *Schizotricha* (cf. also Totton, 1930).

The four species here included in *Schizotricha* are all very similar and it is not apparent what separates most of them. *Schizotricha variablis* appears to be distinct from the others by the constant heteromerous segmentation of its hydrocladia (after Naumov, 1960, 1969). The remaining three species are not easily separable using existing descriptions. They are here kept separate mostly because of biogeographic arguments and because no material for examination was available. *Schizotricha unifurcata* occurs in the Southern hemisphere, mostly around Antarctica, while *S. frutescens* occurs in the subtropical and boreal North Atlantic. *Schizotricha profunda* is most probably conspecific with *S. frutescens*.

Schizotricha frutescens (Ellis & Solander, 1786)

Sertularia frutescens Ellis & Solander, 1786: 55, pl. 6 figs a, A, pl. 9 fig. 1.
Plumularia frutescens; Kirchenpauer, 1876: 26, pl. 1 fig 9, pl. 3 fig. 9.
Schizotricha frutescens; Jäderholm, 1909: pl. 12 fig. 9; Millard, 1975: 368; Cornelius & Ryland, 1990: 154, fig. 4.23; Ramil & Vervoort, 1992a: 150, fig. 38b-d; Cornelius et al., 1995: 108, fig. 4.19.
Polyplumaria frutescens; Broch, 1918: 59; Cornelius, 1995: 166, fig. 39.

Type locality.— Scarborough, U. K.

Distribution.— Widely distributed in the subtropical and temperate Atlantic, including the Mediterranean and the Barents Sea near Bear Island, depth 30 to 1300 m, mostly growing on stones. Records from South Africa are uncertain and need reconfirmation (Millard, 1975).

Remarks.— Good descriptions and figures of this species can be found in Millard (1975), Ramil & Vervoort (1992a); Cornelius & Ryland (1990) and Cornelius (1995). See also discussions under *S. profunda* and *S. unifurcata*.

Schizotricha profunda (Nutting, 1900)

Plumularia profunda Nutting, 1900: 66, pl. 8 figs 2-3.
Polyplumularia profunda; Broch, 1918: 60, fig. 24.
Schizotricha profunda; Bedot, 1921b: 13.

Type locality.— Nutting (1900) did not give a type locality, but his two samples were taken not far apart, east of Jacksonville, Florida, U.S.A.

Distribution.— Florida, North Atlantic, 250 to 2200 m (Nutting, 1900; Broch, 1918).

Remarks.— Nutting (1900) described *Schizotricha profunda* as having unbranched hydrocladia. Later Broch (1918) found more material he assumed to belong to *S. profunda* and noted that the branching of the hydrocladia is varied and apparently depends on the age of the colony. He also noted further important details like the presence of cauline hydrothecae. In the same paper, Broch (1918) also described *Schizotricha frutescens* and thus kept both species implicitely separate. Although he gave good descriptions for both species, it is neither apparent what the real differences between these two species are, nor does Broch discussed such differences. The only feasible difference is that *S. profunda* seems to have regular transverse nodes that put each hydrotheca on its own segment, while those of *S. fructescens* are irregular or absent. However, it is the opinion of the present author, that not too much weight can be put on this difference alone and it is probable that *S. profunda* actually belongs to *S. frutescens*. As it is possible that Broch distinguished both species on some detail not mentioned in the text, both are here provisionally kept separate.

Schizotricha unifurcata Allman, 1883

Schizotricha unifurcata Allman, 1883: 28, pl. 7 fig 1-3; Billard, 1908: 938; Vanhöffen, 1910: 338; Bedot, 1921b: 13; Stechow, 1925b: 489; Totton, 1930: 231, fig 65.
Schizotricha multifurcata Allman, 1883: 29, pl. 7 fig. 4-5; Billard, 1908: 939, Stechow, 1925b: 498.
Schizotricha anderssoni Jäderholm, 1904: 11; Vanhöffen, 1910: 338.
Schizotricha turqueti Billard, 1906: 15, fig. 5.
Plumularia glacialis Hickson & Gravely, 1907: 22, pl. 3 fig. 23-24.
Polyplumaria unifurcata; Billard, 1910: 41, fig. 18.
Polyplumaria multifurcata; Billard, 1910: 42, fig. 19.
Schizotricha turqueti; Vanhöffen, 1910: 337, fig. 49a-b.
Schizotricha unifurcata unifurcata; Stepanjants, 1979: 115, pl. 22 fig 1.
Schizotricha unifurcata turqueti; Billard, 1910: 42; Stepanjants, 1979: 116, pl. 22 fig. 1B.

Type locality.— Christmas Harbour, Kerguelen; 182 m.

Distribution.— Kerguelen; South Georgia; Booth-Wandel Island, East End of Barrier, Antarctica.

Remarks.— Billard (1908) re-examined the type material of *S. unifurcata* and *S. multifurcata* and found that they differ only in the degree of the ramification of the hydrocladia. Billard (1908) also supplemented Allman's description and information on the variability in number and positions of the nematothecae. Later, Totten (1930) carefully re-examined Allman's material and was unable to find a significant difference; he also underlined this by providing a table. Totten (1930) thus sunk *S. multifurcata* into the synonymy of *S. unifurcata*, which appears unquestionable. Stechow (1925b) and Totton (1930) re-examined the material of *Plumularia glacialis* Hickson & Gravely, 1907 and synonymised it with *S. unifurcata*. This was already obvious from Hickson & Gravely's (1907) description. Totton (1930) probably also examined material of *S. turqueti* Billard, 1906 and he referred it to *S. unifurcata*. Stechow (1925b) kept both separate, noticing, nevertheless, a close relationship. Billard (1910) himself admitted that *S. turqueti* did not differ much from *S. unifurcata* and referred to it as a variety of *S. unifurcata*. According to Totton (1930), the size of the hydrothecae of *S. turqueti* does not differ from that in *S. unifurcata* and both species are here also seen as conspecific. *Schizotricha anderssoni* Jäderholm, 1904 was synonymised with *S. uni-*

furcata by Stechow (1925b) and Stepanjants (1979), who are followed here too. *Schizotricha anderssoni* seems only to be unique in having regular, oblique nodes that place every hydrotheca on its own segment (Jäderholm, 1904).

From the existing descriptions of *S. unifurcata* it is not clear what distinguishes it from *S. frutescens* and both nominal species could be conspecific. In view of the wide geographic separation without overlap it seems better to keep both species separate. However, *S. frutescens* does prefer deeper waters down to 1264 m (Broch, 1918; Ramil & Vervoort, 1992a; Cornelius et al., 1995) and thus appears to be adapted to cold water as well.

Schizotricha variabilis (Bonnevie, 1899)

Plumularia variabilis Bonnevie, 1899: 91, pl. 7 fig. 3
Schizotricha variabilis; Naumov, 1969: 507, fig. 357.

Distribution.— Western Barents Sea near Bear Island, depth 349 m.

Remarks.— *Schizotricha variablis* appears to be distinct from the other congeners by the constant heteromerous segmentation of its hydrocladia (after Naumov, 1969).

