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   (c) Table of contents
   (d) Introduction
   (e) Subject-matter of the paper, divided into sections to correspond with those given in table of contents
   (f) Summary, if paper is lengthy
   (g) Acknowledgements
   (h) References
   (i) Abbreviations, where these are numerous

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   ‘As described by Haughton et al. (1927) . . .’

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(continued inside back cover)
ANNALS OF THE
SOUTH AFRICAN MUSEUM

VOLUME 68
*Hydrocorella africana.* Colony on shell, with calcareous processes in foreground.

*Hydractinia altispina.* Colony on shell, with gastrozoooids and gonozoooids.

*Photographs: D. Gerneke.*

*Tubularia warreni.* Hydranth with gonophores.

*Bicorona elegans.*
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ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

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OF SOUTHERN AFRICA

By

N. A. H. MILLARD

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N. A. H. MILLARD

South African Museum, Cape Town

(With 143 figures)

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INTRODUCTION

CONTENT AND CLASSIFICATION

This monograph deals with the hydroid fauna of the African coast south of 20° south latitude, and as such covers all of the Republic of South Africa, most of South West Africa and the southern part of Moçambique as far north as Beira (Fig. 1). Seawards it covers the continental shelf and the Agulhas Bank, where records are abundant to a depth of about 100 m but become increasingly scarce below this.

The classification of the Hydrozoa accepted for the purpose of the monograph is as follows:

Class HYDROZOA

Order 1. Hydrida
Order 2. Actinulida
Order 3. Trachylida
  Suborder 1. Trachymedusae
  Suborder 2. Narcomedusae
Order 4. Hydroida (Leptolina)
  Suborder 1. Athecata (Gymnoblastea, Anthomedusae)
  Suborder 2. Thecata (Calyptoblastea, Leptomediatae)
  Suborder 3. Chondrophora
  Suborder 4. Limnomedusae
Order 5. Hydrocorallida
  Suborder 1. Milleporina
  Suborder 2. Stylasterina
Order 6. Siphonophora

The monograph deals with the marine and brack water Hydroida of the suborders Athecata, Thecata and Limnomedusae. Certain authorities (particularly Picard 1957) consider that the Chondrophora (originally included in the Siphonophora) and the Milleporina are closely related to the athecate hydroids. Evidence in favour of such an affinity appears to be increasing, and Bouillon (1974) evaluates these two groups as families (Vellellidae and Milleporidae respectively) of capitate athecate Hydroidea. However, in the meantime I have retained the old classification and these two groups are not covered in this monograph.

It is usual among hydroid systematists to divide the Athecata into the Capitata and the Filifera, a division which depends on the presence of capitate tentacles in the former and their absence in the latter. It is felt, however, that this fission is not a natural one and it has therefore not been used. In some genera capitate tentacles are present in the immature stages and not in the adult (e.g. Tubularia), while in others they are present in the medusa and not in the polyp (e.g. Bougainvillia).

In all 286 species and subspecies are described, nine of them new to science.* Keys to South African families, genera and species are provided. These keys do

* See also Addendum, p. 483.
Fig. 1. Map of southern Africa showing the localities mentioned in the text.
not necessarily represent systematic relationships but are intended as a tool for identification only. They should be used with caution and the genera and species checked against the diagnoses and diagrams. Material which does not fit the keys may be new species or new records for the country. Some well-known genera not yet recorded from South Africa have been included in the keys but are enclosed in brackets.

The monograph is essentially on the polyp rather than the medusa generation, and the polyp generation has been emphasized throughout, both in the keys and in the descriptions. The medusa generation is described where known, but medusae with unknown polyops are not described. A check-list of South African medusa records is given on p. 481.

Families are arranged in the generally accepted order, which implies a very rough evolutionary sequence. Genera and species are arranged in alphabetical order within the families. Each family has a short introduction outlining its more important features.

The systematic descriptions are preceded by a section on structure and terminology where definitions of terms will be found. Certain terms, which are relevant to particular families only, will be defined in the introduction to those families. The index to scientific terms on p. 497 will give quick access to definitions.

**MEASUREMENTS**

Measurements are not given in detail, for they are intended only as a rough guide to the size. Measurements of a colony are given to the nearest mm and those of a hydrotheca to the nearest 0,1 mm except for those which are less than 0,2 mm which are given to the nearest 0,01 mm. Measurements apply strictly to South African material, as do numbers of tentacles, etc. The depth of a hydrotheca is taken in side-view in the centre, unless otherwise stated, and exclusive of regenerated margins when these occur. When the hydrothecal wall is curved the straight measurement is taken from the base to the edge and across the curvature.

**RECORDS OF DISTRIBUTION AND DEPTH**

At the end of each species the distribution in southern Africa, both from the author's findings and other papers, is briefly summarized. This is done by the use of two figures indicating the latitude/longitude squares. Thus, 35/20 would indicate a latitude between 35 and 36° south and a longitude between 20 and 21° east.

The depth range is added in parenthesis, thus: 35/20 (s), where 's' refers to 'shallow'. For the depth the following key is used:

- l: littoral
- s: shallow (1–99 m)
- d: deep (100–499 m)
- v: very
- a: abyssal (1 000 m and over)
- h: ships' hulls and floating objects

Estuarine records have not been separated; generally they are included in 's'. 
No attempt has been made to indicate relative abundance. In the first place most of the records are from dredgings performed in a random fashion. In the second place many species can be identified only from fertile material, and in such cases sterile records have been omitted rather than risk incorrect identifications. Genera such as Eudendrium, Tubularia and Hydractinia, for instance, are much more abundant than is indicated by the records, which are usually of fertile material only.

Geographical distribution has not been analysed in this monograph, either within southern Africa or as related to world distribution. The matter will be discussed fully in a subsequent paper.

NEMATOCYSTS

Much attention has been paid in recent years to nematocyst type and its use in classification. It appears that within most families nematocysts are not of great diagnostic value since members of a family tend to have the same types. They may be of great value, though, in genera with few other diagnostic characters and are useful for establishing relationships in groups of doubtful affinity. In this monograph they have been described, where possible, for the Athecata only, where the diagnostic characters are fewer than in the Thecata.

For the examination of nematocysts only living material is satisfactory. Whole tentacles, smears or portions of the body should be mounted on a microscopic slide in sea-water. Replacement of the sea-water by distilled water will cause discharge of many types, and further discharge may be facilitated by alternate drying and re-hydration. Suitable stains include neutral red, methylene blue and magenta. A powerful microscope and oil immersion lens is necessary for observation of detail, though the category can often be determined without strong magnification.

SYNONYMY AND REFERENCES

The synonymy given with each species is not intended to be complete, but in each case there has been quoted the original description and, where possible, at least one good description or reference to a synonymy.

The literature on South African hydroids is very scattered, most of the earlier work being limited to descriptions of collections made by expeditions passing through the area. Stechow, in 1925a, published a check-list of 153 species up to that date. The most important records previous to 1925 are those of Warren, who deserves special praise for the accuracy of his descriptions and diagrams, Busk, Kirchenpauer, Allman, Ritchie, Billard, Jäderholm, Marktanner-Turneretscher, Vanhöffen and Stechow himself. Kirchenpauer’s type material was unfortunately nearly all destroyed during the last world war. Some of his species were redescribed by Stechow (1919b), but many were inadequately described in the first place and may now be dropped. Stechow’s slide material has been available to the author on loan. Busk’s material and much of Allman’s material is present in the British Museum (Natural History).
Warren’s material is in part in the British Museum and in part in the Natal Museum. Ritchie’s collection was redescribed by Rees & Thursfield (1965).

Since 1925 the quota of species has been added to by Vervoort, Leloup, Ewer, Kramp, Manton and the present author, and Stechow’s check-list has been almost doubled.

In the list of references on p. 485 all those containing South African records have been marked with an asterisk.

On p. 471 a complete list of species is given together with the authorities for previous records. Thus, any record can be located through the index to species on p. 499, even though it may not be quoted with the description.

Sources of Material

Collections from many sources have contributed material towards this monograph. They may be listed as follows:

The collection in the Zoology Department, University of Cape Town, consisting of some material left by the late Professor T. A. Stephenson from his intertidal survey of the coast, and a large body of material added more recently by Professor J. H. Day and his colleagues during work on estuaries, the bottom fauna of the continental shelf and the littoral area. Type specimens from this collection are housed in the South African Museum.

The collection in the South African Museum, much of it derived from dredgings of the s.s. Pieter Faure at the turn of the century.

The collection from Dr Th. Mortensen’s Java–South Africa Expedition, 1929–1930, and material from the Universitetets Zoologiske Museum, København.

A collection from Inhaca, Delagoa Bay, submitted by the University of the Witwatersrand, Johannesburg.

Material submitted by the Oceanography Department, University of Cape Town.

Material submitted by the Zoology Department, Rhodes University, Grahamstown.

Material submitted by the Division of Sea Fisheries, Cape Town.

Material collected by the R/V Anton Bruun during the International Indian Ocean Expedition, 1964.

Material collected by Professor J. Bouillon, Bruxelles, on the coast of Moçambique in 1969.

Material collected by the author from various parts of the coast.

Structure and Terminology

Accounts of the detailed structure and histology of the Hydrozoa are readily obtainable in textbooks. The present account of the anatomy does not claim to be complete and is intended only to provide a glossary to the terms used in the keys and diagnoses.

The polyp and medusa phases characteristic of the life-history of the Hydroidea are primarily radially symmetrical, though occasionally a secondary bilateral symmetry is superimposed. The polyp, or asexual generation, usually multiplies by vegetative propagation to produce colonies and is typically permanently attached to the substratum. The medusa, or sexual generation, is free-swimming and responsible for distribution of the sexual products.
The polyp has a cylindrical body with a body-wall of ectoderm, endoderm and mesoglea, and it contains a cavity, or coelenteron, with a single opening, the mouth. It consists of a base, the hydrorhiza, an upright stem, the hydrocaulus, and a terminal part bearing the mouth and tentacles, the hydranth.

The hydrorhiza normally takes the form of branching tubes, or stolons, which ramify over the substratum and affix the body of the animal. In certain cases the stolons may fuse with one another to form a continuous mat, said to be incrusting (Fig. 35C). In certain mud- and sand-dwelling forms the hydrorhiza is in the form of slender root-like anchoring filaments (Fig. 13). Forms also occur in which the hydrorhiza is provided with attachment discs or pedal discs with adhesive properties (Fig. 142).

The hydrocaulus rises from the hydrorhiza and bears the hydranth, from which it is often not clearly demarcated. Its body-wall is the coenosarc. Its cavity provides communication between the various parts of a colony; it is usually simple, but in some of the larger polyps may be provided with special
longitudinal ENDODERMAL CANALS, while the main lumen is filled with vacuolated endoderm cells.

The H YDRANTH consists of a main or digestive region containing a swollen GASTRAL CAVITY and an elongated HYPOSTOME, or manubrium, bearing the mouth at its summit. It also bears the TENTACLES.

The endoderm of the hydranth is usually relatively undifferentiated, though mucous cells tend to be more numerous in the hypostome and enzymatous cells in the gastral cavity. In the Thecata the single whorl of tentacles marks a boundary between these two regions. In some thecate families the endoderm of the gastral cavity is differentiated into two parts which may be demarcated externally by a groove, the enzymatous cells being concentrated in the basal part, e.g. Haleciidae, Plumulariidae. In the Sertulariidae some genera possess a BLIND CAECUM, or pouch of endoderm, which grows out from the basal region and is devoid of enzymatous cells (Fig. 81A).

The cavity of the hydranth is normally simple, but in large hydranths, e.g. Myriothenelidae, the surface area may be increased by ingrowths of endoderm to form VILLI (Fig. 18E). In the Tubulariidae a cushion of special endoderm cells projects into the basal part of the gastral cavity functioning as a DIAPHRAGM to prevent the passage of large food particles.

The HYPOSTOME is conical in most families, but in the Eudendriidae and Campanulariidae tends to gape open and is trumpet-shaped.

The TENTACLES vary in structure and arrangement, and may be scattered over the whole body of the hydranth, or concentrated into one or more whorls. When there are two whorls these are said to be ORAL and ABORAL. Rarely tentacles are absent, and rarely they are branched.

There are three types of tentacles:

1. MONILIFORM: very extensile tentacles, with a series of batteries of sting-cells arranged like beads on a string.

![Diagram of Tentacle Types and Structure](image-url)

**Fig. 3. Tentacle types and structure.**
2. **CAPITATE**: short tentacles terminating in a single knob-like battery of sting cells.
3. **FILIFORM**: long, slender tentacles in which the sting-cells are scattered along the length and not concentrated in batteries.

In structure the tentacles may be:

1. **HOLLOW**, in which case they may contain a cavity lined by endoderm and communicating with that of the gastric cavity, but more often the inner sides of the endodermal tube have come into juxtaposition and the cavity is lost. However, in the latter case the endoderm is always more than one layer thick.
2. **SOLID**, in which case there is a central core consisting of one row of large, stiff endoderm cells.

In some of the more primitive families the bases of the tentacles may be connected by an **INTERTENTACULAR WEB** (Fig. 43C).

The Hydroidea are noted for their **POLYMORPHISM**, or ability to exist in different forms. Not only does this term apply to the differentiation between polyp and medusa, but there may be dimorphism or polymorphy of the polyp stage. Thus there may be recognized:

1. **GASTROZOOIDS**: normal feeding individuals with mouth and well-developed tentacles (but without tentacles in the parasitic *Hydricthys*); without reproductive organs.
2. **GONOZOOIDS**: reproductive individuals bearing medusa-buds or degenerate medusae. They are usually modified gastrozooids and show various stages in the reduction and loss of the tentacles. The conversion may occur during the ripening of the reproductive bodies, e.g. *Eudendrium*. Sometimes there is no sign of tentacles at any stage and the hydranth body forms a hollow axis or stalk known as the **BLASTOSTYLE**.
3. **DACTYLOZOOIDS**: defensive individuals richly armed with sting-cells and without the power to feed or reproduce. There are several types:

![Fig. 4. Types of individuals in polymorphic colonies.](image-url)
(i) **Spiral zooids:** modified hydranths without mouth or tentacles but with a gastric cavity. They are characteristic of some of the *Hydractiniidae* and typically perform writhing movements and tend to twist into a spiral.

(ii) **Tentaculozooids:** similar to tentacles in structure, with a solid core of endoderm cells and no mouth or gastric cavity. More delicate and slender than spiral zooids.

(iii) **Nematophores:** highly extensile structures representing reduced hydranths and without mouth or tentacles. Characteristic of the *Plumulariidae*, where they may also be called *sarcostyles*, but also occurring in a number of other families.

The polyps of the *Hydroida* are occasionally solitary, as in the families *Corymorphidae* and *Myriothelidae*, where the individuals are large and provided with various internal elaborations of structure, but they are more often colonial and consist of numerous individuals derived by asexual multiplication but remaining in cellular continuity with one another.

Colonies may be **stolonial**, where growth is horizontal and the hydranths arise direct from a common hydorhiza, or erect, where growth is vertical, producing an upright hydrocaulus bearing the hydranths. Such a hydrocaulus may be unbranched, and bear a terminal hydranth with or without a number of lateral ones, or it may be branched.

The form of erect colonies depends primarily on the type of growth. Kühn (1914) defined three types of growth, and these types have been accepted by modern systematists and are depicted in most textbooks.

1. **Monopodial growth with terminal hydranth (raceme).** The first hydranth on the hydrocaulus is terminal. Below this is a growth-zone, and below this a budding zone. Buds are formed in the budding zone and the

![Diagram of growth and colony formation](image-url)
hydrocaulus elongates above them, so that the first bud is at the base of the stem and the youngest near the top. Each bud then grows in a similar manner and several degrees of branching may occur, each branch topped by its oldest hydanth, e.g. most Athecata: Eudendrium, Bougainvillia, Halocordyle.

2. MONOPODIAL GROWTH WITH TERMINAL GROWING POINT. There is no terminal hydanth, but the stem is topped by a growth-zone. Below the growth-zone is the budding zone, so that as growth proceeds the oldest hydanth is at the base and the youngest just below the tip, e.g. Plumulariidae, most Sertulariidae.

3. SYMPODIAL GROWTH (cyme). The first hydanth is terminal, but it has no growth-zone and the stem does not elongate after completion. A budding zone below the hydanth produces a branch which grows beyond the first hydanth and is topped by the second hydanth. Continuation of this process produces a ‘false axis’ (the SYMPODIUM), which is in reality formed by successive branches (the PODIA), e.g. Haleciidae, Campanulinidae, Campanulariidae. Such a stem is usually zigzag or GENICULATE.