Genus *Antennellopsis* Jäderholm, 1896

Diagnosis.— Halopteridídae with simple, unbranched hydrocladia that either arise directly from the hydrorhiza or from a polysiphonic stem formed by stolon-like tubes. Lateral nematothecae completely fused to hydrotheca, median inferior nematotheca free from hydrotheca.

Type species.— *Antennellopsis integerrima* Jäderholm, 1896 by monotypy.

Remarks.— The genus *Antennellopsis* is characterised by its lateral nematothecae that are fused to the hydrotheca. The validity of this genus has been questioned several times and it was synonymised with *Antennella* (cf. Billard, 1913; Bedot, 1921b; Millard, 1975; Bouillon, 1995), but recently Calder (in press) kept it separate. It is here kept separate too, however, more for pragmatic reasons. The genus comprises only one valid species which occurs in two growth forms. If *Antennellopsis* was not available it would be impossible to decide whether to place it in *Antennella* or in *Corhiza*. The retention of the genus *Antennellopsis* circumnavigates this ambiguity.

Antennellopsis integerrima Jäderholm, 1896

Antennellopsis integerrima Jäderholm, 1896: 16, pl. 2 figs 7-8; 1919: 20; Stechow, 1923b: 232; Rho & Chang, 1972: 101, pl. 3. figs 10-11.
Antennellopsis dofleini Stechow, 1907: 196; 1909: 86, pl. 2 fig. 4, pl. 6 fig. 6.
Antennella integerrima; Stechow, 1907: 196; 1909: 87; Bedot, 1921b: 4; Rho, 1974, 146; Rho & Park, 1986: 91; Park, 1992: 295.

Type locality.— 33°5'N 129°16'E (Japan).

Distribution.— Japan, Korea.

Remarks.— *Antennellopsis integerrima* Jäderholm, 1896 was originally described as an *Antennella*-like colony, although Jäderholm's figure indicated a clustered, tuft-

Table 37. Distinguishing characteristics of *Corhiza* species.

species	*Corhiza bellicosa*	*Corhiza complexa*	*Corhiza fascicularis*	*Corhiza pannosa*	*Corhiza scotiae*	*Corhiza sociabilis*	*Corhiza suensoni*	*Corhiza valdiviae*
colony form	short stem, irregularly branched	stem dichotomous or unbranched	dichotomous, long branches	short stems bushy	long branches originating near base	tree-like	simple stem, not branched	large, irregular colony
companion tube	absent	absent	absent	absent	absent	present	absent	absent
pinnate cormoids	no	no	no	no	no	no	no	yes
hydrotheca adnate (for)	completely	1/2	1/2	1/2	1/2	1/2	1/2	1/2
pairs of lateral nematothecae	3	1	1	2	2	2	1	1
inferior lateral nematothecae	present	absent	absent	absent	absent	absent	absent	absent
axillar nematothecae	absent	present	absent?	absent	absent caulus	absent	absent	pair on
type of lateral nematothecae	bivalved	conical	conical?	spanner	conical	conical	conical	conical

like growth. Stechow (1907, 1909) later described *A. dofleini* and depicted a colony with a long, polysiphonic stem as found in species of *Corhiza*. Jäderholm (1919) considered that *A. dofleini* might be conspecific with *A. integerrima*, a proposal shortly afterwards accepted by Stechow (1923b) without discussion. For descriptions and figures, Jäderholm (1896) and Stechow (1909) should be consulted.

Genus *Corhiza* Millard, 1962

Diagnosis.— Halopteridídae with erect polysiphonic stem, which may be branched or unbranched, composed of intercommunicating tubes of equal diameter and importance, these tubes irregularly giving rise either to hydrocladia or to hydrocauli bearing hydrocladia. Hydrocauli, if present, with cauline hydrothecae and pinnately arranged hydrocladia. Hydrocladia unbranched, occasionally (as a secondary growth-form) arising independently from hydrorhiza. Hydrotheca cup-shaped, with smooth, though sometimes sinuated, rim.

Type species.— *Antennopsis scotiae* Ritchie, 1907b.

Remarks.— The genus *Corhiza* includes several large species, but also some problematic species able to develop colonies typical for the genus *Antennella*. Millard (1975) emended her previous (1962) diagnosis and also allowed the inclusion of species with pinnate cormoids like *C. valdiviae*. This possibly renders the taxon polyphyletic. Several species of *Antennella* and *Halopteris* also demonstrate a *Corhiza*-like mode of growth as an alternative colony form. It is thus probable that the scope of the genus must be revised. The species here included in *Corhiza* are tabulated in table 37. The majority have been excellently described by Millard (1975, 1980). All species are well separable, but *C. fascicularis* and *C. suensoni* should be re-examined. With the exception of *C. suensoni*, all *Corhiza* species are from the southern hemisphere.

Corhiza bellicosa Millard, 1962

Corhiza bellicosa Millard, 1962: 275, fig. 2A-E; 1975: 334, fig. 108A-D; 1978: 190.

Type locality.— Agulhas Bank, South Africa.

Distribution.— Endemic to South Africa.

Remarks.— *Corhiza bellicosa* is unusual by its paired lateral inferior nematothecae in addition to the usual median inferior one and the three pairs of nematothecae lateral to the hydrotheca. It is thus readily distinguished from the somewhat similar *Antennella sibogae*. For further details and descriptions Millard (1962, 1975) should be consulted.

Corhiza complexa (Nutting, 1905)
(fig. 48, table 38)

Antennella complexa Nutting, 1905: 952, pl. 5. fig. 4; Bedot 1917: 123; 1921b: 4.
Corhiza mortenseni Millard, 1968: 274, fig. 5A-D (syn. nov.).
Corhiza mortenseni; Millard, 1975: 335, fig. 108E-H; 1978: 190.

Material examined.

-1) Syntype material of *Antennella complexa*, NMNH 22144, Albatross station 3859 (between Molokai and Maui Island, Hawaiian archipelago), depth 251 m, contains at least three fragmented colonies of *C. complexa* besides a messy mixture of other thecate hydroids and invertebrates.
-2) Holotype material of *Corhiza mortenseni*, ZMC, T. Mortensen expedition station 24, 29°48.5'S 13°18'E, depth 220 m, coll. 22.viii.1929, sandy/muddy bottom.

Description.— Colonies forming erect stems resembling a bottle-brush, stems either branched or unbranched, height up to 10 cm. Stems arising from creeping stolons and composed of a bundle of stolon-like tubes repeatedly bearing hydrocladia on well formed apophyses. Tubes of stem without nodes or nematothecae. Hydrocladia set at right angle to stem, irregularly distributed.

Hydrocladia of variable length, up to 12 mm long, first one or two segments terminated by transverse nodes, without nematothecae, next segment long, with distal oblique node and two to four median nematothecae. Remainder of stem heteromerously segmented by alternating oblique and transverse nodes, thus delimiting main- and intersegments. Main segments with a hydrotheca placed in middle of segment and four nematothecae: one median inferior, a pair of laterals, and one axillar. Intersegments longer than main segments, normally with two nematothecae, rarely three.