Few of the Hydroida are completely naked; most are provided with an external ectodermal skeleton of a horny chitinoid material. In the Athecata the skeleton is confined to the hydrorhiza, or to the hydrorhiza and hydrocaulus, where it encloses the stolons and coenosarc as the PERISARC. The hydanth is usually naked, or ATHECATE, but sometimes a gelatinous or membranous extension of perisarc may enclose the base of the hydanth as the PSEUDOHYDROTHECA, e.g. Bougainvillia, Bimeria (Fig. 33F). In the Thecata the hydanth is contained in a cup-like skeletal structure of definite shape, the HYDROTHECA, into which it can be partly or completely withdrawn, i.e. it is THECATE, and the reproductive buds (GONOPHORES) are contained in a GONOTHECA.

The PERISARC of the stem is sculptured in a fashion characteristic of the species. It is usually divided into segments, or INTERNODES, by partitions, or NODES: the latter are penetrated centrally by the living coenosarc. Less-marked thickenings of perisarc may form TRANSVERSE ANNULATIONS, probably resulting from growth, or internal ridges with a strengthening function, the INTERNODAL SEPTA. In the Thecata each internode may give origin to one or two hydrothecae or branches with great regularity, each from a projecting shoulder, or APOPHYSIS.

The stem, when it consists of a single perisarc-covered tube, is said to be UNFASCICLED. A FASCICLED stem consists of many parallel tubes intercommunicating by pores at intervals (Fig. 105). The central tube is the first-formed and the peripheral tubes grow up around it, arising either from the hydrorhiza or from the stem itself. Branches may arise either from the axial tube or from the peripheral tubes.

Branching of the stem may be quite irregular resulting in shrubby colonies, e.g. Eudendrium, or it may be very regular with the type diagnostic of the genus or species. The following main types occur, although in certain cases two or more may be combined in the same colony:
Fig. 6. Parts of the siphon. On the left a pedicellate and radially symmetrical hydrotheca. On the right a sessile and bilaterally symmetrical hydrotheca, with accompanying nematothecae.

1. Pinnate. The stem is plume-like with two rows of branches on opposite sides and in the same plane. The branches may be alternate if they arise alternately on the right and left, or opposite if they arise in pairs from the same level.

2. Dichotomous. The stem forks to form two limbs of equal thickness. This process may be repeated many times and the length of the two limbs is not necessarily the same. The colony has no obvious ‘main stem’.

3. Whorled. Branches arise from the stem in whorls. In Nemertesia members of one whorl alternate with those of the next, giving double the number of longitudinal rows.

4. Spiral. Branches arise as in a pinnate stem, but the main axis is spirally twisted.

5. Sympodial. In addition to the single erect and hydrotheca-bearing stem resulting from sympodial growth (which is really a ‘false axis’ or symposium, p. 11), subsidial branches may be produced in the same way, i.e. below the terminal hydranth. If the branches arise alternately on the right and left, a scorpoid symposium* results, if the branches always arise from the same side, a helicoid symposium*, the latter tending to curl or twist into a spiral. Two branches arising together on right and left produce a dichotomous symposium.

* These terms are not used consistently in hydroid literature. The definitions adopted here are from Webster’s International Dictionary.
Fig. 7. Types of stem and branching. The hydrocladium (h) corresponds to the stem in B, to a branch of the first order in C, to a branch of the second order in E, and to a branch of the third order in F.
The term HYDROCLADIUM is in use in hydroid literature, and particularly in the Plumulariidae, for hydrotheca-bearing branches. Unfortunately it is not always used in the same sense. Von Schenk (1965) abandoned the term and invented a completely new terminology for the different orders of branches in the Plumulariidae. His system is, however, cumbersome and has not been generally accepted. Complex branching can normally be described by use of the simple terms primary, secondary, tertiary, etc., or branches of the first, second, third order, etc., with the retention of the well-established term HYDROCLADIA for the final branchlets bearing hydranths or hydrothecae. The position may be complicated in species where the colony can exist in two forms. Thus, Antennella secundaria may produce both simple unbranched stems and pinnate stems. In this case the simple stem is synonymous with a hydrocladium and with a branch of the pinnate stem. The same position may arise in some of the Sertulariidae. In colonies with irregular branching the term hydrocladium is best avoided.

The HYDROTHECA (Fig. 6) may be without a stalk and sessile, or with a stalk, or pedicell, and pedicellate. It may be tubular, bell-shaped (campanulate), or saucer-shaped. In the Sertulariidae and Plumulariidae it is bilaterally symmetrical, usually with one wall fused to the stem, or adnate. Since the hydrotheca usually arises at an angle to the stem it is possible to distinguish that side closer to the stem as adcauline and the opposite side as abcauline. In the genus Silicularia and some species of Campanularia the hydrotheca tends to be grossly thickened on two opposite sides, thus imparting a bilateral symmetry on an otherwise radially symmetrical family (the Campanulariidae) (Fig. 66). The hydrotheca is often ornamented by transverse annulations or longitudinal striations.

The margin of the hydrotheca may be smooth or dentate. The MARGINAL TEETH vary in shape and number and provide a useful diagnostic character.

The hydrotheca may also have internal perisarcal thickenings. A DIAPHRAGM commonly occurs in the base where the hydranth narrows to join the coenosarc. A true diaphragm takes the form of a definite perisarcal shelf on which the base of the hydranth rests, e.g. Clytia, Obelia; sometimes an ANNULAR THICKENING of a less definite nature occupies the same position (Fig. 66). In the sessile and bilaterally symmetrical hydrothecae of the Sertulariidae and Plumulariidae there is an inturmed base similar in appearance to a diaphragm. It is penetrated by the HYDROPORE.

Internal and transverse shelves or ridges of perisarc in the hydrotheca are termed INTRATHECAL SEPTA. These may form useful attachment points for the hydranth, facilitating its withdrawal.

INTERNAL TEETH, situated within the hydrotheca just below the margin, are characteristic of certain Sertulariidae. Their function is not clear; the number and position are diagnostic in certain species.

In certain families the hydrotheca is provided with a lid, or OPERCULUM, consisting of one or more valves meeting in the centre. Broch (1918) showed
that in some members of the Campanulinidae the opercular valves are formed from the distal part of the hydrotheca, and simply fold inwards to close the aperture. In other campanulinids and in the Sertulariidae the operculum is formed from the primary covering of the hydrotheca and the opercular segments are seated and hinged in embayments of the hydrothecal margin.

The arrangement of the hydrothecae on the stem and branches varies. There may be a single row of hydrothecae on one surface, two rows of hydrothecae on opposite surfaces (with OPPOSITE OR ALTERNATE arrangement), many longitudinal rows, or the arrangement may be quite irregular. If the hydrothecae are not quite opposite or not quite alternate the terms SUBOPPOSITE and SUBALTERNATE are used. When the hydrothecae are borne on one surface, or face towards one surface, that surface is said to be the ANTERIOR FACE and the opposite surface the POSTERIOR FACE. Hydrothecae may be borne on the stem (CAULINE HYDROTHERCAE) and all its branches, or they may be restricted to the branches or the hydrocladia.

NEMATOTHECAE contain the nematophores. They are characteristic of the Plumulariidae and a few genera of Lafoeidae and Haleciidae. They may be sessile or pedicellate, one-chambered or two-chambered, movable or immovable. They may be quite irregularly arranged on the colony, or grouped in a definite manner around the hydrothecae. In the Plumulariidae there is typically one below each hydrotheca, the MEDIAN INFERIOR NEMATOTHECA, and one on each side, the LATERAL NEMATOTHETECAE (Fig. 6). There may also be one or two above the hydrotheca, the SUPERIOR NEMATOTHETECAE, and some on the stem, CAULINE NEMATOTHETECAE (Fig. 106).

The GONOTHECA encloses the reproductive bodies of the hydranth generation (GONOPHORES). It is usually more or less spindle-shaped, and may be smooth, annulated or spiny, and may be provided with an operculum. The gonothecae

---

Fig. 8. Types of nematothecae.
may be borne singly, or may be aggregated into compound bodies or protected by special outgrowths.

In the Lafœidae aggregations of gonothecae, often accompanied by specially modified nematothecae, form COPPINIAE, or nest-like structures round the larger stems. In the plumulariid genera Aglaophenia and Thecocarpus aggregations of gonothecae are borne on specially modified hydrocladia forming CORBULÆ. Protective branchlets for the gonothecae are termed PHYLACTOCARPS. They may be formed from a modified hydrocladium or as an appendage to a hydrocladium.

![Diagram of gonothecae](image)

**Fig. 9. Types of structures protecting the gonothecae.**

In addition to the external skeleton considered so far, some hydroids possess an INTERNAL SKELETON in the sense that it is contained within, or covered by, living cells. However, such a skeleton is always ectodermal in origin and its position is probably secondary. In Hydractinia, for example, the adpressed stolons of the hydrorhiza may lose the outer perisarc during development, so that the layer is covered externally by epithelium—the NAKED COENOSARC. The basal layer of perisarc may produce spines which penetrate the surface. Hydrocorella is similar, except that the skeleton is impregnated with lime. In Rosalinda and Teissieria the internal skeleton of the hydrorhiza consists of anastomosing ribs, or TRABECULÆ, which produce spines. The culmination of this process is reached in Solanderia where the trabeculae rise up to form an erect and elaborately branching stem, covered superficially by naked ectoderm.

A typical MEDUSA is radially symmetrical with a convex upper surface, the EXUMBRELLA, and concave lower surface, the SUBUMBRELLA. The shape varies from flat and disc-shaped to deep bell-shaped or conical. The mouth is borne on
a HYPOSTOME, or manubrium, which hangs from the centre, and opens into a STOMACH, or gastric cavity. From the latter lead RADIAL CANALS, which communicate with a CIRCULAR CANAL round the margin. From the margin a VELUM, or horizontal ectodermal shelf, projects inwards and demarcates a SUBUMBREL-LAR CAVITY within the bell. The margin also bears the MARGINAL TENTACLES. At the top of the exumbrella a projecting cone may form an APICAL PROCESS and may contain an APICAL CANAL communicating with the stomach.

The RADIAL CANALS are usually four in number and impart a tetramerous symmetry to the whole. From their position the 'axes' or radii of the medusa are derived. The radial canals lie in the PERRADII; alternating with these are the INERRADII, and between the perradii and the interradii are the ADRADII. Occasionally the radial canals are branched or multiplied.

The MOUTH may be simple and circular, e.g. Sarsia, or it may be drawn out into ORAL LIPS which may be folded or crenulated, e.g. Leuckartiara. It may also bear simple or branched ORAL TENTACLES. The latter may be borne on the edge of the mouth or may be set back, as in Bougainvillia, so as to arise just above it.

The STOMACH and HYPOSTOME may be short, not reaching the edge of the bell, or may be long and extensile, hanging well below the bell. The jelly of the upper part of the bell may bulge down into the base of the stomach forming a PEDUNCLE.

The MARGINAL TENTACLES may be SOLID OR HOLLOW, FILIFORM, CAPITATE OR MONILIFORM, these terms being used as in the hydranth (Fig. 3). They arise from a swelling of the margin, the MARGINAL BULB, but in some Limnomedusae this
bulb is absent. There is usually a tentacle to each bulb, but occasionally marginal bulbs lack tentacles or one bulb bears a group of tentacles. Rarely the tentacles are branched (Cladonemidae). The surface of the tentacle facing towards the centre is said to be adaxial and the outer surface abaxial. In addition to normal tentacles, reduced tentacles or cirri may occur; these are without marginal bulbs and may be spirally coiled.

The medusa bears the sexual products in gonads. The gonads are borne either
(1) on the stomach wall, where they may form a single mass surrounding the stomach or be split into horizontal or radial segments, or
(2) on the radial canals, where they may vary in shape (oval or elongated, folded, sinuous, flattened, etc.).

Gonads borne on the stomach may, however, also spread on to the radial canals, and those on the radial canals may reach the stomach at their inner ends.

Most medusae possess sense-organs, normally borne on or near the margin. Several types occur:
1. Statocysts, or organs of orientation and equilibrium. They are absent in the Athecata, but occur in the Thecata and Limnomedusae. There are two kinds:
   (i) Ectodermal Statocysts (Marginal Vesicles), in the form of hollow pits or vesicles situated in the velum and lined by ectoderm. They contain statoliths, or concretions of calcium carbonate. They may be open, with an opening facing towards the subumbrellar cavity, or closed, when they hang below the velum.
   (ii) Endodermal Statocysts, in the form of sensory clubs growing from the circular canal. There is a solid axis of endodermal cells of which one or two terminal ones contain concretions. They may be free, and project through the margin of the bell, or enclosed, and contained in an ectodermal vesicle.

2. Ocelli, or organs of sight, borne on the marginal bulbs and either adaxial or abaxial in position. The structure varies from simple patches of red, brown or black pigment to elaborate organs containing a lens.

3. Cordyli, club-like structures of unknown function borne on the bell margin. Medusae may also possess so-called excretory pores, which are openings from the radial canals to the subumbrellar surface.

The typical medusa is free-swimming and able to feed and grow, but among the hydroids there are numerous cases where the medusa remains attached to the hydranth as a gonophore and is reduced to a varying degree; its development appears to be arrested at a certain stage. It is usual to distinguish the following stages in medusa reduction (originally defined by Kühn 1914):
1. Eumedusoid. Marginal tentacles and sense organs absent or reduced. No mouth. Velum not penetrated. Radial canals present, but sometimes without a cavity. May be freed and perform pulsations, but cannot feed or develop fully.
2. CRYPTOMEDUSOID. Radial canals absent, but a single layer of endoderm, the endodermal lamella, present lining the exumbrellar ectoderm. Subumbrellar cavity distinct, reduced or absent.

3. HETEROMEDUSOID. Endodermal lamella absent. Outer ectoderm two or more-layered, often enclosing the remnant of a subumbrellar cavity. This may form an acrocyst for the retention of eggs.

4. STYLOID. A simple evagination covered with ectoderm and lined with endoderm; the latter with its cavity forming the spadix. The sex cells develop between the two layers.

These stages have a doubtful value in classification since some species are sexually dimorphic, with one sex more reduced than the other, e.g. in Tubularia indivisa and T. regalis the male gonophore is cryptomedusoid and the female eumedusoid, and in Euclaomedea flexuosa and E. calceolifera the male gonophore is styloid and the female heteromedusoid. It is, however, important to distinguish between medusae which develop fully and can be keyed out by typical adult characters and those which are degenerate and cannot feed or grow. Therefore propose to follow Rees's dictum (1957) and retain 'separate genera for hydroids with fixed gonophores and for hydroids with free medusae . . .'. The term fixed sporosacs will be used for all degenerate medusoid stages, including the four described above.
It is thus apparent that although in the 'typical hydroid' the polyp and medusa stages alternate and are of more or less equal importance, in some families, and particularly in the Plumulariidae and Sertulariidae where fixed sporosacs are the rule, evolution in the polyp generation has outpaced that in the medusa. In contrast there are some families in which the evolution of the medusa generation is highly advanced while the polyp is small and inconspicuous. In these cases the hydranth, if known, is often of little use in diagnosis and keys have of necessity to be based on the medusae. This applies to the Linnomedusae, the Campanulinidae and to several families of Athecata.

Species are said to be monoecious if the male and female sex products are borne on the same colony or individual, and dioecious if on separate colonies or individuals. Hermaphrodite individuals occur rarely.

Development of the fertilized egg produces two kinds of larvae:

1. The planula, an oval or pear-shaped, ciliated body consisting of solid endoderm surrounded by ectoderm (Fig. 34D). It settles to the bottom, attaches by the broader anterior end and develops into a polyp.

2. The actinula, resembling a small polyp with two circles of tentacles (Fig. 15D). It settles to the bottom where it rests on the aboral tentacles, attaches by the aboral end and develops into a polyp.

The eggs may be fertilized in the sea or be retained in the gonophore of the polyp generation or gonad of the medusa for the initial stages of development. In some Thecata the eggs may be extruded from the gonotheca but retained in an acrocyst for the initial stages of development. Special brood-chambers or marsupia may also occur.

THE STING CELLS

Sting-cells, or nematocysts (cnidocysts), are always present, and are particularly abundant on the tentacles, the hypostome and certain special tracts on the hydranth and medusa.

The nematocyst consists of a round, oval or elongated capsule, containing a coiled tube. It discharges the tube by eversion. The tube may or may not have a thicker basal portion, the butt, and is usually armed in part or in whole by spirally arranged spines.

The classification of nematocyst types presented by Weill (1934) has been adopted here. Weill originally distinguished 17 types in the Cnidaria; since then additional types have been named, and in 1974 Mariscal listed a total of 26. Not all of these occur in the Hydroida. A key to the identification of the most common hydroid types is given below.

1. Discharged tube rolled up like a corkscrew, tube closed at tip DESMONEME (volvent) 2
   - Discharged tube not rolled up, tube open at tip  
   2. Without butt (haploneme)  
   - With butt (heteroneme)  
   3. Tube tapering and slightly thicker at base (anisorhiza), armed, and with larger spines near base HETEROTRICHIOUS ANISORHIZA 4
   - Tube of equal diameter throughout (isorhiza)  

2
3
6
4
4. Tube without well-defined spines (glutinant)  ...  ...  ...  ...  ...  ATRICHOUS ISORHIZA  
   — Tube with well-defined spines  ...  ...  ...  ...  ...  5  
5. Spines in basal region only  ...  ...  ...  ...  ...  BASITRICHOUS ISORHIZA  
   — Spines in middle region only  ...  ...  ...  ...  ...  MEROTRICHOUS ISORHIZA  
6. Butt of equal diameter throughout, tube continued beyond butt (MASTIGOPHORE)  ...  ...  ...  7  
   — Butt of unequal diameter  ...  ...  ...  ...  ...  8  
7. Butt not more than 3 times length of capsule  ...  ...  ...  ...  ...  MICROBASIC MASTIGOPHORE  
   — Butt at least 4 times length of capsule  ...  ...  ...  ...  ...  MACROBASIC MASTIGOPHORE  
8. Butt dilated at base  ...  ...  ...  ...  ...  STENOTELE (penetrant)  
   — Butt dilated at distal end (EURYTELE)  ...  ...  ...  ...  ...  9  
9. Butt not more than 3 times length of capsule  ...  ...  ...  ...  ...  MICROBASIC EURYTELE  
   — Butt at least 4 times length of capsule  ...  ...  ...  ...  ...  MACROBASIC EURYTELE  

The total ensemble of nematocyst types possessed by a species is known as its Cnidome.

Nematocysts are occasionally concentrated on special stalks or processes known as Cnidophores. These may occur in the polyp generation (e.g. Eudendrium racemosum) or in the medusa (Zanclea, Proboscidactyla).

![Diagram of Nematocyst Structure and Type](image-url)

Fig. 12. Nematocyst structure and type.
ECOLOGY

ASEXUAL REPRODUCTION is responsible for colony-formation and budding off of medusae. A form of asexual reproduction known as STOLONIZATION may also occur in the polyp generation, when the ends of the stem or branches produce tendril-like stolons which reattach and form new colonies. Sometimes the ends of such stolons separate off (SCHIZOGENY) forming bodies similar to planulae, e.g. Coryne pusilla (Fig. 19G).

BUDDING of medusae may also occur, either from the stomach wall (e.g. Rathkea) or from the marginal bulbs (Hybocodon). FISSION is more rare, but occurs in Staurocladia and Craspedacusta. The medusa Cytaeis tetrastyla buds off young hydranthids from the stomach wall (Kramp 1959).

REGENERATION, or regrowth after injury, is common. Colonies may die down and regenerate later from the hydrorhiza or from the hydrocaulus. Many forms are provided with HINGE-JOINTS (Fig. 78, 115C), which are strongly marked oblique nodes in the perisarc where movement can occur and where rupture is easy (comparable to the ‘breaking point’ in a lizard’s tail). Hinge-joints often occur in pairs with a short internode between them.

In the Thecata regeneration of hydrothecae may occur. In Halecium the new hydrotheca develops from within the old one and repetition of this process results in a tier of hydrothecae one within the other (Fig. 46). Sometimes only the margin regenerates resulting in a hydrotheca with numerous margins and often adding considerably to the depth (Fig. 56A). This is common in the Laffoeidae and Sertulariidae.

In the Moerisiidae special resting bodies or podocysts can survive death of the colony to regenerate later.

The Hydroida often have close relationships with other animals. The larvae may settle and grow on almost any animal, including other hyroids, simply using them as a convenient substratum. Such forms are said to be EPIZOOTIC. In some cases the relationship is closer, and there seems to be a definite selection of the host by the epizoite. Hyroids which live on the shells of molluscs or hermits are well known and are well represented in South Africa. It is often difficult to draw a boundary between epizoism and COMMENSALISM, where both animals obtain benefit from the association. Proboscidiaclyla (Lar), which lives on polychaet tubes, has been proved to be an obligatory commensal.

Table 1 gives a list of South African host animals and the hyroids which have been recorded on them as epizoites, commensals or parasites, but hyroids acting as hosts have not been included. In addition to these, sessile barnacles, the common shore mussels and the red-bait Pyura may carry a thick population of hyroids.

In a few members of the Plumulariidae and Laffoeidae colonies may be epizootic on the same species of hyroid or on closely related species. Such forms are said to be AUTO-EPIZOOTIC (Millard 1973). This commonly results in the stunting of the epizoite in whole or in part, so that its appearance is abnormal, and it is difficult to recognize.
Some hydroids occur only on algae and may have special adaptations for this substratum. In *Plumularia filicaulis* the gonothecae are recumbent and cemented to the alga. In *Lineolaria* the hydrothecae are fused for almost their entire length to the alga.

### Table 1

A list of host animals with their recorded hyroid epizoites, commensals or parasites.

<table>
<thead>
<tr>
<th>Host</th>
<th>Hydroid</th>
<th>Family</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>SPONGES</strong></td>
<td><strong>Hybocodon unicus</strong></td>
<td>Tubulariidae</td>
</tr>
<tr>
<td></td>
<td><strong>Zyzyxus solitarius</strong></td>
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<tr>
<td></td>
<td><strong>Sphaerocoryne hedoti</strong></td>
<td>Corynidae</td>
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<tr>
<td></td>
<td><strong>Zanclea sp.</strong></td>
<td>Zanceliidae</td>
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<tr>
<td></td>
<td><strong>Zanclea sp.</strong></td>
<td>Zanceliidae</td>
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<tr>
<td><strong>CORALS</strong></td>
<td><strong>Proboscisactyla sp.</strong></td>
<td>Proboscisactylidae</td>
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<td></td>
<td><strong>Clytia hemisphaerica</strong></td>
<td>Campanulariidae</td>
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<tr>
<td><strong>POLYZOA</strong></td>
<td><strong>Laonome sp.</strong></td>
<td>Campanulariidae</td>
</tr>
<tr>
<td></td>
<td><strong>Sabella penicillus L.</strong></td>
<td>Campanulariidae</td>
</tr>
<tr>
<td></td>
<td><strong>Lepas sp.</strong></td>
<td>Campanulariidae</td>
</tr>
<tr>
<td><strong>POLYCHAETS</strong></td>
<td><strong>Clytia hummelinki</strong></td>
<td>Bougainvillidae</td>
</tr>
<tr>
<td><strong>CIRRIPEDES (stalked)</strong></td>
<td><strong>Obelia dichotoma</strong></td>
<td>Bougainvillidae</td>
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<td></td>
<td><strong>Codonophilus (Meinertia) imbricata (Fabr.)</strong></td>
<td>Bougainvillidae</td>
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<td><strong>Dicoryne conferta</strong></td>
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<td><strong>Hydrocorrella africana</strong></td>
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<td><strong>Clavaclina multientunctulata</strong></td>
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<td><strong>Leuckartiara octona</strong></td>
<td>Pandeidae</td>
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Table 1 (cont.)

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<th>Family</th>
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<td>Thais squamosa (Lam.)</td>
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<td>&quot;Turitella sp.&quot;</td>
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<tr>
<td>Vermetus sp.</td>
<td>Hydrocorella africana</td>
<td>Hydractiniidae</td>
</tr>
</tbody>
</table>

PTEROPODS

Diacria trispinosa Les.  
Clytia gravieri  
Campanulariidae

FISH

Ambassis safgra (Forsk.)  
Hydrichthys boycei  
Pandeidae

Chaetodon lunula (Lac.)  
Hydrichthys boycei  
Pandeidae

Mugil sp.  
Hydrichthys boycei  
Pandeidae

Squalus fernandinus Molina  
Obelia dichotoma  
Campanulariidae

TURTLES

Caretta caretta (L.)  
Obelia dichotoma  
Campanulariidae

Eretmochelys imbricata (L.)  
Clytia hemisphaerica  
Campanulariidae

N.B. Ritchie (1907b) records Nassa crepulida as a host for Podocoryne carnea, and Stechow (1925a) records Oliva auricularia as a host for Hydrocorella africana and Sipho islandicus for Styelactis siphoni. These three molluscs are not known from South Africa and are omitted from the table.

ORDER HYDROIDA

Diagnosis. Hydrozoa typically with alternating asexual polyp and sexual medusa generations. Polyp generation typically sedentary, rarely planktonic, with perisarc and well-developed tentacles. Medusa generation budded from polyp generation and typically free-swimming though sometimes reduced to a fixed sporosac; with velum and sense-organs in the form of ocelli, statocysts or cordyli.

KEY TO SUBORDERS

1. Polyp generation planktonic, in the form of polymorphic colonies with a central gastrozooid  
   - Polyp generation usually sedentary, if planktonic not as above  
     2

2. Hydranth with a definite hydrotheca of definite shape. Medusa, when present, usually flattened; with gonads on radial canals; with or without statocysts and if present ectodermal  
   - Hydranth with no definite hydrotheca. Medusa, when present, usually deep; with gonads on radial canals or stomach; with or without statocysts and if present endodermal  
     3

3. Medusa without statocysts and usually with ocelli; with gonads on stomach  
   - Medusa with or without statocysts, without ocelli; with gonads on stomach or radial canals  
     4

SUBORDER ATHECATA

Diagnosis. Hydranth with no definite hydrotheca or gonotheca, though a gelatinous or membranous pseudohydrotheca may cover the base of the body. Producing fixed sporosacs or free medusae. Medusa usually deep bell-shaped; with gonads on stomach but rarely extending perradially on subumbrella; without statocysts; usually with ocelli.
KEY TO FAMILIES

[Families in which the polyp generation is not represented in South Africa are bracketed]

1. Mature hydranth with at least some tentacles capitate (with the exception of one non-South African genus of Zancleidae: *Pieroclava*), or with tentacles absent. If absent, hydranth not parasitic .......................... .......................... .......................... .......................... 2
   — Mature hydranth with all tentacles filiform (with a few exceptions in non-South African genera of Corymorphidae), or with tentacles absent. If absent, hydranth parasitic .......................... .......................... .......................... .......................... .......................... 15

2. Hydranths solitary .......................................................... .......................... .......................... .......................... 3
   — Hydranths colonial, united by a common hydrocalus or hydrorhiza .......................... .......................... .......................... .......................... 5

3. Hydranth tentacles all capitate, numerous and scattered .......................... MYIOTHETIDAE, p. 42
   — At least some tentacles not capitate, at least some arranged in definite whorls .......................... 4

4. Oral tentacles scattered and capitate; aboral tentacles in one whorl and filiform (or rarely absent) .......................... .......................... .......................... .......................... [ACaulidae]
   — Tentacles in three whorls, one oral and capitate, two aboral and imperfectly moniliform .......................... .......................... .......................... .......................... [Tricyclusidae]

5. Hydranth with capitate oral tentacles and with 'branched' aboral tentacles bearing several rows of capitulae .......................... .......................... .......................... .......................... CLADOCORYNIDAE, p. 64
   — Hydranth without 'branched' tentacles .......................................................... .......................... .......................... 6

6. Skeleton internal .......................................................... .......................... .......................... 7
   — Skeleton, if present, external .......................................................... .......................... .......................... 9

7. Skeleton forming erect, branching stems .......................................................... SOLANDERIIDAE, p. 58
   — Skeleton restricted to inerusting hydrorhiza .......................................................... .......................... 8

8. Hydranth with an oral whorl of capitulate tentacles only .......................... [HYDROCORYNIDAE]
   — Hydranth with scattered capitulate tentacles .......................................................... ZANCLEIDAE, p. 66

9. Stem pinnate. Aboral tentacles of hydranth long, filiform and in one whorl; oral tentacles capitate and scattered .......................................................... HALOCORDYLIDAE, p. 40
   — Stem not pinnate. Tentacles of hydranth not as above .......................................................... 10

10. Oral tentacles in one whorl, capitate; aboral tentacles scattered, moniliform .......................................................... ASYNSYNIDAE, p. 63
    — All tentacles usually capitate, sometimes an aboral whorl of vestigial filiform tentacles as well, rarely tentacles absent .......................................................... 11

11. Medusa, when present, with simple tubular mouth and 2-4 simple marginal tentacles. Polyp generation stolonal or with erect branched stem with firm perisarc .......................................................... CORYNIIDAE, p. 48
    — Medusa, when present, not as above. Polyp generation always stolonal, often polymorphic .......................................................... 12

12. Hydranth with scattered tentacles. Medusa with 2-4 marginal tentacles bearing stalked cnidophores .......................................................... ZANCLEIDAE, p. 66
    — Hydranth with one whorl of capitulate tentacles or tentacles absent. Medusa, when present, without cnidophores .......................................................... 13

13. Hydranth with one whorl of capitulate tentacles, with or without a vestigial whorl of aboral filiform tentacles. Medusa creeping, with numerous branched tentacles provided with adhesive discs .......................................................... CLADONEMIDAE, p. 55
    — Colony poly- or dimorphic, with gastrozooids and dactylozooids, of which at least some lack tentacles. Producing fixed sporosacs .......................................................... 14

14. Gastrozooids and dactylozooids without tentacles, but with lateral or terminal nematocyst clusters .......................................................... [HALOCORYNIDAE]
    — Gastrozooids without tentacles, dactylozooids with one whorl of capitulate tentacles .......................................................... [PTILOCODIIDAE]

15. Hydranth with two whorls of tentacles, one oral and one aboral, with gonophores borne on blastostyles between them .......................................................... 16
    — Hydranth not as above .......................................................... 18

16. Hydranth pelagic, solitary and without stem .......................................................... [MARGELOPSISIDAE]
    — Hydranth sedentary, with well-developed stem .......................................................... 17
17. Stem with perisarc, which reaches to base of hydranth body and is usually stiff
   
   — Perisarc feebly developed, restricted to base of stem. Anchoring filaments
   present
   TUBULARIIDAE, p. 30
   
   — Hydranth tentacles irregularly scattered over body. Medusa, when present, with 4
   lips with a continuous row of nematocyst clusters along margin
   CLAVIDAE, p. 69
   
   — Hydranth tentacles concentrated at oral end, either in one whorl or 2-4 whorls
   close together, or tentacles absent
   
   19
   
   — Hydranth with trumpet-shaped hypostome. No medusae. Sporosacs borne on
   body of hydranth below tentacles
   EUDENDRIDI, p. 77
   
   — Hydranth with conical hypostome. Medusa present or absent
   
   20
   
   — Hydranth borne on definite perisarc-covered stem which is usually branched.
   Medusa, when present, with branched or unbranched oral tentacles inserted
   above mouth-rim, marginal tentacles often in groups
   BOLGAINVILLIDAE, p. 88
   
   — Polyp generation stolonal. Medusa, when present, not as above
   
   21
   
   21. Medusa with unbranched oral tentacles borne on mouth-rim and 4 marginal
   tentacles. Hydranths never polymorphic; medusa-buds borne directly on hydro-
   rhiza
   CYTAELIDAE, p. 118
   
   — Medusa, when present, without true oral tentacles, but with 4 lips which may be
   drawn out to form oral arms
   
   22
   
   — Medusa, when present, with 4 oral arms bearing clusters of nematocysts. Hydranth
   naked
   
   23
   
   — Medusa without oral arms; lips usually without clusters of nematocysts. Hydranth
   with or without perisarc
   
   24
   
   23. Medusa, when present, with solitary marginal tentacles. Hydranths polymorphic,
   with gonophores borne on gonozooids
   HYDRACTINIDAE p. 104
   
   — Medusa with marginal tentacles in 8 groups. Hydranths not polymorphic, with
   very extensive thread-like tentacles; medusa-buds borne directly on hydro-
   rhiza
   
   [RATHKEIDAE]
   
   24. Marginal tentacles of medusa swollen at base, without a terminal cluster of nemato-
   cysts
   PANDIDAE p. 121
   
   — Marginal tentacles of medusa not swollen at base, with a terminal cluster of nemato-
   cysts
   [CALYCOPSIDAE]

Family Corymorphidae

Diagnosis. Large, solitary hydroids with a cylindrical hydrocaulus and terminal
hydranth. Perisarc feebly developed. Hydrocaulus usually with anchoring
filaments. Hydranth with conical hypostome and two sets of tentacles: oral and
aboral. Oral tentacles filiform, moniliform or capitate. Aboral tentacles filiform
or moniliform. Gonophores borne immediately above aboral tentacles, usually
on branching blastostyles, in the form of fixed sporosacs or free medusae.