Hydrotheca cup-shaped, walls in lateral view nearly parallel, rim sometimes slightly flared, adcauline wall adnate for about half its length, angle of opening with hydrocladial axis 30 to 50°.

Nematothecae all two-chambered and probably all movable. Median inferior conical, straight, inner wall of upper chamber lowered. Lateral nematothecae seated on pedicel of similar length as nematotheca itself, conical, walls straight, wall of upper chamber lowered on inner side. Nematotheca in upper axil of hydrotheca smaller, position median, one side of upper chamber missing. Nematothecae of intersegments like median inferior ones.

Gonothecae of both sexes on same stem. Female gonotheca pear-shaped, 0.65 mm

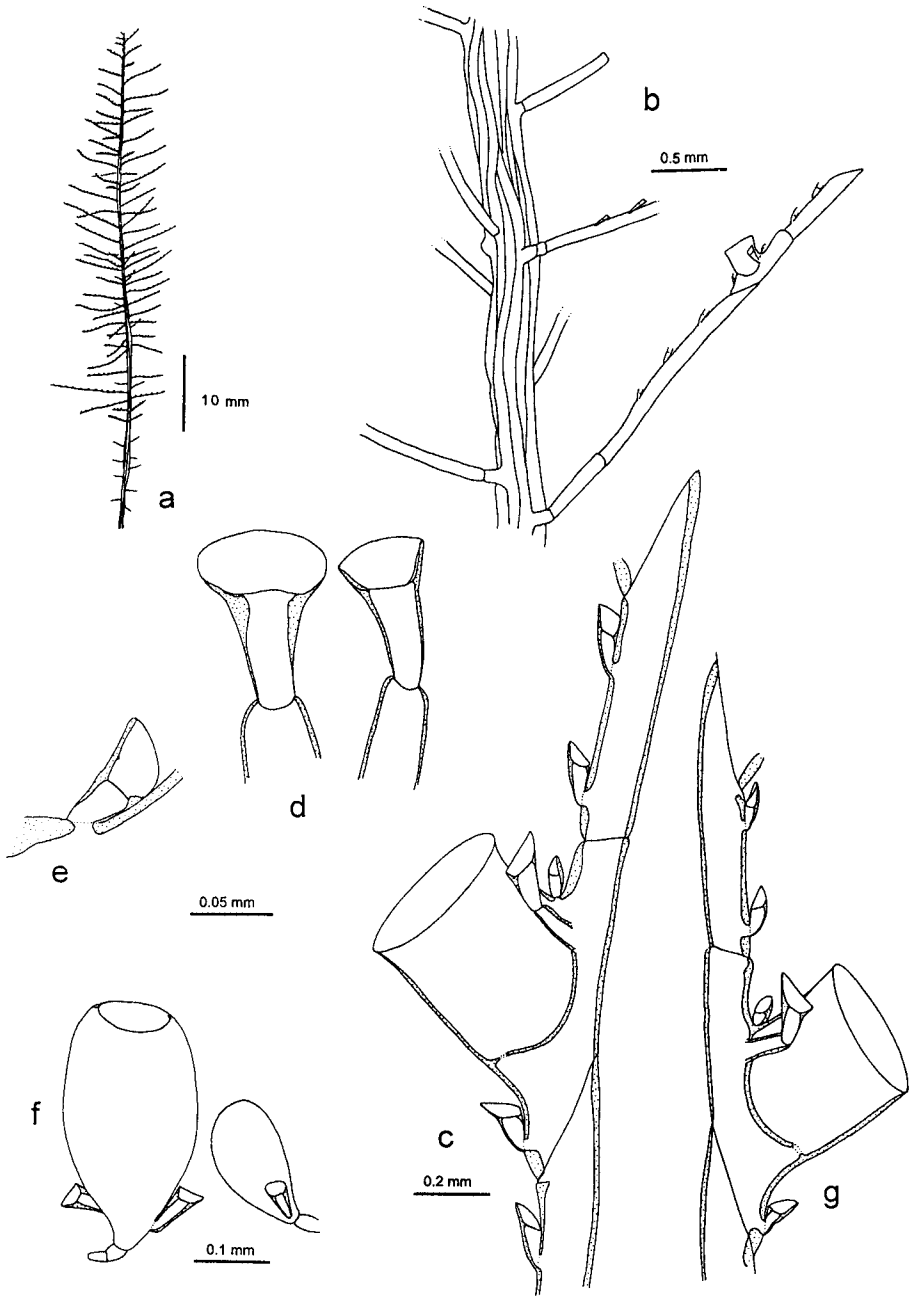

Fig. 48. *Corhiza complexa* (Nutting, 1905); after syntype material of *A. complexa* (g-h) and holotype of *C. mortenseni* (g); a, colony aspect; b, part of stem with bases of hydrocladia; c, part of hydrocladium; d, two lateral nematothecae; e, median inferior nematotheca, same scale as d; f, female (left) and male (right) gonotheca; g, part of hydrocladium, same scale as b.

Table 38. Dimensions of *Corhiza complexa*, in µm.

sample no.	1	2
main segment	390-500	350-400
intersegment	520-620	400-550
abcauline side hydrotheca	190-220	170-190
free adcauline side hydrotheca	120-150	110-140
diameter hydrotheca	220-240	190-220

long, straight, with truncated, operculate distal end, with two large nematothecae near base, pedicel composed of two segments. Male gonotheca about 0.33 mm long, with rounded end, one nematotheca near base, pedicel one-segmented.

Type locality.— Nutting's type material is from Molokai and Maui Island, Hawaiian Archipelago.

Distribution.— Hawaiian Islands; South Africa; 88 to 250 m.

Remarks.— *Antennella complexa* Nutting, 1905 has a polysiphonic stem and must thus be referred to the genus *Corhiza*. After examination of type material of both *Corhiza complexa* and *C. mortensi* it became obvious that both samples are almost identical. *Corhiza mortensi* only had insignificantly smaller hydrothecae (see table 38, and fig. 48) and the stem was branched. Because Millard (1968) also described unbranched stems of *C. mortensi*, no significance can be attributed to this difference. *Corhiza mortensi* is thus indistinguishable from *C. complexa* and was synonymised with the latter. Gonotheca of South African material are not known so far and the possibility remains that they differ from the Hawaiian material. *Corhiza complexa* is a rare species and confined to deeper waters.

No lectotype is designated here because not all of Nutting's syntype material could be examined and the remaining could be in better condition.

Corhiza fascicularis (Allman, 1883)

Antennularia fascicularis Allman, 1883: 24, pl. 4 figs 5-6; Billard, 1908: 759.
Corhiza fascicularis; Millard, 1968: 276.

Type locality.— Nightingale Island, Tristan da Cunha , South Atlantic, 183-275 meters.

Distribution.— Known from type locality only.