Medusa, when present, with simple circular mouth, four radial canals and
one to four capitates or moniliform marginal tentacles. No exumbrellar nemato-
cyst tracts or ocelli. Gonad completely surrounding hypostome.

Introduction. There are several theories on evolution among the athecate fami-
lies. Rees (1957) believes that the basic stock is to be found amongst the simpler
Corymorphidae, e.g. Euphysa aurata Forbes, where the hydranths are of simple
construction, with two whorls of tentacles and poorly developed perisarc.
Within the family, however, there has been a trend among certain forms to an
increase in size and elaboration of structure, culminating in the giant Branchio-
cerianthus. These structural elaborations include:
1. The presence of longitudinal endodermal canals in the hydrocaulus, e.g. *Corymorpha* and *Branchiocerianthus*. These occur in the periphery of an otherwise diffuse and parenchymatous endoderm which often fills the whole cavity of the coenosarc.

2. The presence of a transverse diaphragm of soft tissue in the hydranth dividing the cavity into an oral and an aboral chamber, presumably for the support of the aboral tentacles. (This diaphragm is not comparable with that found in the Thecata.)

3. The elaboration of a system of branched or unbranched 'radial canals' in the hydranth immediately above the diaphragm.

4. An increase in the number of tentacles.

5. The development of a bilateral symmetry in *Branchiocerianthus* to permit feeding in strong currents at great depths.

The perisarc is in general poorly developed and in the form of a gelatinous sheath, which sometimes fits quite loosely. It never extends on to the body of the hydranth and is usually restricted to the basal part of the hydrocaulus. In *Branchiocerianthus* and *Corymorpha* the hydrorhiza is in the form of anchoring filaments, slender root-like tubes covered with thin perisarc. These are adaptations for anchoring the body in a substratum of mud or sand.

Tentacles are always in two sets, oral and aboral, and may be moniliform, capitrate or filiform.

The aboral tentacles are usually in one whorl, but the oral tentacles may be in several, or many, close whorls concentrated around the mouth.

The gonophores are borne immediately above the aboral tentacles, usually on hollow, branching blastostyles. They may develop into free medusae or remain attached as fixed sporosacs. In many medusa species the hydranth generation is still unknown.

The subdivision of the Corymorphidae is still far from settled. It has been discussed in papers by Rees (1938, 1957), Kramp (1949) and Prévot (1959).

In the key which follows only a few of the more important genera with known hydranth generations have been included, and the diagnostic characters have been taken from Brinckmann-Voss (1970).

**KEY TO GENERA**

[Genera not represented in South Africa are bracketed]

1. Hydranth bilaterally symmetrical, with two sets of filiform tentacles
   - Hydranth radially symmetrical ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... 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Genus *Branchiocerianthus* Mark, 1898

Syn. *Branchiaria* Stechow, 1921.

*Diagnosis.* Hydranth bilaterally symmetrical and excentrically seated on hydrocaulus, with diaphragm, radial canals and two sets of filiform tentacles. Hydrocaulus rooted by anchoring filaments. Perisarc rudimentary. Gonophores in the form of fixed sporosacs borne on blastostyles arising immediately above the aboral tentacles.

Type species: *Branchiocerianthus urceolus* Mark, 1898.

One species only from South Africa.

*Branchiocerianthus imperator* (Allman, 1885)

Fig. 13

*Monocaulus imperator* Allman, 1885: 753, fig. 265. Allman, 1888: 5, pl. 3.

*Branchiocerianthus imperator:* Miyajima, 1900: 235, figs 1–2, pl. 14–15.


*Diagnosis.* Body very large, over 2 m in length when mature. Hydrocaulus tubular, narrowest distally and separated from hydranth by a diaphragm and an annular constriction, widening proximally and ending in a bulbous swelling bearing anchoring filaments. Base of hydrocaulus and anchoring filaments covered with thin perisarc. Coelenteron filled with vacuolated endoderm cells but containing a circle of longitudinal endodermal canals at periphery; these visible externally as longitudinal striations.

Hydranth disc-shaped, bilaterally symmetrical, especially in young individuals, with an excentric ('ventral') insertion of hydrocaulus and an excentric ('dorsal') hypostome; mouth directed at an angle of 45° to hydrocaulus. Hypostome round in section. Aboral tentacles 100–250 in number and reaching 300 mm, in one, or in two closely alternating whorls, the series broken in the ventral axis where new tentacles develop. Oral tentacles 48–180 in number and reaching 55 mm, in several close whorls. Internal cavity divided by a transverse diaphragm with a circular opening at level of aboral tentacles. Many unbranched radial canals present immediately above diaphragm and ending blindly at periphery.

Blastostyles 96–160 in number, in 1–3 whorls, the youngest ventral, branching 6–8 times, reaching 63 mm, bearing in total up to 600 sporosacs. Each branch terminating in a battery of nematocysts.

Colour: reddish, varying from pale pink to scarlet and maroon.

*Remarks.* Since the only material from the South African coast was not in good condition (Vervoort 1966b), the dimensions and tentacle numbers given above have been taken from Brattström's summary (1957).

*Distribution outside South Africa.* Pacific and Indian Oceans, in tropical and warm temperate waters. Type localities: North Pacific and Japan.

*Distribution in South Africa.* One record only, off Moçambique in 730 m. 25/35 (vd)
Fig. 13.

*Branchiocerianthus imperator*. Redrawn from Miyajima (1900). Scale in cm.
Genus Corymorpha M. Sars, 1835

Syn. Steenstrupia Forbes, 1846.

Diagnosis. Hydranth radially symmetrical, with diaphragm and two sets of filiform tentacles but no radial canals. Hydrocaulus rooted by anchoring filaments. Perisarc a transparent membranous sheath over hydrocaulus. Gonophores producing free medusae, borne on blastostyles immediately above aboral tentacles. Medusa with pointed apex and apical canal, with one moniliform marginal tentacle.

Type species: Corymorpha nutans M. Sars, 1835.

One species only from South Africa.

Corymorpha sp.


Diagnosis. Hydranth 14 mm in length, with at least 18 oral tentacles and 18 aboral tentacles. Oral tentacles in two close whorls. Reproduction unknown.

Remarks. Only one infertile specimen has been found, and it is impossible to delegate it to a species.

Distribution in South Africa. Durban Bay, in mud. 29/31 (s).

Family Tubulariidae

Diagnosis. Athecate, solitary or colonial hydroids with erect stems covered in perisarc to immediately below the hydranth. Hydranth large, with conical hypostome and two sets of filiform tentacles (aboral and oral) in adult, the oral tentacles capitate in the young stages. Gonophores borne on blastostyles which arise immediately above the aboral tentacles, in the form of fixed sporosacs or free medusae. Medusa, when present, with four radial canals, gonad completely surrounding hypostome, one to four perradial marginal tentacles, without ocelli. An actinula stage present in the life-history.

Introduction. The Tubulariidae are characterized by tall perisarc-covered stems and large terminal hydranthas. In most species the stem is unbranched and connected with other stems only by the reticular hydorhiza. In Zyzzyzu however, the hydranthas are solitary and in a few species of Tubularia the stem branches irregularly.

Growth occurs at the distal end of the stem where the newly formed perisarc is thin and where the coenosarc is dilated. During growth groups of annulations are formed at this level. These occur quite irregularly in the stem and their formation is apparently influenced by external factors. At this point, too, the hydranth may be shed in unfavourable conditions, to be regenerated later from the living coenosarc.

The histology is comparatively elaborate, second only to that in the Corymorphidae. The endoderm of the stem in many species forms longitudinal
ridges, visible as striations in external view. These ridges may meet in the centre, so dividing the coelenteron into longitudinal canals, or may themselves contain canals. In *Zyzyzus* separate endodermal canals are present within the normal vacuolated endoderm similar to those in the Corymorphidae. The canals communicate distally with the gastric cavity of the hydranth.

As in the Corymorphidae the endoderm of the hydranth is thickened round the base of the body as a diaphragm or cushion of large vacuolated endoderm cells bulging towards the centre and constricting the coelenteron. It may be separated from the endoderm of the aboral tentacles by a lamella of mesogloea. Similarly the endoderm of the oral tentacles may be separated from that lining the hypostome by a mesogloeval lamella.

These specializations are associated with the large size of the hydranth.

The gonophores, which are borne on blastostyles arising immediately above the aboral tentacles, may be in the form of fixed sporosacs (*Tubularia* and *Zyzyzus*) or become freed as medusae (*Ectopleura* and *Hybocodon*). The degree of development of the sporosacs varies between species and sometimes within the same species. The medusa is little modified and close to the hypothetical ancestral condition postulated by Rees (1957). In *Ectopleura* the medusa is radially symmetrical usually with four marginal tentacles, but in *Hybocodon* it is asymmetrical with one or a group of tentacles on one edge and the tentacles are moniliform.

All the Tubulariidae possess an actinula larva, which is released either by the sporosac or by the medusa. The eggs are large and yolky and only a few develop into actinulae at the expense of the others. The actinula possesses one whorl of filiform aboral tentacles and one whorl of capitate oral tentacles of which the latter may only develop after release. It does not swim, but sinks passively to the bottom where it rests mouth upwards on the aboral tentacles. Growth of the aboral pole produces a short stalk which then achieves attachment to the substratum by the developing perisarc. The young hydranth thus possesses filiform and capitate tentacles. As development proceeds the oral tentacles lose their capitula.

Rees (1957) considers that the Tubulariidae evolved from the unspecialized members of the Corymorphidae by the development of firm perisarc, loss of anchoring filaments and partial atrophy of the stem canals and diaphragm. *Zyzyzus* represents an intermediate stage in its solitary habit, its soft perisarc and its endodermal canals. It is included in the Tubulariidae by virtue of the actinula larva. It possesses rooting processes which, however, are not homologous with the rooting filaments of Corymorphids but are adaptations to a habitat in sponges.

**KEY TO GENERA**

1. Hydranth solitary, with rooting processes and soft perisarc .... *Zyzyzus* p. 38
   - Hydranths usually colonial with a common hydorhiza, without rooting processes and with firm perisarc .... .... .... .... .... 2
2. Gonophores in the form of fixed sporosacs .... .... .... .... .... *Tubularia* p. 35
   - Gonophores released as free medusae .... .... .... .... .... 3
3. Medusa radially symmetrical, with two or four marginal tentacles . . . Ectopleura p. 32
   Medusa asymmetrical, with one or a group of marginal tentacles . . . Hybocodon p. 32

Genus Ectopleura L. Agassiz, 1862


Type species: Tubularia dumortieri van Beneden, 1844.
   One polyp species only from South Africa.

Ectopleura bethae (Warren, 1908)

Fig. 14A–D

Tubularia bethersi Warren, 1908: 280, pl. 45 (figs 10–11), pl. 46 (fig. 12).

Diagnosis. Hydorhiza branching, giving rise to unbranched stems up to 33 mm in length, each bearing a single terminal hydranth. Perisarc firm, irregularly annulated, especially near base, becoming very thin distally where it terminates on a dilation of the coenosarc just below the hydranth. Hydranth with 9–17 long aboral tentacles and 10–17 shorter oral tentacles. Oral tentacles capitate in young hydranth, filiform in mature hydranth but with concentration of nematocysts at distal end.

   Blastostyles arising just above aboral tentacles, bearing irregular clusters of medusa-buds. Medusa-bud with four capitate marginal tentacles, reaching at least 0.2 mm in diameter before release. Adult medusa unknown.

Distribution outside South Africa. S.E. Madagascar.

Distribution in South Africa. Natal and Inhaca. Type locality: between Park Rynie and Alexander Junction. 30/30 (1), 26/32

Genus Hybocodon L. Agassiz, 1862

Diagnosis. Hydranths colonial, without rooting processes. Hydrocaulus with firm perisarc. Gonophores released as free-swimming medusae. Medusa asymmetrical with margin at oblique angle, with 1–3 marginal tentacles arising from a single large marginal bulb, the remaining three marginal bulbs rudimentary.

Type species: Hybocodon prolifer L. Agassiz, 1862.
   One species only from South Africa.

Hybocodon unicus (Browne, 1902)

Fig. 14E–H

Amphicodon unicus Browne, 1902: 276.

Diagnosis. Hydorhiza branching within the sponge Hymeniacodon perlevis.
Fig. 14.

Ectopleura bethae. A, colony; B, mature hydranth with medusa-buds; C, young hydranth with capitate oral tentacles; D, oldest medusa-bud found.

Hybocodon unicus. E, mature hydranth with medusa-buds; F and G, recently hatched medusae, G in ventral view; H, nematocysts, from left to right a desmoneme, stenotele, atrichous isorhiza, microbasic mastigophore.

Scale: A in cm, H in μm, the rest in mm/10.
(Montagu), giving rise to unbranched stems up to 19 mm in height, each bearing a single terminal hydranth. Perisarc firm, not annulated, becoming membranous and swollen immediately below hydranth. Hydranth with 12–19 long aboral tentacles and 15–28 shorter oral tentacles, the latter in two close whorls. Blastostyles arising just above aboral tentacles, short and branching, bearing clusters of medusa-buds.

Medusa on release 0.75 mm in height and 0.65 mm in maximum diameter; with a single marginal tentacle arising from an enlarged marginal bulb; bell asymmetrical, bulging on side of marginal tentacle and with margin slightly oblique; the three small marginal bulbs produced over exumbrellar surface for a short distance; hypostome cylindrical and reaching practically to bell margin; with four unbranched radial canals; with scattered nematocysts on exumbrellar surface. Marginal tentacle about 1.3 mm when extended, moniliform, with 26 batteries of nematocysts. Adult medusa (not reported from South Africa) bell-shaped, 3 mm in height and 2 mm in diameter, with gonad surrounding hypostome from base almost to mouth.

Colour: hydranth transparent with orange-red stomach and hypostome, sometimes with darker longitudinal streaks on hypostome. Medusa transparent with orange-yellow hypostome and marginal bulbs.

Nematocysts of four types;

(i) Desmonemes, 4.8 × 3.0 – 6.6 × 5.4 μm. Capsule oval, undischarged thread in two coils.


(iii) Microbasic mastigophores, 9.0 × 4.8 – 10.8 × 4.8 μm. Capsule elongate-oval. Butt approximately equal to capsule in length.

(iv) Atrichous isorhizas, 9.0 × 7.2 – 10.2 × 7.2 μm. Capsule oval to spherical. Rare.

Remarks. The absence of nematocyst tracks on the bell of the medusa clearly distinguishes this species from the well-known *H. prolifer*. There is also no sign of the asexual budding so characteristic of the latter species. In the young living medusa the marginal bulb at the base of the tentacle is single and bean-shaped, not double as described by Browne & Kramp for *H. unicus*. The double appearance is assumed on contraction during fixation. I have assigned the species to *H. unicus* on the scattered nematocysts, the long hypostome and the distinctive process of the three small marginal bulbs which ‘is attached to and curls over the margin of the umbrella’ (Browne & Kramp 1939).

This is apparently the first discovery of the hydranth of *H. unicus*, and the first record of the genus from South Africa.

*Distribution outside South Africa.* South Atlantic and India. Type locality: Falkland Islands.

*Distribution in South Africa.* Sea Point only, lower littoral under ledges. 33/18 (1)
Genus *Tubularia* Linnaeus, 1758

*Syn. Parapha L. Agassiz, 1862.*

**Diagnosis.** Hydranths colonial, without rooting processes. Hydrocaulus with firm perisarc. Gonophores in the form of fixed sporosacs, either eumedusoid or cryptomedusoid.