Remarks.— *Corhiza fascicularis* resembles *C. complexa*, but Allman (1883) did not describe an axillar nematotheca. Because Allman otherwise did not pay attention to axillar nematothecae (e.g. see *H. buskii*), he may well have overlooked them here. Unfortunately, Allman's type material cannot be re- examined as it is reportedly lost (Billard, 1908).

Corhiza pannosa Millard, 1962

Corhiza pannosa Millard, 1962: 278, fig. 3A-B, D-G; 1968: 276; 1975: 337, fig. 109F-K; 1978: 190.

Type locality.— Agulhas Bank, South Africa, depth 11 m.

Distribution.— Endemic to South Africa.

Remarks.— *Corhiza pannosa* resembles *C. scotiae* in some respects, but has a different colony and distinctively shaped lateral nematothecae (spanner-type). *Corhiza pannosa* can also occur in the *Antennella*-like form. For further details and descriptions table 37 and Millard (1968, 1975) should be consulted.

Corhiza scotiae (Ritchie, 1907b)

Antennopsis scotiae Ritchie, 1907b: 543, pl. 3 fig. 3; 1909: 90, fig. 8.
Corhiza scotiae; Millard, 1962: 281, fig. 3C; 1968: 276; 1975: 338, fig. 109A-E; 1978: 190.

Type locality.— Saldanha Bay, South Africa, depth 46 m.

Distribution.— Endemic to South Africa.

Remarks.— For details and descriptions Millard (1962, 1975) should be consulted.

Corhiza sociabilis Millard, 1980

Corhiza sociabilis Millard, 1980: 146, figs 5c-e, 6a-c.

Type locality.— 32°15.5'S 29°09.7'E (off Transkei), depth 600-650 m.

Distribution.— Known from type locality only.

Remarks.— *Corhiza sociabilis* is unique among it congeners in having so called companion tubes. This companion tube is a superficial tube that accompanies the axis and each branch of the stem; it is unbranched and bears hydrothecae. It represents a modified hydrocladium that adheres to stem and branches; it is not comparable to a hydrocaulus.

Corhiza suensoni (Jäderholm, 1896)

Antennella suensoni Jäderholm, 1896: 13, pl. 2 fig. 5; Stechow, 1909: 86; Bedot, 1917: 122, 126; 1921b: 5.

Type locality.— Japan, between 33°10'-33°15'N and 129°16'-129°15'E, depth 82 m.

Distribution.— Known from type locality only.

Remarks.— According to the description of Jäderholm (1896) *Antennella suensoni* has a polysiphonic stem reaching a height of 10 cm from which simple hydrocladia branch off. Therefore, the correct name must be *Corhiza suensoni*. *Corhiza suensoni* is similar to *Corhiza complexa* (Nutting, 1905), but according to the description of Jäderholm (1896) the former has no axillar nematothecae. The type material should be re-examined to confirm the absence of axillar nematothecae, but no material could be made available for this study.

Corhiza valdiviae (Stechow, 1923a)

Heteroplon valdiviae Stechow, 1923a: 15.
Thecocaulus (?) *valdiviae*; Stechow, 1925b: 495, figs 42-43.
Halopteris valdiviae; Millard, 1957: 228, fig. 14B; 1962: 290, fig. 4H-J.
Corhiza valdiviae; Millard, 1975: 340, fig. 110A-E; 1978: 190.

Type locality.— Plettenberg Bay, South Africa, depth 100 m.

Distribution.— South Africa.

Remarks.— *Corhiza valdiviae* is a large halopterid reaching heights of up to 40 cm. It is remarkably similar to *H. tuba* in the arrangement and structure of its hydrocladia, but differs from it in its polysiphonic stem, and proportions of the hydrotheca in which the depth is almost invariably greater than the width (Millard, 1962). *Corhiza valdiviae* also differs from all its congeners by the possession of pinnate cormoids with a hydrocaulus bearing hydrothecae. For more details table 37 and Millard (1975) should be consulted.

Genus *Gattya* Allman, 1886

Synonym.— *Paragattya* Warren, 1908.

Diagnosis.— Halopteridae with simple pinnate cormoids arising either directly from a hydrorhiza or from a main axial tube of an erect, polysiphonic stem of stolon-like tubes. Hydrocauli in monosiphonic colonies with hydrothecae; main axial tube in polysiphonic stems without hydrothecae or nematothecae. Hydrocladia normally unbranched. Hydrotheca cup-shaped, margin with more than one cusp.

Type species.— *Gattya humilis* Allman, 1886.

Remarks.— The genus *Gattya* is only distinguished from *Halopteris* and *Corhiza* by the possession of more than one cusp on the rim of the hydrotheca. Although

Table 39. Distinguishing characters for *Gattya* species.

species character	*G. aglaophe-niaformis*	*Gattya trebilcocki*	*Gattya balei*	*Gattya conspecta*	*Gattya heurteli*	*Gattya humilis*	*Gattya multithecata*	*Gattya tropicalis*
stem polysiphonic	no	no	no	no	yes	no	no	no
stem branched	no	no	no	no	yes	no	no	no
abcauline wall hydro-theca	straight or slightly concave	straight	slightly convex	straight	straight	double curvature	straight	straight
abcauline cusp	present	present	present	present	present	present	present	present
lateral cusp or cusps	1 broad, 1 pointed	± 1 broad, 1 rounded	1 broad only	1 broad only	1 broad only	1 broad only	only 1 very shallow	3 present
adcauline cusp	absent	absent	present	present	present	present	present	present
abcauline cusp curved	not or slightly	not	not or slightly	not	not	not	strongly	not
pairs of lateral nematothecae	1	1	1	1	1	1	1	2
nematotheca in axil of hydrotheca	1	1	1	1	1	1	1	absent
intrathecal septum	absent	absent	present	absent	absent	absent	absent	absent
intersegments in cladia	present	present	present	absent	absent	absent	present	variable
nematothecae/inter-segment or superior nematothecae	1	1	1	2	0-2	absent	2	absent or 1
female gonotheca	unknown	unknown	flabellate	? whelk-shaped	unknown	pear-shaped	unknown	unknown

some species of *Gattya* are rather distinct, others like *G. trebilcocki* have varied cusp lengths and it is sometimes difficult to draw a dividing line, especially so because many species of *Halopteris* also may have a variably sinuated hydrothecal rim.

All known *Gattya* species are tabulated in table 39. The species are mostly quite distinct and easily separable, only *G. aglaopheniaformis* and *G. trebilcocki* are similar. The species are ordered according to their distribution.

It is interesting to note that all *Gattya* species exclusively occur in the southern hemisphere. Moreover, they are mainly distributed in a triangle spanning the Indian Ocean coasts of South Africa, the Seychelle Islands, and southern Australia. This restricted zoogeographic distribution argues in favour of *Gattya* being a monophyletic genus that had a rather recent evolutionary radiation.

Gattya aglaopheniaformis (Mulder & Trebilcock, 1909) (fig. 49, table 40)

Plumularia aglaopheniaformis Mulder & Trebilcock, 1909: 32, pl. 1 fig. 7.
Thecocaulus aglaopheniaformis; Bedot, 1921b: 9.
Gattya aglaopheniaformis; Watson, 1973: 186.