Type species: *Tubularia indivisa* Linnaeus, 1758.

**KEY TO SPECIES**

(Doubtful species not included, for these see p. 38)

1. Stem unbranched. Apical processes of female gonophores laterally compressed *T. warreni*  
   - Stem branched. Apical processes of female gonophores conical  . . .  *T. larynx*

   **Tubularia larynx** Ellis & Solander, 1786

   *Fig. 15H–J*


   **Diagnosis.** Hydrorhiza a matted reticulum, giving rise to irregularly branched stems reaching a maximum height of 70 mm, each branch bearing a terminal hydranth. Perisarc firm, smooth for the most part, but with scattered groups of shallow annulations, becoming thin distally and terminating below the hydranth body. Cavity of coenosarc divided longitudinally by 2–4 endodermal ridges which may meet in the centre and may contain canals. Hydranth with up to 27 long aboral tentacles and up to 19 shorter oral tentacles.

   Blastostyles arising just above aboral tentacles in 1–3 closely alternating verticils, male and female usually on separate hydranths. Blastostyle branched or unbranched, bearing the gonophores in clusters. Gonophores without radial canals or marginal tentacles, oval to spherical, with three or four rounded tubercles at distal end. Eggs developing into actinulae *in situ*.

   Actinula at liberation with no oral tentacles or with rudiments of 3–5, with 6–13 long aboral tentacles with swollen tips. Oral tentacles not capitiate on settling. (From the literature, not observed in South Africa.)

**Distribution.** Cosmopolitan.

**Distribution in South Africa.** Two records only, one from a ship's hull in Table Bay and another from the Agulhas Bank in 126 m. 33°18' (h), 35°20' (d)

**Tubularia warreni** Ewer, 1953

   Frontispiece; Figs 15A–G


   **Diagnosis.** Hydrorhiza a matted reticulum giving rise to clusters of unbranched stems 50–100 mm in length, each bearing a single terminal hydranth. Perisarc
**Fig. 15.**

*Tubularia warreni.* A, colony; B, hydranth with female blastostyles; C, newly settled hydranth with capitate oral tentacles; D, actinula; E, nematocysts, from left to right a desmoneme, stenotele, heterotrichous anisorhiza, basitrichous isorhiza; F, female gonophore with crests and protruding spadix; G, male gonophore.

*Tubularia larynx.* H, female gonophore with tubercles; J, male gonophore.

Scale: A in cm, B in mm, E in μm, the rest in mm/10.
firm, smooth for the most part but with scattered groups of 3–7 annulations, becoming very thin distally where it terminates in a groove round a dilation of the coenosarc just below the hydranth. Cavity of coenosarc divided longitudinally by two or more endodermal ridges which may contain canals. Hydranth with up to 31 long aboral tentacles (5 mm or more) and up to 27 shorter oral tentacles (1 mm or more).

Blastostyles arising just above aboral tentacles in two or three closely alternating verticils, 6–12 in each, the oldest ones oral and the youngest aboral, male and female on separate hydranths. Each blastostyle with a slender axis, sometimes with a few lateral branches, bearing the gonophores singly or in clusters. Gonophores without radial canals or marginal tentacles. Male oval to spherical, normally smooth. Female oval to spherical, with eight laterally compressed distal crests, containing one or two eggs which develop into actinulae in situ.

Actinula at liberation normally with eight aboral tentacles and rudiments of four oral tentacles. Oral tentacles capitate in newly settled hydranth.

Nematocysts of four types:

(i) Desmocemes, $4.2 \times 2.4 - 5.4 \times 4.2 \mu$. Capsule oval, discharged thread with three coils. Numerous.

(ii) Stenoteles, $4.8 \times 4.2 - 10.8 \times 9.6 \mu$. Capsule oval, butt about two-thirds length of capsule. Numerous.

(iii) Heterotrichous anisorhizas, $7.8 \times 7.2 - 9.6 \times 9.6 \mu$. Capsule spherical or almost so. Thread coiled horizontally when undischarged, armed with spiral bands of short spines. Rare.*

(iv) Basitrichous isorhizas, $7.8 \times 2.4 - 9.0 \times 3.0 \mu$. Capsule elongate-oval, thread coiled longitudinally when undischarged, armed with short spines for the first part of its length. Rare.

Colour, endoderm of hydranth and spadix of gonophore deep red, tentacles transparent. General impression of living colonies orangy-red.

Variation. The longitudinal endodermal ridges in the stem vary in number from two to five (though usually two or three) and also in strength. Thus they may be very low indeed, or they may be high enough to meet in the centre when they may contain canals.

The oral tentacles of the hydranth are in one verticil in the extended state but on contraction alternate tentacles get pushed inwards, giving the impression of two verticils.

The male gonophores, though usually quite smooth, may occasionally bear four or five rudimentary conical processes at the distal end. In the female gonophores the distal processes vary in size and may rarely be absent. One or more may be swollen and distended. The spent female gonophores are elongated-oval or cylindrical. The spadix of the gonophore usually protrudes through the aperture in the female, and occasionally in the male.

* This classification is from Ewer (1953). I was not able to verify personally the fact that the thread tapers.
The number of tentacles in the newly released actinula varies from 5 to 12 aboral and up to 6 oral.

**Observations on living material.** This is one of the harder species of hydroids, growing abundantly in dock areas in spite of severe pollution. In the laboratory thousands of actinulae may be released and become established on the walls of the tank. The living hydranth readily accepts brine-shrimp larvae which are stung by the aboral tentacles and transferred to the mouth. The pendulous blastostyles when at rest hand down between the tentacles to a length of about 10 mm but perform rhythmical contractions, sweeping upwards towards the mouth.

The newly released actinula rests with the mouth directed upward and the aboral tentacles held alternately elevated and depressed, the downward-directed ones supporting it on the substratum. It does not swim but performs slow exploratory crawling movements. At this stage the slender aboral tentacles are slightly swollen at the tips and the oral tentacles mere lobes. By the time settling occurs the aboral part of the body has lengthened to form a short stem covered with perisarc and the oral tentacles are distinctly capitate and about 0,1 mm in length. Young hydranths of 2,5 mm have about 12 aboral tentacles and 6 capitate oral tentacles. The capitulum of the oral tentacles is densely covered with nematocysts. The aboral tentacles have nematocysts scattered along both oral and aboral surfaces, but the aboral ones are more numerous.

**Distribution.** Endemic to South Africa. Type locality: Durban harbour.

**Distribution in South Africa.** Langebaan to Durban, common in dock areas on pylons and on ships' hulls. 33/18 (1, h), 34/18 (h), 34/22 (1), 34/23 (h), 29/31 (h)

Doubtful species

*Tubularia crocea* (L. Agassiz, 1862)

*Parypha crocea* L. Agassiz, 1862: 249, pls 23–23a.

**Remarks.** Broch (1914) has reported this species from Lüderitz Bay in South West Africa, but the specimens were young and no description was given. The material is probably referable to *T. warreni*.

*T. crocea* differs from *T. warreni* in details of nematocysts, blastostyles and actinula.

**Genus Zyzzyus** Stechow, 1921

**Diagnosis.** Hydranths solitary, with rooting hydrorhizal processes. Hydrocaulus with soft perisarc. Gonophores in the form of fixed sporosacs.

Type species: *Tubularia solitaria* Warren, 1906a.

One species only from South Africa.
Fig. 16.

*Zyzyzus solitarius*. A, hydranth growing in sponge and showing rooting structures; B, mature hydranth with gonophores and escaping actinulae
*Halocordyle disticha*. C, stem; D, part of stem and hydrocladia; E, hydranth with gonophores; F, gonophore; G, large stenotele.

Scale: C in cm, G in μm, the rest in mm/10.
"Zyzyzyus solitarius" (Warren, 1906)

Fig. 16A–B


**Diagnosis.** Hydranths growing in sponges, reaching 13 mm in maximum total length, and embedded for about half this length. Hydorhiza and hydrocaulus not clearly demarcated externally, covered with smooth, soft perisarc which terminates in a circular groove below hydranth. Hydorhiza forming slender supporting ‘rootlets’ and fleshy storage ‘tubers’. Coenosarc of stem with about 16 longitudinal endodermal canals contained within the normal reticular endoderm and communicating distally with the gastric cavity of the hydranth. Hydranth with 15–34 aboral tentacles and 16–21 oral tentacles.

Blastostyles arising just above aboral tentacles, each bearing a cluster of 3–5 gonophores; male and female on same hydranth but on separate blastostyles. Gonophores cryptomedusoid, with a subumbrellar cavity opening to exterior, but no marginal tentacles or radial canals; female containing many eggs, of which one or two develop into actinulae. Actinula with 9–12 aboral tentacles.

Colour: hydranth body and gonophores rose-red, hydrocaulus and tentacles translucent white.

Nematocysts of at least three types:

(i) Large, oval capsules (?stenoteles). 7,2 × 5,9 – 12,1 × 11,6 μ.
(ii) Desmonemes. Small oval capsules. 4,5 × 3,6 – 6,3 × 3,6 μ.
(iii) Bean-shaped capsules (?basitrichous isorhizas). 8,1 × 3,6 – 9,0 × 3,6 μ.

**Distribution outside South Africa.** Cape Verde Islands, Trinidad.

**Distribution in South Africa.** Saldanha Bay to Moçambique, littoral. Never common. Type locality: Natal. 33/18 (1), 34/18 (1), 33/27 (1), 30/30 (1), 29/31 (1), 25/32, 21/35

**Family Halocordylidae**

Syn. Pennaridae.

**Diagnosis.** Upright, branching colonies with firm perisarc. Stem pinnate, bearing alternate hydrocladia. Hydrocladia bearing ramules on upper surface only. Hydranth borne on the summits of the stem, hydrocladia and ramules. Hydranth with an aboral whorl of long filiform tentacles and an oral set of capitate tentacles of which some or all form a whorl around the mouth. Gonophores borne on the hydranth above the aboral tentacles.

**Introduction.** This is one of the few athecate families with an upright stem and a regular scheme of branching. The arrangement of the side-branches, which arise alternately and bear the hydranths on short ramules on one surface only, is similar to that found in the pinnate Plumulariidae, and the same term is used for them, namely hydrocladia. Firm perisarc clothes the stem and all branches; it is usually divided into internodes, and annulated in certain areas, particularly
in the neighbourhood of the nodes. It terminates in a groove round the base of each hydranth.

The hydranth is comparatively large and flask-shaped, very similar in general structure and appearance to that of the Corymorphidae and Tubulariidae. Here also there is an aboral whorl of long filiform tentacles, but the oral tentacles are capitate and in most cases scattered over the whole of the oral region.

The gonophores are in the form of eumedusae, with four permanently stunted marginal tentacles and four radial canals. They may or may not have a short free-swimming existence, and this has in the past been used erroneously to separate species.

Mammen (1963) described the release of actively pulsating medusoids in *Halocordyle disticha*, and these settled on the bottom within a few hours. For the same species Brinckmann-Voss (1970) stated ‘The medusae may shed their sexual products while still attached to the hydranths or they may break free; they do not swim but sink immediately to the bottom. Liberated and non-liberated medusae occur on the same colony.’ Since there is no mouth, the medusae cannot feed and have a limited life.

One genus only.

Genus *Halocordyle* Allman, 1872


*Diagnosis*. As for family.

Type species: *Globiceps tiarella* Ayres, 1854.

One species only in South Africa.

*Halocordyle disticha* (Goldfuss, 1820)

Fig. 16C–G


*Pennaria australis* Bale, 1884: 45.


*Diagnosis*. Stem unfascicled, reaching a maximum height of 139 mm, divided by straight nodes into regular internodes, each bearing a hydrocladium near distal end, annulated at base and above each node. Hydrocladia alternate, the two rows in one plane, gently curved, those near the centre of the stem longer than those at the base and distal end, the longer ones divided by straight nodes into internodes, each internode bearing a ramule on the upper surface, annulated at base and above each node. Ramules unsegmented, annulated at least in basal region.

Hydranths borne on summits of stem, hydrocladia and ramules, with an aboral whorl of 8–15 long filiform tentacles and an oral set of 8–17 short capitate
tentacles which may be irregularly scattered or have a roughly verticillate arrangement.

Gonophores borne on hydranth between the two sets of tentacles, developing into eumedusae, which may have a short free-living life, male and female on separate colonies. Gonophores deeper than wide, with four radial canals, four rudimentary marginal tentacles, a long hypostome and no ocelli.

Nematocysts of at least three kinds:

(i) Stenoteles, large ones (to $47 \times 25 \mu$) on capitate tentacles, and small ones ($8 \times 5 - 14 \times 10 \mu$) on all tentacles, abundant.
(ii) Desmonemes, $6.5 \times 5.5 \mu$, on all tentacles.
(iii) ?Microbasic mastigophores, $11.5 \times 5 \mu$, on all tentacles, scarce.

Colour (preserved): stem dark-brown to black, becoming lighter towards the extremities which are transparent, hydranths reddish, gonophores with reddish longitudinal stripes.

Variation. The amount of annulation on the stem and branches has been shown by many authors to be variable, so that it is probably no longer correct to retain var. *australis* (Bale 1884), which is distinguished mainly by the paucity of annulations on the hydranth-bearing ramules.

The stem may have as many as 20 annulations at the base and up to 11 above each node, though more commonly four or five. The hydrocladia may have true annulations or spiral ridges. The ramules usually have one or two rings at the base, but there may be a large number, and there may also be a group at the distal end. Additional groups of annulations may occur anywhere on the stem or its branches. The South African material can be assigned to var. *australis* if this should be retained.

Distribution. Circumglobal in tropical and subtropical waters.

Distribution in South Africa. East coast, from just south of Durban to Moçambique, lower littoral region to 3 m, and on ships’ hulls. 30/30 (1), 29/31 (1, h), 27/32 (1), 26/32 (1), 24/35 (s), 23/35 (1), 21/35

Family Myriothelidae

Diagnosis. Large solitary hydranths attached to substratum by special perisarcal anchoring structures. Tentacles all capitate, numerous, scattered. Gonophores borne either on special blastostyles or direct on hydranth body.

Introduction. The Myriothelidae is a family of solitary hydranths in which some species have attained great size with accompanying elaborations of internal structure, a process paralleling that in the Corymorphidae. Thus, the endoderm is thrown into villi projecting into the coelenteron and the mesogloelal layer is thickened and bears lamellae on its outer surface supporting the longitudinal muscles (Fig. 18E). These features occur to a greater or lesser extent in the larger species and culminate in the giant *Myriothela penola* which can reach a length of 850 mm and has about 330 000 body tentacles (Manton 1940).
The body is normally cylindrical but can perform active contractile movements involving changes of shape. The distal and major part is thickly covered with tentacles, while the base is permanently attached to the substratum. A perisarcal sheath covers the basal region in *Arum* and *Monocoryne*, but in *Myriothela* the body is entirely naked, and perisarc is limited to the adhesive structures. The latter are processes of the body and may be (1) tubular with sucker-like distal ends, e.g. *Arum cocksi*, (2) tentacle-like, e.g. *Myriothela phrygia* and *M. capensis*, or (3) root-like, e.g. *Monocoryne gigantea*. In the first and second types the processes are fastened to the substratum by chitinoid ATTACHMENT DISCS which are in continuity with the mesogloea, and in *Myriothela capensis* the underlying ectoderm disappears. If torn away these discs cannot be reattached, although new adhesive structures may be formed (Manton 1941).

The tentacles are always capitate; single and scattered in *Arum* and *Myriothela*, but attached to one another in groups of three or four in *Monocoryne*. Each tentacle contains a lumen separated from that of the main body cavity, and the mesogloea often expands in the capitulum to form a thick apical pad (Fig. 18C). In *Myriothela* new tentacles are continually formed at the oral end, while the basal ones are progressively reduced and absorbed, and this is probably also the case in the other genera.

Reproduction, so far as is known, is always by means of fixed sporosacs, and the eggs, at any rate in *Myriothela*, develop into actinulae. The gonophores may be borne directly on the body (*Monocoryne*) or may arise from special blastostyles (*Myriothela* and *Arum*). The blastostyles arise from a budding zone between the attachment processes and the lowest body tentacles; they may be branched or unbranched and with or without capitate tentacles similar to those of the body.