Material examined.
- 1) Holotype, MVM slide F57967, as *Plumularia aglaopheniaformis*, Torquay, Australia, ex collection Trebilcock, labelled as type on original label, therefore type designation by original author. Slide contains one infertile plume.
- 2) Pearson Island, South Australia, MVM slide F42025, *Gattya aglaopheniaformis*, ex. collection Watson (Watson, 1973), station G, 18-24 m, 12.i.1969.
- 3) Pearson Island, South Australia, MVM slide F42026, *Gattya aglaopheniaformis*, ex. collection Watson (Watson, 1973), station A, 27-30 m, 7.i.1969.

Description.— Colony forming up to 7 mm high plumes.

Hydrocaulus monosiphonic, unbranched, with basal part devoid of hydrothecae and hydrocladia and longer distal part bearing hydrothecae and hydrocladia. Basal part divided into segments by up to three straight nodes and an oblique node at end of basal part. Stem above basal part homomerously segmented by oblique nodes, up to ten hydrocladia per side. Segments of stem bear one hydrocladium on alternate sides, a hydrotheca, and six nematothecae: one median inferior, one pair of laterals, one in upper axil of hydrotheca, and two superior ones on distal part of segment.

Hydrocladia inserted on well-formed apophyses lateral to cauline hydrothecae. Apophysis without nematotheca. First segment of hydrocladium quadrangular, without nematotheca. Second segment longer than first, with one median nematotheca on upper side. Remaining part of hydrocladia heteromerously segmented by alternating oblique and transverse nodes. Main segments with four nematothecae: one median inferior, a pair of laterals, and one in upper axil of hydrotheca. Intersegments with one nematotheca only.

Hydrotheca broad, abcauline and adcauline walls almost straight in lateral view. Margin with five cusps: one pointed abcauline, one blunt and broad anterio-lateral on each side, one pointed posterio-lateral at site of lateral nematothecae. There is no cusp in adcauline position. Hydrotheca adnate for half of adcauline length, angle of opening with hydrocladial axis c. 50°.

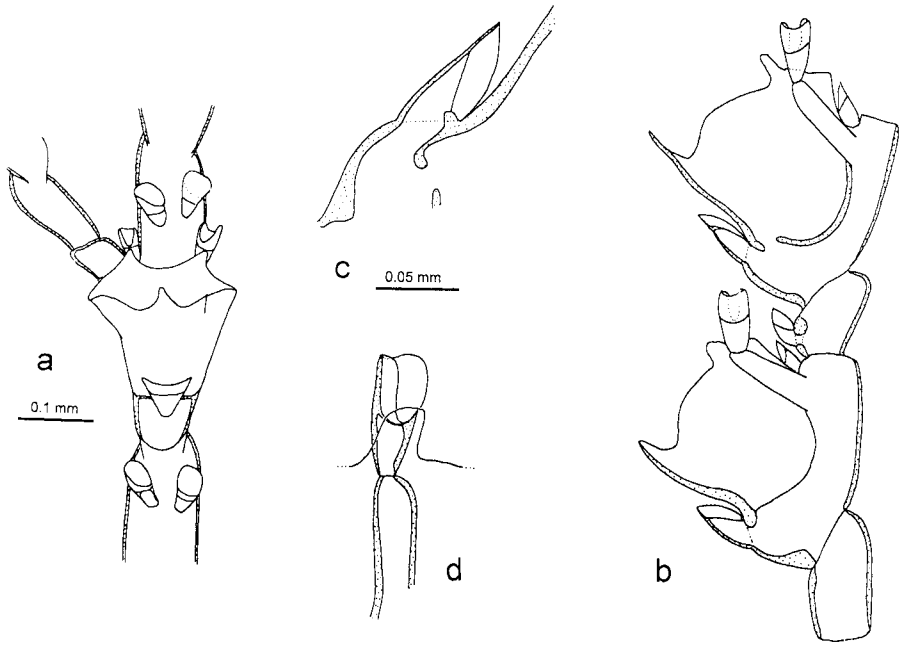

Fig. 49. *Gattya aglaopheniaformis* (Mulder & Trebilcock, 1909); a after sample no. 2, b-d after holotype; a, part of hydrocaulus with one base of hydrocladium, frontal view; b, part of hydrocladium, same scale as a; c, median inferior nematotheca; d, lateral nematotheca seen from inside of hydrotheca, note presence of posterior lateral marginal cusp, same scale as c.

Nematothecae of stem and hydrocladia all two-chambered. Median inferior nematothecae reaching hydrothecal base, with short adcauline wall, adcauline wall of upper chamber missing. Lateral nematothecae on long pedicels reaching almost to rim of hydrotheca. Lateral nematothecae conical, mobile, lower chamber as long as upper one, margin of upper chamber straight and emarginated on adcauline side down to bottom, bottom oblique. Nematothecae of intersegments and occasional superior ones on caulus similar to basalmost median inferior ones, but with longer free adcauline wall and mobile.

Gonothecae unknown.

Type locality.— Torquay, Australia.

Table 40. Dimensions of *Gattya aglaopheniaformis*, measurements in µm.

sample no.	1	2
caulus segments	420-480	400-410
cladial main segments	270-300	250-270
cladial intersegments	130-140	120-140
abcauline side hydrotheca	180-210	180-200
free adcauline side hydrotheca	60-80	50-80
diameter hydrotheca	190-260	200-210

Distribution.— South Australia to Victoria, Australia.

Remarks.— Because no figures are available besides those in Mulder & Trebilcock (1909) published in a rather obscure serial, *Gattya aglaopheniaformis* is here figured and redescribed. Watson (1973) also gives a good description. For the distinction from the similar *G. trebilcocki* see remarks under the latter.

Gattya balei (Bartlett, 1907)
(fig. 50, table 41)

Plumularia balei Bartlett, 1907: 65, pl. ; Mulder & Trebilcock, 1909: 29, pl. 1 figs 1-3.
Thecocaulus balei; Bedot, 1921b: 8.
Gattya balei; Watson, 1973: 186.

Material examined:
- 1) Two syntype slides MVM F57665, as *Plumularia balei*; one slide with label of National Museum Victoria no. 62764, labelled: Type presented by G. Conrad Bartlett 15.xi.20; this slide is therefore seen as holotype specimen through designation by original author. The other slide of this series is labelled as second type and bears gonothecae.
- 2) Barwon Heads, Victoria, Australia, MVM slide F77649, as *Plumularia balei*, ex collection Trebilcock, contains infertile stems.
- 3) Point Lonsdale, Victoria, Australia, MVM slide F77650, as *Plumularia balei*, ex collection Trebilcock, from 3.i.1921; contains 5 well preserved plumes of which some with gonothecae.
- 4) MVM slide F77651, as *Plumularia balei*, ex collection Trebilcock, locality unknown, one infertile plume.

Description.— Colony forming up to 10 mm high plumes arising from ramified, tubular stolons.

Hydrocaulus monosiphonic, unbranched, with basal part devoid of hydrothecae and hydrocladia and longer distal part bearing hydrothecae and hydrocladia. Basal part divided into segments by two or three transverse nodes, last segment ending in oblique node. Segments of basal part with several nematothecae in double row. Stem above basal part homomerously segmented by oblique nodes. Segments of stem each bear one hydrocladium on alternate sides, up to 11 hydrocladia per side. Segments with a hydrotheca and up to six nematothecae: one median inferior, one on each side of hydrotheca, one in axil of hydrotheca, and up to two on distal part of segment.

Hydrocladia inserted on long apophyses developing lateral to cauline hydrothecae. Apophysis without nematotheca. First segment of hydrocladium quadrangular, often with indicated partition into two parts of equal size, without nematotheca. Second segment longer than first, with one median nematotheca on upper side. Remaining part of hydrocladium heteromerously segmented by alternating oblique and transverse nodes. Main segments with four nematothecae: one median inferior, a pair of laterals, and one in upper axil of hydrotheca. Intersegments with one nematotheca only.

Hydrotheca broad, abcauline wall with a deep constriction in middle forming an intrathecal shelf, adcauline wall almost straight. Rim with teeth: one pointed abcauline, one blunt and broad on each side, and a shallow one in adcauline position. Sometimes there are small cusps behind the pedicels of the lateral nematothecae. Hydrotheca adnate for half its adcauline length, angle of opening with hydrocladium 40 to 50°.

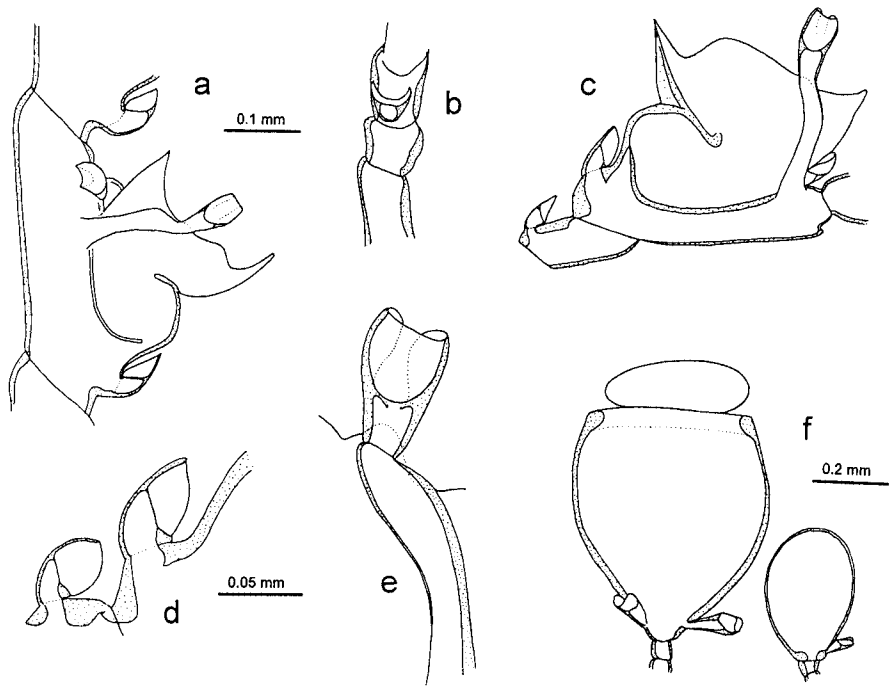

Fig. 50. *Gattya balei* (Bartlett, 1907); from sample no. 1; a, segment of hydrocaulus; b, basal part of hydrocladium, same scale as a; c, part of hydrocladium with intersegment and main segment, same scale as a; d, median inferior (right) and nematotheca of intersegment (left); lateral nematotheca, same scale as d; f, female (left) and male gonotheca (right).

Nematothecae of stem and hydrocladia all two-chambered. Median inferior nematothecae not reaching to hydrothecal base, adcauline wall of lower chamber short, adcauline wall of upper chamber missing. Lateral nematothecae on long pedicels reaching to rim of hydrotheca, conical, mobile, lower chamber as long as upper one, margin of upper chamber slightly rolled inwardly and emarginated on adcauline side down to bottom, bottom oblique. Nematothecae of intersegments and occasional superior ones on caulus similar to basalmost median inferior ones, but with longer free adcauline wall and mobile.

Gonothecae of both sexes on same stem. Female gonotheca up to 0.6 mm long, flabellate with broad, truncated end bearing a lid, walls rather thick and with annular thickening around lid, base tapering, straight, with two or three nematothecae. Pedicel consists of one segment and an apophysis. Male gonothecae up to 0.45 mm long, evenly oval, with one nematotheca at base, pedicel consists of one segment and a short apophysis.

Type locality.— Thompsons Creek (= Bream Creek), near Torquay, Victoria, Australia.

Distribution.— Victoria and South Australia, Australia.

Remarks.— There is no recent description of *Gattya balei* available and it was therefore redescribed here, and some previously unpublished material collected by

Table 41. Dimensions of *Gattya balei*, in µm if not stated otherwise.

sample no.	1	2
caulus height [mm]	6	10
max. number of cladia per side	9	11
length of apophysis	100-120	100-110
length of 2nd cladial segment	110-130	130
cladial main segments	280-300	310-320
cladial intersegments	100-110	110
abcauline side of hydrotheca	170-230	200-240
free adcauline side of hydrotheca	100-150	120-150
diameter of hydrotheca	280-290	230-240
pedicel of lateral nematothecae	120	130-140

Trebilcock is included. Mulder & Trebilcock (1909) noted the presence of a single nematotheca behind all hydrothecae. This could be confirmed for the type material too. *Gattya balei* is easily separated from all congeners by its pronounced intrathecal septum that gives the hydrotheca a folded appearance (fig. 50a, c).

Gattya trebilcocki Watson, 1973

Gattya trebilcocki Watson, 1973: 186, figs 48-52.

Type locality.— Pearson Island, South Australia.

Distribution.— Pearson Island, South Australia.

Remarks.— *Gattya trebilcocki* closely resembles *G. aglaopheniaformis*, but can be distinguished from it by the shape of the posterior lateral cusps of the hydrothecal rim, which in *G. trebilcocki* are rounded and broad, while in *G. aglaopheniaformis* they are narrow and rather pointed. Both species were found by Watson (1973) at the same locality. Watson noted that *G. trebilcocki* occurs on algal substrates and *G. aglaopheniaformis* epizoically. This, however, contradicts her own description (1973: 186) reporting *G. aglaopheniaformis* on the red alga *Callophyllis*. Both *G. trebilcocki* and *G. aglaopheniaformis* are rare species and more material is needed to consolidate the identity of both species. Gonothecae are unknown in both species and could possibly offer more distinguishing characters.

Gattya conspecta (Billard, 1907)

Plumularia conspecta Billard, 1907: 362, fig. 11.
Thecocaulus conspectus; Bedot, 1921b: 9.
Gattya conspecta; Millard, 1975: 343, fig. 111A-C; 1978: 192.