**KEY TO GENERA**

[Genera not represented in South Africa are bracketed]

1. Tentacles grouped ........................................ *Monocoryne* p. 43
   - Tentacles single ........................................ 2

2. Proximal end of hydranth naked; perisarc present only on tips of anchoring filaments ........................................ *Myriothela* p. 45
   - Proximal end of hydranth and anchoring filaments sheathed in perisarc ........................................ *Arum*

**Genus Monocoryne** Broch, 1909

*Symplectanea* Fraser, 1941.

**Diagnosis.** Proximal end of hydranth and anchoring filaments surrounded by a perisarcal sheath. Distal end of hydranth bearing tentacles attached to one another in groups. No blastostyles; gonophores borne on body, in the form of fixed sporosacs.

Type species: *Coryne gigantea* Bonnevie, 1898.

One species only from South Africa.
Fig. 17.

Monocoryne minor. A, complete individual; B, a typical group of four tentacles.
Myriothela tentaculata. C, nematocysts, from left to right: large desmoneme, small desmoneme, heteroneme, atrichous isorhiza, stenotele.
Myriothela capensis. D, nematocysts, from left to right: undischarged and discharged large desmoneme, small desmoneme, heteroneme, ?atrichous isorhiza, stenotele, ?haploneme.

Scale: C and D in μm, the rest in mm/10.
Monocoryne minor Millard, 1966

Fig. 17A–B

Monocoryne minor Millard, 1966a: 435, fig. 1.

Diagnosis. Hydranth cylindrical, about 5 mm in length. Basal part (one-quarter) sheathed in transparent perisarc and giving rise to anchoring filaments. Distal part (three-quarters) naked, bearing about 110 capitate tentacles usually in groups of two, three or four united at the base; usually one tentacle of a group longer than the others.

Gonophores (?male) scattered on distal part of body, pear-shaped, reaching a diameter of 0.3 mm.

Nematocysts of at least three kinds:

(i) Desmonemes, 9.0 × 6.3 − 13.5 × 10.8 μ. Capsule oval, thread in about two coils. Abundant.
(ii) Stenoteles, 15.3 × 13.0 − 18.0 × 15.3 μ. Capsule oval, butt about half length of capsule. Fairly common.
(iii) Undetermined heteronemes, 16.2 × 6.3 − 18.9 × 7.6 μ. Capsule elongated, butt about ⅔ length of capsule. Rare.

Distribution. Endemic to South Africa.

Distribution in South Africa. Type locality and only record: Agulhas Bank in 77 m. 34/25 (s)

Genus Myriothela M. Sars, 1851

Syn. Candelabrum de Blainville, 1830 (nomen oblitum).

Diagnosis. Proximal end of hydranth without perisarc, bearing adhesive processes with perisarc only at the tips. Distal end of hydranth bearing separate, scattered tentacles. Gonophores in the form of fixed sporosacs, borne on blasto-styles arising below the area of body tentacles. An actinula stage in the life history.

Type species: Lucernaria phrygia Fabricius, 1780.

KEY TO SPECIES

1. Blastostyles about 1.5 mm long, with about 5 capitate tentacles at distal end  M. capensis
   – Blastostyles long and tendril-like, up to 20 mm, with over 25 scattered capitate tentacles

   M. tentaculata

Myriothela capensis Manton, 1940

Fig. 17D, 18A, F–G

Myriothela capensis Manton, 1940: 276, figs 7, 8b, 9, pl. 1 (figs 12–13), pl. 3 (fig. 27). Millard, 1966a: 437.

Diagnosis. Hydranth cylindrical, naked, reaching 25 mm in length, usually attached to weed. Basal part of body (one-tenth) bearing 20–30 adhesive processes capped by chitinoid discs. Distal part (nine-tenths) bearing 400–600 densely packed capitate tentacles.
Blastostyles arising from basal part of body (above adhesive processes) in a single whorl of about 20, unbranched, reaching 4 mm in length, bearing up to nine gonophores in proximal region, the oldest distal, and 4–7 capitate tentacles in distal region, of which some may be adhesive. Male and female on separate hydranths. Female gonophore sessile, spherical, reaching 0.9 mm in diameter, releasing up to three actinulae.

Nematocysts of possibly five types:

(i) Desmonemes, $7.8 \times 5.4 - 16.8 \times 12.6 \mu$. Capsule oval, thread in one to three coils.
(ii) Stenoteles, $9.9 \times 8.1 - 11.4 \times 7.2 \mu$. Capsule oval, butt just over half length of capsule.
(iii) Undetermined heteronemes, $11.7 \times 3.6 - 19.2 \times 6.0 \mu$. Capsule elongated, butt almost entire length of capsule.
(iv) Undetermined haplonemes, $10.8 \times 9.9 \mu$. Capsule wide-oval.
(v) ?Atrichous isorhizas, $18.0 \times 6.0 \mu$. Capsule elongated, no butt, thread coiled mainly in longitudinal plane. Not always present.

Colour variable. In one individual the capitula of most of the body tentacles were purple-brown, with amongst them white tentacles fewer in number and in roughly longitudinal bands; the gonophores had about seven longitudinal purple-brown stripes and two apical rings; the rest of the body was creamy white. In another individual the capitula of the body tentacles and tips of the gonophores were bright magenta, fading to pink on the stalks of the tentacles and white on the base of the body. A third individual was uniformly pink.

Variation. Various algae are used as hosts, including Ecklonia maxima (Osbeck) and Codium sp. It has also been found attached to a crustacean appendage and inside an empty limpet shell.

Distribution. Endemic to South Africa.

Distribution in South Africa. Lüderitz Bay to East London, littoral to 27 m. Type locality: Aquarium rocks, East London. 26/15 (1), 32/18 (s), 34/18 (1, s), 33/27 (1)

Myriotheta tentaculata Millard, 1966

Fig. 17C, 18B–E

Myriotheta tentaculata Millard, 1966a: 437, fig. 2.

Diagnosis. Hydranth cylindrical, naked, reaching 31 mm in length, attached to encrusting polypoans. Basal part of body (two-fifths) bearing about nine short, adhesive processes capped by chitinoid discs. Distal part (three-fifths) bearing densely packed capitate tentacles.

Blastostyles arising from basal part of body (above adhesive processes) in a single whorl of 17; unbranched, long and tapering and generally coiled, reaching 20 mm, bearing 4–8 gonophores in the proximal region, the oldest distal, and over 25 capitate tentacles on distal region and scattered amongst the gonophores. Tentacles not adhesive and resembling boot-buttons. Male gono-
Fig. 18.

*Myriotheia capensis.* A, complete individual extended; F, male blastostyle, contracted; G, female blastostyle, extended.

*Myriotheia tentaculata.* B, individual attached to polyzoan; C, l.s. body tentacle; D, l.s. blastostyle tentacle; E, t.s. body wall including origins of two tentacles on lower side of diagram.

Abbreviations: *e:* ectoderm; *m:* mesogloea; *ml:* mesogloea lamella; *mp:* apical pad of mesogloea; *n:* nematocysts; *v:* endodermal villi.

Scale: A, B, F and G in mm, C–E in mm/10.
phores spherical, reaching 2 mm in diameter, pedicellate. Female gonophores unknown.

Nematocysts of four types:

(i) Desmonemes, 10.2 × 7.2 – 18.0 × 14.4 μ. Capsule oval, thread in two or three coils.

(ii) Stenoteles, 14.4 × 10.8 μ. Capsule oval, butt over half length of capsule.

(iii) Undetermined heteronemes, 44.1 × 8.1 – 45.9 × 8.1 μ. Capsule banana-shaped, butt almost entire length of capsule.

(iv) Atrichous isorhizas, 15.3 × 4.0 – 19.8 × 7.2 μ. Capsule elongate-oval.

Variation. The tentacles are well developed at the distal end of the body, with large capitula and long stalks, but become progressively reduced as they approach the blastostyle region.

Distribution. Endemic to South Africa.

Distribution in South Africa. Type locality and only record: off Slangkop on the west coast of the Cape Peninsula, in 43 m. 34/18 (s)

Family Corynidae

Diagnosis. Colonial hydroids with erect stems and firm perisarc. Hydranth with conical hypostome, with capitate tentacles only or with short filifrom tentacles below the capitule ones. Gonophores borne on or below hydranth body, in the form of fixed sporosacs or free medusae. Medusa, when present, with simple circular mouth, four radial canals, gonads completely surrounding stomach, 2–4 hollow marginal tentacles and ocelli.

Introduction. In this family the tentacles of the hydranth are very varied in structure and arrangement so that allocation into genera is difficult. All possess capitate tentacles, and these may be arranged in definite whorls located on definite regions of the body (two well-separated whorls in Bicorona and Dicyclocoryne, one aboral whorl in Sphaerocrone, one oral whorl in some species of Dipuren) or they may be spread over the whole of the body. In the latter case there are usually three or four tentacles grouped around the mouth and the rest of the tentacles may show an indistinct whorling, but for ease of terminology they are here referred to as 'scattered'.

In addition to the capitate tentacles some species possess an additional whorl of vestigial filifrom tentacles round the base of the hydranth. The presence or absence of filifrom tentacles has in the past been used as a diagnostic generic character, but it has been shown that they may occur in some hydranthos of a colony and not in others, or that they may occur in primary and secondary hydranthos but not in tertiary ones (Rees 1957; Brinckmann-Voss 1970). I have, therefore, followed Brinckmann-Voss in uniting Stauridiosarsia with Sarsia, and Staurocrone with Coryn. Rees (1957) suggests that there has been a general trend amongst the Corynidae towards the loss of filifrom tentacles and the addition of whorls of short capitate tentacles.
Free-swimming medusae are formed in *Dicycloccoryne*, *Dipurena*, *Sarsia* and *Sphaerocoryne*. In some cases differentiation of the medusa generation appears to have advanced further than the hydranth generation. For instance the hydranths of *Dipurena* and *Sarsia* are almost identical, but their medusae are distinct, and in this case I prefer to retain the two genera and have not united them as was done by Brinckmann-Voss. Furthermore the hydranth of *Dipurena reesi* is very similar to that of *Cladonema radiatum* whose medusa belongs to a completely different family.

An actinula larva occurs in the genus *Actigia* Stechow, 1921, a genus which can probably be included in *Coryne*, and actinula-like buds have been shown by Rees (1957) to occur in *Sarsia tubulosa*.

**KEY TO GENERA**

[Genera in which the hydranth generation is unknown in South Africa are bracketed]

1. Capitate tentacles limited to one whorl or two closely alternating whorls near base of hydranth ... ... ... ... ... ... *Sphaerocoryne* p. 54
   - Capitate tentacles not as above ... ... ... ... ... ... ... ... ... ... ... ... 2
2. Capitate tentacles in two distinct and widely separated whors, one oral and one aboral ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... 3
   - Capitate tentacles scattered or indistinctly whorled over whole body, or limited to an oral whorl ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... 4
3. Producing fixed sporosacs ... ... ... ... ... ... ... ... ... ... ... ... ... ... *Bicorona* p. 49
   - Producing free medusae ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... [Dicycloccoryne]
4. Producing fixed sporosacs ... ... ... ... ... ... ... ... ... ... ... ... ... ... *Coryne* p. 51
   - Producing free medusae ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... 5
5. Medusa with undivided gonad ... ... ... ... ... ... ... ... ... ... ... ... ... ... *Sarsia* p. 52
   - Medusa with gonad in two or more rings round stomach ... ... ... ... ... ... ... ... [Dipurena]

**Genus Bicorona** Millard, 1966

*Diagnosis*. Colonies with erect, branched stems. Mature hydranth with two widely separated whors of capitate tentacles, one oral and one aboral. No filiform tentacles. Gonophores in the form of fixed sporosacs borne on the body of the hydranth.

Type species: *Bicorona elegans* Millard, 1966.

One species only.

*Bicorona elegans* Millard, 1966

*Frontispiece; Fig. 19A–E*

*Bicorona elegans* Millard, 1966a: 441, fig. 3.

*Diagnosis*. Stem unfascicled, reaching 58 mm in height, giving rise to alternate branches which may rebranch in a similar manner. Perisarc closely annulated throughout except for a smooth area on the origin of each branch, terminating as a gelatinous layer over the base of each hydranth.

Hydranths borne on summits of stem and branches, 1–2 mm in length, with an aboral whorl of 10–21 capitate tentacles and an oral whorl of 4–7
Fig. 19.

*Bicorona elegans*. A, stems; B, mature hydranth bearing gonophores; C and D, young hydranths; E, nematocysts: large and small stenoteles.


Scale: A in cm, E in mm/100, the rest in mm/10.
shorter capitate tentacles. Aboral tentacles held alternately elevated and depressed in life, oral tentacles held erect. Aboral tentacles of young hydranth in three alternating verticils.

Gonophores borne on about seven short blastostyles arising immediately above aboral tentacles, 2–4 on each, oval to spherical, in the form of fixed sporosacs, male and female on separate colonies. Female gonophore reaching 0,4 mm in diameter, containing 29–84 small eggs. Male gonophore reaching 0,6 mm in diameter.

Nematocysts: stenoteles, \(13,5 \times 7,2 - 26,1 \times 17,1 \mu\). Capsule oval.

Colour: colony a rich plum-colour, shading to dark-red on the stems and rose-pink on the hydranth tentacles.

**Distribution.** Endemic to South Africa.

**Distribution in South Africa.** Saldanha Bay, west coast of Cape Peninsula, East London, littoral. Type locality: Saldanha Bay. 33/18 (1), 34/18 (1), 33/27 (1)

**Genus Coryne** Gaertner, 1774

*Syncoryne* Ehrenberg, 1834.

**Diagnosis.** Hydranth with capitate tentacles scattered, or in rough whorls, over whole of body, and sometimes with a whorl of short filiform tentacles below them. Gonophores in the form of fixed sporosacs borne on the hydranth.

Type species: *Coryne pusilla* Gaertner, 1774.

One species only from South Africa.

**Coryne pusilla** Gaertner, 1774

Fig. 19F–G

*Coryne pusilla* Gaertner, 1774: 40, pl. 4 (fig. 8). Hincks, 1868: 39, pl. 7 (fig. 1). Warren, 1908: 289, fig. 4. Brinckmann-Voss, 1970: 51, fig. 57. ?Millard & Bouillon, 1974: 13, fig. 1B, C.

**Diagnosis.** Stem unfascicled, reaching about 13 mm in height, branching irregularly. Perisarc strongly annulated at least in distal part, annulations often becoming irregular and indistinct in lower part, terminating on base of hydranth but not expanded.

Hydranth spindle-shaped, about 1,3 mm in length, with 20–30 scattered capitate tentacles.

Gonophores borne on hydranth amongst the tentacles, in the form of fixed sporosacs.

Nematocysts: stenoteles, \(8,4 \times 4,8 - 16,7 \times 11,2 \mu\).

**Variation.** A dwarf form of *Coryne* also occurs, which reaches about half the size. The hydranth has 10–19 tentacles and is 0,4–0,8 mm in length. Since
gonophores have not been recorded for this form it is not certain that it is the same species. Such records are indicated with a query below.

The dwarf form may produce 'regeneration bodies', which are budded off from the tips of branches. In appearance they resemble planula larvae; they represent a form of asexual reproduction.

**Distribution outside South Africa.** Common in the North Atlantic from the Arctic to the Mediterranean. Scattered records, some of them doubtful, from the Indian Ocean (Madagascar and Kerguelen) and the Pacific (Japan).

**Distribution in South Africa.** Natal and ?Inhaca, littoral. 30/30 (1), 26/32 (1)

*Genus Sarsia* Lesson, 1843


**Diagnosis.** Hydranth with capitate tentacles scattered, or in rough whorls, over whole of body, and sometimes with a whorl of short filiform tentacles below them. Gonophores borne on body of hydranth, developing into medusae. Medusa with gonad forming a continuous ring around stomach.

Type species: *Oceania tubulosa* M. Sars, 1835.

One species only from South Africa.

*Sarsia eximia* (Allman, 1859)

*Fig. 20A–D*

*Coryne eximia* Allman, 1859: 141.

*Syncoryne eximia:* Allman, 1872: 282, pl. 5. Hincks, 1868: 50, pl. 9 (fig. 2).


**Diagnosis.** Stem erect, reaching a height of 53 mm, unfascicled, branching profusely and irregularly, though final branches with a tendency to unilateral arrangement. Perisarc mainly smooth but annulated on base of stem, on origin of branches and sometimes for entire length on smallest branches; terminating as a very delicate layer below the first tentacles of the hydranth.