Type locality.— Fort Dauphin, Madagascar.

Distribution.— Madagascar; South Africa.

Remarks.— Millard (1975) should be consulted for description and figures.

Gattya heurteli (Billard, 1907)

Plumularia heurteli Billard, 1907a: 360, figs 9-10.
Thecocaulus heurteli; Bedot, 1921b: 9.
Plumularia quadridentata Jarvis, 1922: 348, pl. 26 fig. 22.
Paragattya heurteli; Stechow, 1923b: 233; Millard, 1958: 208, fig. 10E.
Gattya heurteli; Millard, 1968: 276; 1975: 344, fig. 111J-L; 1978: 192.

Type locality.— Macalonga in Moçambique, depth 22 m.

Distribution.— South Africa; tropical East Africa (Millard, 1975)

Remarks.— Millard (1975) should be consulted for description and figures. Synonyms are given following Millard (1959, 1975).

Gattya humilis Allman, 1886

Gattya humilis Allman, 1886: 156, pl. 24 figs 5-7; Nutting, 1900: 87, pl. 17 figs 10-11; Millard, 1962: 281; 1975: 346, fig. 111D-H; 1978: 192.
Paragattya intermedia Warren, 1908: 323, figs 16, pl. 47 fig. 27; Bedot, 1921a: 6; Stechow; 1923b: 234; 1925b: 494; Millard, 1957: 230; 1958: 209.

Type locality.— ? Port Elizabeth, South Africa.

Distribution.— Endemic to South Africa (Millard, 1975).

Remarks.— Millard (1962) re-examined Allman's type material of *Gattya humilis* and Warren's cotypes of *Paragattya intermedia* and concluded that they must belong to the same species. Already Stechow (1923b) corrected some of Warren's (1908) observations. Millard (1975) should be consulted for description and figures.

Gattya multithecata (Jarvis, 1922)

Plumularia multithecata Jarvis 1922: 346, pl. 25 fig. 19.
Halopteris multithecata; Stechow, 1923b: 232.
Gattya multithecata; Millard, 1975: 348, fig. 112A-B; 1978: 190.

Type localities.— Zanzibar and Wasin.

Distribution.— South Africa to tropical East Africa (Millard, 1975)

Remarks.— Millard (1975) should be consulted for description and figures.

Gattya tropicalis Millard & Bouillon, 1973

Gattya tropicalis Millard & Bouillon, 1973: 79, fig. 10A-D.

Type locality.— Mahé, Beau Vallon, Seychelles.

Distribution.— Seychelles.

Remarks.— *Gattya tropicalis* is easily distinguishable from other congeners by its two pairs of lateral nematothecae. The second pair is placed in the axil of the pedicel of the first pair of laterals. The hydrothecal rim also has more cusps than other *Gattya* species.

Genus *Calvinia* Nutting, 1900

Diagnosis.— Halopteridídae with colonies having erect, branched, polysiphonic stems. Hydrocladia arise alternately from main axial tube on surface of stem. Main axial tube with hydrotheca. Rim of hydrothecae smooth. From anterior side of each cladial hydrotheca arises a long, tapering, segmented branch with nematothecae.

Type species.— *Calvinia mirabilis* Nutting, 1900.

Remarks.— Due to the presence of cauline hydrothecae, this genus must be included in the Halopteridídae, as has already been done by Bouillon (1985).

Calvinia mirabilis Nutting, 1900
(fig. 51)

Calvinia mirabilis Nutting, 1900: 77, pl. 14 figs 1-3; Bedot, 1921b: 17.

Material examined.— Syntype slides NMNH 18577; Albatross station 2666 (30°48'N 79°49'W, Florida), type designation by Nutting (1900).

Type locality.— 30°48'N 79°49'W, Florida, U.S.A.; depth 494 m.

Remarks.— *Calvinia mirabilis* is rather unique and easily identified by the processes developing below the hydrocladial hydrothecae (fig. 51). Contrary to similar structures in other plumularids, they are not used to protect the gonothecae but the hydrothecae. Probably they are modified secondary hydrocladia. For a complete description and more figures, Nutting (1900) should be consulted. *Calvinia mirabilis* is a rare species from deeper waters.

Distribution.— Atlantic side of Florida, USA; depth 494 to 805 m.

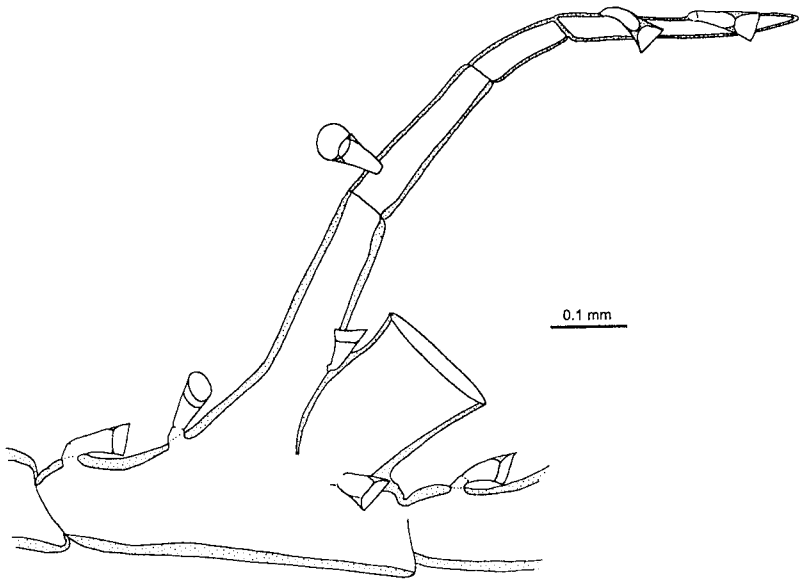

Fig. 51. *Calvinia mirabilis* Nutting, 1900; after syntype slide; hydrocladial segment with accessory structure.

Genus *Nuditheca* Nutting, 1900

Diagnosis.— Halopteridídae forming colonies with erect, branched, polysiphonic stems. Hydrocladia arising from main axial tube with hydrothecae, branched. Hydrothecae without cusps, completely adnate. Median inferior nematotheca not fused to hydrotheca, lateral nematothecae not movable, fixed to pedicel.

Remarks.— Until recently, *Nuditheca* was included in the Aglaopheniidae. Calder (1996) re-examined *Nuditheca dalli* and found hydrothecae on the hydrocaulus. Thus, *Nuditheca* must be placed in the Halopteridídae, to which it obviously shows a close relationship. Formally, *Nuditheca* only differs from *Schizotricha* by its completely adnate hydrothecae and the immovable lateral nematothecae. Although it is not clear whether all nominal *Nuditheca* species have cauline hydrothecae, all three known species are here included. Unfortunately, no material could be examined. The species can be distinguished by characters given in table 42 and taken from Naumov (1960, 1969). See also discussion under *Anarthroclada*.