Hydranth tubular, reaching 1.7 mm in height, with 15–26 scattered capitate tentacles, four or five of which form a verticil round the mouth; bearing medusa-buds amongst the tentacles.

Medusa at liberation reaching 1 mm in height and diameter, with thin jelly, four moniliform marginal tentacles, four black ocelli on the marginal bulbs and scattered nematocysts on the bell. Mature medusa (not recorded from South Africa) reaching 3–4 mm in height and 2 mm in diameter, with four per-radial marginal tentacles and four ocelli. Hypostome not extending beyond margin of bell, female with a few large eggs.

Nematocysts of hydranth: stenoteles of variable size, 5.4 × 4.0 – 17.1 ×
Sarsia eximia. A, hydranth with medusa-buds; B, colony; C, newly liberated medusa; D, nematocysts, from left to right a stenotele from the hydranth, an undischarged and discharged desmoneme from the medusa.
Sphaerocoryne bedoti. E, hydranth with medusa-buds, redrawn from Warren (1908, as Clavatella multitentaculata).
Asyncoryne ryniensis. F, hydranth with medusa-buds, redrawn from Warren (1908).
Scale: B in mm, D in μm, the rest in mm/10.
12.6 μ. Butt length approximately equal to capsule length and bearing three large spines and three spiral rows of small spines on its distal half.

Nematocysts of medusa of two types:
(i) Stenoteles, $8.1 \times 5.4 - 10.4 \times 8.1$ μ. Structure as in hydranth.
(ii) Desmonemes, $6.3 \times 3.2 - 9.0 \times 4.5$ μ.

**Observations on living material.** This species releases abundant medusae during the summer months of December to February and even as late as April; these live well in the laboratory during their early stages, but have not been reared to maturity in this country. Nor have fully mature medusae been reported from the plankton. Newly hatched medusae have alternate swimming and resting phases. They swim with rhythmical contractions of the bell and velum, holding the tentacles in a contracted state. During resting the bell relaxes and the tentacles extend to about double the height of the bell, trailing in the water in the 'fishing' position. The tentacles bear about 20 nematocyst batteries, of which the terminal one is the largest. The largest size reached in the laboratory is $2.8 \times 2.7$ mm, with no gonads visible.

Colour: hydranth orange-pink, medusa transparent with reddish-brown marginal bulbs and hypostome.

**Distribution outside South Africa.** North Atlantic from America to Europe and from Iceland to France, Mediterranean, west coast of North America, New Zealand. Medusae also from Brazil, Valparaiso and the N.W. Pacific. Type locality: Great Britain.

**Distribution in South Africa.** Common in the environs of Cape Town, on ships' hulls, pylons and floating objects, and also on rocky shores. Certainly present from Lüderitz Bay in South West Africa to Llandudno on the west coast of the Cape Peninsula, with doubtful (infertile) records from False Bay, the south coast and Inhaca in Moçambique. 26/15 (1), 33/18 (1, h), 34/18 (1), ?34/22 (1), ?34/23 (1), ?26/32 (1)

Genus *Sphaerocoryne* Pictet, 1893

**Diagnosis.** Hydranth with capitate tentacles in one whorl or two closely alternating whorls round lower part of body. No filiform tentacles. Gonophores borne on body of hydranth, developing into medusae. Adult medusa unknown.

Type species: *Sphaerocoryne bedoti* Pictet, 1893.

One species only in South Africa.

*Sphaerocoryne bedoti* Pictet, 1893

Fig. 20E


*Clavatella multitentaculata* Warren 1908: 278, pl. 45 (figs 7–9).

**Diagnosis.** Hydrorhiza embedded in sponge, ramifying, giving rise to solitary hydranths on long stems with a maximum total height of 13 mm. Pedicel with smooth perisarc terminating just above a groove below hydranth, increasing in diameter from base to distal end.

Hydranth pear-shaped, reaching a maximum height of 0.8 mm, with 15–35 solid capitate tentacles arranged in two closely alternating whorls on lower part of body. No oral tentacles. Hypostome conical.

Gonophores borne in clusters on hydranth body immediately above tentacles, in the form of medusa-buds.

Medusa (not recorded from South Africa) on liberation nearly spherical, 0.5–0.6 mm in diameter, with four marginal bulbs. On maturity with four marginal tentacles bearing spirally arranged clusters of nematocysts and four abaxial ocelli; male nearly ovoid, reaching 3.5 mm in height and 3.0 mm in diameter; female deeper, reaching 4.5 mm in height and 3.0 mm in diameter. (From Yamada & Konno.)

Colour: chalky white round mouth, below this a band of lemon-yellow and below this an irregular band of bright red just above the tentacles. (From Warren.)

Nematocysts: stenoteles and desmonemes in polyp; stenoteles, desmonemes and basitrichous haplonemes in medusa.

*Distribution outside South Africa.* India (type locality), Queensland, Madagascar, Japan.

*Distribution in South Africa.* Natal and Moçambique, intertidal. Rare. 30/30 (1), 21/35

**Family Cladonemidae**

*Diagnosis.* Hydranths colonial, arising directly from a creeping stolon, with or without perisarc, with an oral whorl of capitate tentacles, with or without an aboral whorl of short filiform tentacles. Gonophores borne on hydranth body, producing free medusae. Medusa with simple, tubular mouth which may be armed with nematocyst clusters; with a variable number of radial canals, simple or branched. Marginal tentacles hollow, branched, one branch with one or more adhesive discs. Ocelli present.

*Introduction.* This family includes the three genera *Cladonema*, *Eleutheria* and *Staurocladia*. Most modern authors divide these genera between the two families Cladonemidae (*Cladonema*) and Eleutheriidae (*Eleutheria* and *Staurocladia*), but I have followed Naumov (1960) and Prévet (1959) in maintaining that both hydranth and medusa generations have too many characters in common to merit distinction at the familial level.

The hydranth is very simple and resembles some of the more primitive Corynidae. The perisarc is poorly developed, if present, and the hydranth has
an oral whorl of a few capitate tentacles and sometimes an aboral whorl of short filiform tentacles as well.

The medusa generation, on the other hand, is highly evolved and specialized. It has received more attention than usual in this monograph because the single South African species (of Staurocladia) has a creeping habit and is commonly encountered on weed in rock-pools and shallow bays. *Eleutheria* also has a creeping medusa, but in *Cladonema* the medusa normally swims and only comes to rest as a temporary measure.

Creeping is made possible by the presence of adhesive discs on the marginal tentacles. The marginal tentacles, which are usually numerous, branch, several times in *Cladonema*, only once in *Eleutheria* and *Staurocladia*. The oral branch bears the adhesive discs and the aboral branch bears one or more clusters of nematocysts resembling the capitula of capitate tentacles.

The mouth of the medusa is armed with nematocyst clusters resembling capitate tentacles in *Cladonema*. This armature is normally absent in *Eleutheria* and *Staurocladia*, but Ralph (1947) has found vestigial clusters in *Staurocladia vallentini* in New Zealand. *Eleutheria* and *Staurocladia* possess a thickened ring of nematocysts round the umbrella margin.

Asexual reproduction by the production of buds or vertical fission of the medusa has been reported in several species.

The medusae may be dioecious or hermaphrodite. In *Eleutheria* the fertilized eggs are retained in a brood-pouch, situated above the stomach, to the planula stage.

KEY TO GENERA

[Genera not represented in South Africa are bracketed]

1. Marginal tentacles of medusa with several branches ... ... ... [**Cladonema**]  
   - Marginal tentacles of medusa bifurcating ... ... ... ... ... ... ... ... ... ... 2

2. Hydranth with capitate tentacles only. Medusa with aboral branch of tentacle bearing one nematocyst cluster only ... ... ... ... ... ... ... ... ... ... [**Eleutheria**]  
   - Hydranth with capitate and filiform tentacles. Medusa with aboral branch of tentacle bearing more than one nematocyst cluster ... ... ... ... ... ... ... ... **Staurocladia** p. 56

Genus **Staurocladia** Hartlaub, 1917


*Diagnosis.* Hydranth with both filiform and capitate tentacles. Medusa of creeping habit, without nematocyst armature on mouth, with thick ring of nematocysts around margin, without brood-pouch; gonads well developed, either in ectodermal pockets or completely surrounding stomach; sexes separate; with six or more radial canals; with numerous bifurcated marginal tentacles, the oral branch with a terminal adhesive disc, the aboral branch with several clusters of nematocysts.

Type species: *Eleutheria vallentini* Browne, 1902.

One species only from South Africa.
**Staurocladia vallentini** (Browne, 1902)

Fig. 23D–G

*Eleutheria vallentini* Browne, 1902: 279.

*Cnidonema capensis* Gilchrist, 1919: 509, pl. 30.


*Cnidonema vallentini*: Ralph, 1947: 414, fig. 1, pl. 35.

**Diagnosis.** Hydranth borne on a slender hydrocaulus arising direct from a creeping hydrophyza, minute, reaching 1.5 mm in length, slender at base and increasing in diameter distally, with 3–4 capitate oral tentacles and 4–6 filiform aboral tentacles. Hydrocaulus reaching 2 mm in length, covered with thin perisarc. Medusa-buds borne at or slightly above level of aboral tentacles, with about six bifurcated tentacles at liberation, the aboral branch with one nematocyst cluster.

Mature medusa about twice as wide as deep, reaching 3.3 mm in diameter. Marginal tentacles increasing in number with age and reaching about 40 in large individuals, oral branch bearing a single terminal adhesive disc, aboral branch bearing median, crescent-shaped clusters of nematocysts: one terminal, 2–4 abaxial and sometimes one adaxial. Radial canals six, unbranched. Stomach with six pouches. Gonads above and around stomach, in six ectodermal pockets. Asexual reproduction common in young medusae.

Nematocysts of two types:

(i) Desmonemes, 9.6 × 4.2 μ.
(ii) Stenoteles, 10.8 × 6.6 – 18.6 × 12.6 μ.

**Colour:** Hydranth transparent with reddish endoderm. Medusa mostly transparent, with reddish-brown circular canal and stomach, dark brown to black ocelli, and opaque, white radiating lines on upper surface.

**Variation and remarks.** The arrangement of the nematocyst clusters on the aboral branch of the medusa tentacle is variable. They are, however, always median in position, and there is always one terminal one. In most populations all the remaining clusters are abaxial, but I have seen one population in which they are alternately abaxial and adaxial as described by Gilchrist. Occasionally there is a cluster on the abaxial side of the tentacle before the bifurcation.

When the medusa is at rest the adhesive discs are attached to the substratum and the aboral branches of the tentacles elevated. Creeping is accomplished by releasing and re-attaching the discs.

**Distribution outside South Africa.** Falkland Islands (type locality). Australasia. ?Bermuda.

**Distribution in South Africa.** Lüderitz Bay to False Bay. Medusa locally common on weed at certain seasons, hydanth recorded only once. Hydanth: 34/18 (1). Medusa: 26/15 (1), 33/18 (1), 34/18 (1).
Family Solanderiidae

Diagnosis. Upright, branching colonies with an internal skeleton of chitinous trabeculae which may protrude through the surface as spines or hydrophores. Hydranths all alike, cylindrical, with scattered capitate tentacles, of which four or five usually form a whorl around the mouth. Gonophores, where known, in the form of fixed sporosacs borne directly on coenosarc.

Introduction. The Solanderiidae is one of the few groups of hydroids to possess an internal skeleton. This skeleton consists of an anastomosing meshwork of chitinous trabeculae which rises from an incrusting base to form an erect and elaborately branching stem. The entire colony is covered externally, and permeated internally, by living coenosarc, which bears the hydranths and gonophores on the surface. Though the skeleton is morphologically internal, it is not 'mesogloea', and has been shown by Vervoort (1966a) to be ectodermal in origin and everywhere covered or lined by cellular ectoderm. The condition is comparable with that in some Hydractiniidae (Hydractinia) and Zancleidae (Rosalinda and Teissieria).

The hydranths are borne over the whole surface of the stem and branches and are usually supported by bracket-like hydrophores arising from the trabeculae of the skeleton and projecting through the superficial coenosarc. These hydrophores may be scoop-shaped, bilobed, or double and with two lateral triangular shields. Spiny or spatulate projections, the latter resembling abortive hydrophores, may also occur in some species.

The highly extensile hydranths are very homogeneous and there is no approach to polymorphism. The shortly stalked capitate tentacles are arranged irregularly over the body, although a group of four or five usually forms a whorl around the mouth.

The gonophores, where known, are borne directly on the coenosarc. They are stalked eumedusoids without marginal tentacles, but sometimes with radial canals. No free-swimming life has been observed. Colonies are dioecious, though no differences in structure between male and female colonies have been seen.

One genus only.

Genus Solanderia Duchassaing & Michelin, 1846

Syn. Ceratella Gray, 1868.
Dehitella Gray, 1868.
Dendrocoryne Inaba, 1892.
Spongiocladium Jäderholm, 1896.

Diagnosis. Colony erect and strongly branched, generally fan-shaped and with the ramifications more or less in one plane, arising from a flattened base of hydorhizal fibres. Skeleton usually forming bracket-like hydrophores which support the hydranths. Gonophores borne direct on the coenosarc.

Type species: Solanderia gracilis Duchassaing & Michelin, 1846.
KEY TO SPECIES
(Doubtful species not included. For these see p. 61)

1. Hydrophores scoop-shaped, rarely bilobed or double. Hydranth with about 15 tentacles
   — Hydrophore always double, one half on each side of hydranth. Hydranth with up to
   33 tentacleless
   → Solanderia minima (Hickson, 1903)

Solanderia minima (Hickson, 1903)
Fig. 21C–E

Ceratella minima Hickson, 1903: 113, pl. 13.
Solanderia minima: Vervoort, 1967: 25, fig. 2, pl. 3 (figs 3–4). Millard & Bouillon, 1973: 16,
fig. 2A–B, pl. 1.

Diagnosis. Colony fan-shaped, reaching 70 mm in height and 70 mm in spread, branching in one plane. Main stem thick; round or irregular in section. Hydranths and hydrophores borne irregularly on stem and branches, though restricted to two opposite sides in certain areas. Small spines sometimes present in older regions.

Hydrophore double, consisting of a pair of shields, one on each side of hydranth. Shield broadly triangular with smoothly rounded apex, sometimes very poorly developed and inconspicuous, usually not supported by ribs from the trabeculae, seldom more than 0.1 mm in height. Hydranth with up to 29 tentacles.

Gonophores (not reported from South Africa) scattered, arising directly from coenosarc, oval, shortly stalked, reaching 0.4 × 0.3 mm.

Colour: larger stems dark purple, smaller branches mauve, hydranths white. Dark brown to creamy white after preservation.

Nematocysts: stenoteles of varying size, 6.3 × 4.5 – 12.6 × 10.8 μ, and possibly other types too.

Variation. This species is more delicate in appearance than S. procumbens and the branches more closely set and spreading, giving a reticulate appearance. The origin of the branches is irregular, though there is a tendency for an alternate arrangement in the younger parts.

The hydrophores vary in degree of development, and though they are always double they may be large and triangular or mere elevations of the trabeculae. They are always smaller than those of S. procumbens.

Distribution outside South Africa. Tropical East Africa and the Seychelles. Type locality: Wasin, East Africa.

Distribution in South Africa. Santa Carolina, Moçambique, only. 21/35

Solanderia procumbens (Carter, 1873)
Fig. 22

Ceratella procumbens Carter, 1873: 10.
Ceratella spinosa Carter, 1873: 12.
Solanderia procumbens: Millard, 1966a: 444, fig. 4, pl. 1.
**Cladocoryne floccosa.** A, hydranth bearing male gonophores; B, macrobasic eurytele, discharged and undischarged.

**Solantheria minima.** C, stem; D, part of stem with hydranths; E, hydrophores.

Scale: C in cm, B in mm/100, the rest in mm/10.
Diagnosis. Colony large, fan-shaped, reaching 400 mm in height and 380 mm in spread, branching in one plane. Main stem of old colonies very thick and flattened in plane of branching. Smaller branches and main stem of young colonies round in section. Hydranths and hydrophores borne irregularly on stem and branches. Spines present in older regions only.

Hydrophore normally scoop-shaped, up to 0.5 mm in height, supported on lower surface by longitudinal ribs continuous with trabeculae of branch. Ribs not normally reaching margin. Hydranth with about 15 tentacles.

Gonophores scattered, arising directly from coenosarc, spherical, shortly stalked, containing four radial canals in male.