Table 42. Distinguishing characters of *Nuditheca* species.

species	*N. dalli*	*N. dogieli*	*N. tetrandra*
hydrocladial segmentation	homomerous	homomerous	heteromerous
median inferior nematotheca	near base of hydrotheca	far below hydrotheca	far below hydrotheca
distal end of gonotheca	broad	narrow, slightly curved	narrow, strongly curved

Nuditheca dallii (Clark, 1876)

Macrorhynchia dallii Clark, 1876: 230, pl. 11.
Nuditheca dalli; Nutting, 1900: 129, pl. 34 figs 4-6; Naumov, 1960: 479, fig. 370; 1969: 517, fig. 370.

Type locality.— Unalaska, Alaska, USA.
Distribution.— Rare species, only found near the coast of Alaska.

Nuditheca dogieli Naumov, 1952

Nuditheca dogieli Naumov, 1952: 37, fig. 5; 1960: 479-480, fig. 371, pl. 18 fig. 1; 1969: 518, fig. 371, pl. 18 fig 1.

Type locality.— Not specified.
Distribution.— Pacific Coast of southern Kuriles and South Kurile Strait, depth 36 to 48 m.

Nuditheca tetrandra Naumov, 1960

Nuditheca tetrandra Naumov, 1960: 480-481, figs 372, 373; 1969: 518, figs 372- 273.

Type locality.— Not specified.

Distribution.— Bering Sea near Medny Island and central Sea of Japan, depth 110 to 823 m.

Genus *Astrolabia* Naumov, 1955

Synonym.— *Tetranema* Fraser, 1937b [not *Tetranema* Haeckel, 1879].

Diagnosis.— Halopteridídae with pinnate cormoids arising directly from hydrorhiza. Hydrocaulus mono- or polysiphonic, if polysiphonic with main axial tube only bearing hydrothecae and hydrocladia. Hydrocladia branched. Hydrotheca deep, completely adnate, cauline and cladial hydrothecae differ in morphology. Hydrocladial hydrothecae with two pairs of lateral nematothecae, most proximal hydrotheca of hydrocladium can have one pair only; lateral nematothecae well separated, immobile, fused to pedicel.

Type species.— *Astrolabia heterotheca* Naumov, 1955.

Remarks.— Fraser (1937b) established the genus *Tetranema* for his *T. furcata*. However, *Tetranema* is preoccupied by *Tetranema* Haeckel, 1879. Although Haeckel's genus name for a Hydromedusa is no longer in use (Kramp, 1961; Bouillon, 1985), *Tetranema* Fraser, 1937b is an invalid junior homonym (Calder, in press). Calder (in press) replaced it by *Astrolabia* Naumov, 1955 (see Naumov, 1960, 1969) with type species *A. heterotheca*. The latter resembles Fraser's *T. furcata* closely and the scope of both *Tetranema* Fraser, 1937b and *Astrolabia* Naumov, 1955 is very similar. *Tetranema* is basically characterised by its two pairs of lateral nematothecae, which are immobile and widely separated.

For the distinction of the two known species of this genus see under *A. furcata*. Both seem to be exceedingly rare.

Astrolabia furcata (Fraser, 1937b)

Tetranema furcata Fraser, 1937b: 193, pl. 44 fig 233a-e.

Type locality.— Kaison Bank, west coast of Moresby Island, Queen Charlotte Island, depth 201 m.

Distribution.— Possibly known from type locality only.

Remarks.— *Astrolabia furcata* is quite similar to *A. heterotheca* Naumov, 1955, but the latter has only one pair of nematotheca lateral to the most proximal hydrotheca of the hydrocladia. *A. furcata* has always two pairs. Furthermore, *A. furcata* has a gonotheca with a curved distal end, while Naumov (1960, 1969) described the gonotheca of *A. heterotheca* as having a slit-like opening on the side of the distal end. Both species seem to lack nematothecae on their gonothecae. The difference observed in the gonothecae could well be due to sexual differences and new material will hopefully clarify the picture. Both species could differ in the presence or absence (*A. furcata*) of internal septae, but the description of Naumov (1960, 1969) is not detailed enough on that matter.

Astrolabia heterotheca Naumov, 1955

Astrolabia heterotheca Naumov, 1955: 22, fig. 5; 1960: 477-478, fig. 369; 1969: 516, fig. 369.

Type locality.— Astrolabe Strait, Kuriles.
Distribution.— Only known from type locality.

Genus *Anarthroclada* Naumov, 1955

Diagnosis.— Halopteridídae with colonies having polysiphonic, pinnate stems with main axial tube bearing hydrothecae. Hydrocladia not branched, not segmented, devoid of inner septae. Hydrothecae completely adnate. Lateral nematothecae immovable, fused to pedicel, outer wall elongated in the form of a scutum. Gonothecae with nematothecae.

Type species.— *Anarthoclada parmata* Naumov, 1955.

Remarks.— The presence of cauline hydrothecae in *Anarthoclada* was demonstrated by Calder (in press) and he moved the genus from the Aglaopheniidae to the Halopteridídae. *Anarthroclada* shows close affinities with *Nuditheca* and only differs from it by the special shape of the lateral nematothecae and the unbranched hydrocladia. The absence of segmentation can hardly be accepted as a character to separate genera, as it is variable even at the species level. A future generic revision of the Halopteridídae will most probably drop the genus *Anarthroclada*. *Anarthroclada* is a monotypic genus.

Anarthroclada parmata Naumov, 1955

Anarthroclada parmata Naumov, 1955: 20, fig. 2; 1960: 475-476, fig. 367, pl. 20; 1969: 514, fig. 367, pl. 20.

Type locality.— Sea of Okhotsk near Island St. Jonas.
Distribution.— Only known from type locality.

Genus *Pentatheca* Naumov, 1955

Diagnosis.— Halopteridídae with colonies having polysiphonic, pinnate stems with main axial tube bearing hydrothecae. Stem occasionally branched. Hydrocladia not branched, given off from two sides of stem. Hydrocladia homomerously segmented, each segment with a completely adnate hydrotheca and two widely separated pairs of lateral nematothecae, median nematothecae lacking. Nematothecae immovable, fused to pedicel. Gonothecae with nematothecae.

Type species.— *Pentatheca angulifera* Naumov, 1955.

Remarks.— Calder (in press) demonstrated that *Pentatheca angulifera* Naumov, 1955 has hidden cauline hydrothecae and must thus be transferred from Aglaopheniidae to Halopteridídae. *Pentatheca angulifera* is somewhat unusual in lacking median nematothecae, however, they are also occasionally absent in *Antennella varians*. *Pentatheca* is further characterised by its immovable nematothecae that are fused to their pedicel. *Pentatheca* is a monotypic genus.

Pentatheca angulifera Naumov, 1955

Pentatheca angulifera Naumov, 1955: 21, fig. 3; 1960: 477, fig. 368, pl. 17 fig. 1; 1969: 515, fig. 368, pl. 17 fig. 1.

Distribution.— Paramushir Island and Boussole Strait (Kuriles).

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