Colour: dark brown on stem and larger branches with occasional tinges of purple, shading to yellowish-brown or ochre on smaller branches (preserved or dry material).

Nematocysts: large stenoteles 15.3 × 11.7 – 24.3 × 18.0 μ and several other types of unknown category.

Variation. This species is very variable in its general appearance and growth-form. The branching may be dichotomous, alternate or unilateral, and a strong development of the last arrangement may give a procumbent appearance to the colony (possibly due to wave-action or currents). The branches may be thick and stumpy with rounded tips, or slender with pointed tips, possibly due to a difference in growth-rate. In older parts of the stem the trabeculae have a reticulate appearance, but in younger parts the longitudinal ones predominant. They may be surmounted by prominent chitinous crests. Spines are only found in older parts of the colony, and may be pointed or spatulate, but tend to be eroded away.

The hydrophores are particularly variable, and bilobed and double varieties are common. In old colonies the edges may become eroded between the supporting ribs producing a serrated appearance.

A form occurs with more slender branches and lighter coloration than the normal one, and with hydrophores predominantly of the double type.

Distribution. Endemic to South Africa. Type locality: Natal.

Distribution in South Africa. West coast of Cape Peninsula to Natal in 12–130 m. 33/18 (s), 34/18 (s), 34/21 (s), 34/22 (s), 33/25, 34/25 (s), 29/31 (d), 29/32 (s)

Doubtful species

Solandra atrorubens (Gray, 1868)


Remarks. This species is said to differ from other species of Solandra by the more bushy nature of the colony. The type locality is in doubt, as also is its occurrence in South African seas. Gray gave the type locality as Australia with a query. Brazier reported it from Algoa Bay, but gave no description. Spencer, quoting Gray's descrip-
Fig. 22.

*Solanderia procumbens.* A, stem of normal form (left) and slender form (right); B, l.s. young gonophore; C, stenotele; D, part of stem with hydranths and gonophores; E, hydrophores and spines.

Scale: A in cm, C in mm/100, the rest in mm/10.
tion, gave the locality as Delagoa Bay, Africa, which is probably a mistake. Marshall's material from Port Natal, which was illustrated, was assigned to *S. procumbens* by Millard (1966a).

*Solanderia labyrinthica* (Hyatt, 1877)

*Ceratella labyrinthica* Hyatt, 1877: 551, pl. 17 (fig. 30).


**Remarks.** This species is too inadequately described for there to be any certainty about its identification. Hyatt mentions one specimen from Mauritius and another from the Cape of Good Hope.

*Solanderia rugosa* Marshall, 1892


**Remarks.** This species was founded on material from Port Natal. The description, which was not illustrated, is too vague for definite recognition.

**Family Asyncorynidae**

**Diagnosis.** Colonial hydroids with polystomal or erect habit. Perisarc present on hydrorhiza and hydrocaulus, not covering hydranth. Hydranth with conical hypostome, one whorl of capitiate oral tentacles, and scattered moniliform aboral tentacles. Gonophores borne on hydranth amongst the aboral tentacles, forming free medusae. Medusa with marginal tentacles bearing cnidophores.

**Introduction.** This family was originally created for the stolonial species *Asyncoryne ryniensis* from South Africa, in which the arrangement of tentacles differs from that in any other form. Picard (1957) assigned to the same genus *Zancloidea philippina* Hargitt, 1924, which has a similar arrangement of tentacles on the hydranth, but an erect and branching stem with better developed perisarc.

These two species have medusoid gonophores in which the marginal tentacles bear stalked cnidophores similar to those of the Zancleidae, but the adult medusa is still unknown.

Picard included *Asyncoryne* and *Pteronema* Haeckel, 1879 in the family Pteronematididae, but *Pteronema*, the type genus, is known only from a somewhat problematical medusa.

One genus only.

**Genus Asyncoryne** Warren, 1908

**Diagnosis.** As for family.

Types species: *Asyncoryne ryniensis* Warren, 1908.

One species only from South Africa.

*Asyncoryne ryniensis* Warren, 1908

Fig. 20F


**Diagnosis.** Hydranth reaching 3 mm or more in height, spindle-shaped, with
4–6 short, capitate oral tentacles and about 25 scattered moniliform aboral tentacles. Perisarc present on hydrorhiza and continued over the short hydrocaulus for 0.6–0.9 mm, not annulated.

Medusa-buds borne in clusters on hydranth body between the moniliform tentacles. Medusa at release with marginal tentacles bearing cnidophores. Adult medusa unknown.

Nematocysts of three types (from Bouillon):

(i) Stenoteles. Capsule subspherical, large or small. Present in oral and aboral tentacles of hydranth and in medusa.

(ii) Macrobasic euryteles. Present in stolon and aboral tentacles of hydranth and in medusa.

(iii) Microbasic euryteles. Present, but rare, in medusa.

Warren mentions large nematocysts of 27.0 × 19.5 µ, which are probably the large stenoteles, and small ones 10.0 × 8.0 µ, which are probably the small stenoteles.

Distribution outside South Africa. Seychelles.

Distribution in South Africa. Type locality and only record: Park Rynie, Natal, littoral. 30/30 (1)

Family Cladocorynidae

Diagnosis. Hydranths borne on long, perisarc-covered stems arising from a creeping hydrorhiza; with a conical hypostome, one whorl of capitate oral tentacles, and one or more whorls of branched, capitate aboral tentacles. Gonophores borne on hydranth body amongst the aboral tentacles.

Introduction. The Cladocorynidae are distinguished from all other athecate families by the nature of the aboral tentacles. For nearly a hundred years Cladocoryne was the only genus, but in 1963 Mammen added two more: Lobocoryne and Cladocorynopsis.

The hydranth is comparatively large and conspicuous. There is one whorl of a few capitate oral tentacles. The aboral tentacles are rather fleshy and bear several rows of capitula, a condition known as ‘branched’ or ‘coryniform’ in the literature. The capitula are sessile in Lobocoryne, but stalked in Cladocoryne and Cladocorynopsis.

The hydrocaulus is generally long, unbranched and covered with perisarc to immediately below the hydranth.

Reproduction is by fixed sporosacs (Cladocoryne) or medusae (Cladocorynopsis), but the nature of the adult medusa is unknown.

The Cladocorynidae are closely related to the Asyncorynidae, from which they may have arisen by the concentration of the nematocyst batteries of the aboral tentacles on to capitula (Vervoort 1966a).
KEY TO GENERA
[Genera not represented in South Africa are bracketed]

1. Capitula of aboral tentacles sessile. Aboral tentacles in three whors [Lobocoryne]
   - Capitula of aboral tentacles stalked .. .. .. .. .. .. .. .. 2

2. Aboral tentacles in one whorl .. .. .. .. .. .. [Cladocorynopsis]
   - Aboral tentacles in several whors .. .. .. .. .. .. Cladocoryne p. 65

Genus Cladocoryne Röth, 1871

Diagnosis. Oral tentacles of hydranth stalked. Aboral tentacles in several whors, bearing stalked capitula in three longitudinal rows. Tentacles solid, septate.

Gonophores borne amongst the aboral tentacles of hydranth which may be reduced to a blastostyle, in the form of fixed sporosacs.

Type species: Cladocoryne floccosa Röth, 1871.

One species only.

Cladocoryne floccosa Röth, 1871

Fig. 21A–B


Diagnosis. Stem unbranched, or rarely with one lateral branch, reaching a maximum height of 12 mm; perisarc smooth or irregularly corrugated or annulated near base, becoming thinner distally to terminate below hydranth.

Hydranth cylindrical, large, 0.5–0.9 mm in height, with a single whorl of 4–7 stalked and capitate oral tentacles, and up to 18 branched aboral tentacles in 3–4 alternating verticils. Capitula of aboral tentacles up to 17 in number, stalked, arranged in three longitudinal rows, two rows of 4–7 on latero-aboral edges and one of 1–3 mid-oral.

Gonophores borne on hydranth among the aboral tentacles on short pedicels, spherical, reaching 0.34 mm in diameter, forming fixed sporosacs of the cryptomedusoid type.

Colour: hydranth red with chalky white area around mouth, perisarc horn-coloured:

Nematocysts of three types:

(i) Macrobasic euryteles. On hydranth body and on gonophores. Capsule bean-shaped, 28.8 × 11.7 – 31.2 × 15.0 μ. Thread in three sections, the first unarmed and about 200 μ long; the second increasing gradually in width and armed with spiral bands of fine spines, about 90 μ long; the third unarmed and narrow.

(ii) Large stenoteles. Fairly common in capitula of tentacles. Capsule ovoid, 12.6 × 10.8 – 14.4 × 12.0 μ.

(iii) Small stenoteles. Abundant in capitula of tentacles and also present on hydranth body. Capsule ovoid 6.0 × 5.0 – 6.7 × 5.7 μ. Not seen discharged.

Variation. In the South African material the fertile hydranths are normal with
well-developed tentacles, but Behner has shown that in European material gonophore-bearing hydranths may be reduced to blastostyles with the gradual reduction and loss of the tentacles.

**Distribution.** Circumglobal in tropical and subtropical waters, occasionally extending into temperate areas. Type locality: Herm, Channel Islands.

**Distribution in South Africa.** Natal and Moçambique, in rock-pools. 30/30 (1), 27/32 (1), 26/32 (1), 25/32

**Family Zancleidae**

**Diagnosis.** Colonial hydroids with a stolonal habit. Hydrorhiza either reticular or incrusting. Skeleton variously developed; either external and forming a feeble sheath around base of polyp, or consisting of trabeculae contained within the incrusting coenosarc and projecting through the surface as spines. Hydranths either all alike or polymorphic; tentacles scattered, usually capitate (always in South African genera), rarely filiform. Gonophores borne on hydranth body, developing into free medusae.

Medusa with, or without, exumbrellar nematocysts confined to specialized tissue in form of oval or club-shaped patches or elongated tracks; with simple circular mouth; with four radial canals; with interradial gonads; with two or four solid marginal tentacles, each with abaxial stalked capsules (cnidophores) containing nematocysts, or without marginal tentacles; with or without ocelli (Russell 1953; Bouillon 1974).

**Introduction.** This family is distinguished mainly by the very characteristic medusa, whereas the polyp generation has few characters in common. Bouillon (1974) recognizes four polyp genera: *Zanclea* Gegenbaur, 1856; *Rosalinda* Totton, 1949; *Pteroclava* Weill, 1931 and his own new genus *Teissiera*. Most of the other medusa genera ascribed to the family by Kramp (1961) have either been transferred to other families or are of doubtful affinity.

The polyp is typically cylindrical and unbranched, with scattered capitately tentacles and a conical hypostome, bearing medusa-buds in the lower region. *Pteroclava* alone has filiform tentacles. In *Rosalinda* and *Pteroclava* all the hydranths are alike, but in *Zanclea costata* fertile hydranths may be devoid of tentacles at certain stages of colony development (Russell & Rees 1936). There is thus an approach to polymorphism with the differentiation of gonozooids or blastostyles. In *Teissiera* polymorphism is firmly established, but has evolved differently, with the differentiation of separate non-feeding dactylozooids similar to those of *Millepora*, and the retention of unmodified polyps for the dual function of feeding and reproduction.

In *Zanclea* and *Pteroclava* the hydrorhiza may be covered with a perisarcal sheath, which may extend over the hydrocaulus to the base of the hydranth. This perisarc may be firm, or soft and membranous, and it may be absent in young colonies. In *Teissiera* and *Rosalinda* the hydrorhiza forms an incrusting
Zanclea sp. A, hydranth of Form 2; B, hydranth of Form 1; C, stenotele.
Staurocladia vallentini. D, hydranth with medusa-bud, redrawn from Gilchrist (1919, as Cnidonema capensis); E, young medusae, the upper one is about to divide and has three hypostomes, the lower three have recently divided; F, a single tentacle from medusa; G, nematocysts of medusa, from left to right an undischarged and a discharged desmoneme, stenotele.

Scale: C and G in mm/100, the rest in mm/10.
basal coenosarc similar to that of *Hydractinia*, and within this coenosarc is a trabecular skeleton of a chitin-like material. From it arise spines of various sizes and shapes. This skeleton, although ‘internal’ and covered by cellular material (except on the tips of the spines), is ectodermal in origin.

The most obvious character of the medusa is the presence of stalked capsules, or *cniDophores*, containing batteries of nematocysts, on the marginal tentacles. Other features include the restriction of exumbrellar nematocysts to areas of special tissue, the tendency to lose the ocelli and the splitting of the gonad into four interradial groups.

**KEY TO GENERA**

[Genera not represented in South Africa are bracketed]

1. Skeleton either absent or consisting of a perisarcal sheath round basal part of polyp.  
   Hydrorhiza not incrusting  
   – Skeleton consisting of trabeculae contained within an incrusting hydorhiza and giving off spines  
   2

2. Tentacles capitate  
   – Tentacles filiform  
   3

3. Colony polymorphic, with dactylozooids and gastro/gonozoooids  
   – Colony not polymorphic, hydranthals all alike  
   2

**Genus Zanchea** Gegenbaur, 1856

*Syn. Gemmaria* McCrady, 1858.  
*Halocharis* L. Agassiz, 1862.

**Diagnosis.** Hydrorhiza reticular, not incrusting. Skeleton external and consisting of a feebly developed perisarcal sheath enveloping the hydrorhiza and sometimes extending on to the base of the hydrocaulus. Hydranth with scattered capitate tentacles, 3–6 forming a whorl around the mouth.

Medusa with exumbrellar nematocysts; without brood-pouch above stomach; without oral tentacles; with four simple radial canals; with two or four marginal tentacles carrying cnidophores.

Type species: *Zanchea costata* Gegenbaur, 1856.

One or two species from South Africa.

**Zanchea** sp.

Fig. 23A–C

*Zanchea* sp. Millard & Bouillon, 1974: 14, fig. 1F–L.

**Diagnosis**

Form 1. Colony commensal with coral. Hydrorhiza ramifying on coral skeleton, giving rise to erect, unbranched hydrocauli which penetrate the soft body of the coral and emerge through pores at the surface. Hydrorhiza and hydrocaulus with firm perisarc, which becomes membranous at point of emergence.

Hydranth (plus hydrocaulus) reaching 1.1 mm in height, with 18–28
stalked capitate tentacles, of which six form an oral whorl and the rest are irregularly scattered.

Nematocysts of two types:

(i) Stenoteles, $6,0 \times 4,8 - 10,8 \times 9,0 \mu$, abundant on tentacles and hydranth body. Capsule almost spherical.

(ii) Small bean-shaped capsules, $13,8 \times 6,0 \mu$, on lower part of hydranth body.

Form 2. Colony commensal with polyzoan. Hydorhiza ramifying in body of host, giving rise to erect, unbranched hydrocauli. Hydorhiza and hydrocaulus with thin perisarc terminating at point of emergence or slightly above.

Hydanth (plus hydrocaulus) reaching 0,8 mm in height, with 11–24 capitate tentacles, of which 3–5 form an oral whorl and the rest are irregularly scattered. Tentacles mostly with very short stalks and some completely sessile, the oral whorl with larger capitula than the rest.

Medusa-buds borne on hydranth amongst or below the lowest tentacles, the largest 0,16 mm in diameter and with rudiments of marginal bulbs.

Nematocysts of two types:

(i) Stenoteles, $6,0 \times 4,8 - 11,4 \times 10,8 \mu$, abundant on tentacles and also present on hydranth body. Capsule almost spherical.

(ii) ?Macrobasic euryteles, $19,2 \times 10,8 - 22,8 \times 7,8 \mu$, present on hydranth body and hydrocaulus. Capsule bean-shaped.

Remarks. These colonies cannot be diagnosed with certainty until the medusae have been reared, nor is it certain whether one or two species are involved. Both are closely related to Zanclea costata Gegenbaur, 1856.

Distribution in South Africa. Inhaca only. 26/32 (s)

Family Clavidae

Diagnosis. Solitary or colonial, radially symmetrical polyps with conical hypostome, undifferentiated endoderm and scattered filiform tentacles. Perisarc present at least on hydorhiza, absent to well developed on rest of body. Reproduction by fixed sporosacs or free medusae.

Adult medusa, when present, with mouth with four lips with continuous row of nematocyst clusters along margin; with interradial gonads; with four simple radial canals; with numerous solid margin tentacles not in groups; with adradial ocelli (Kramp 1961).

Introduction. In the Clavidae the colonies are either stolonial or erect and branching. Erect stems may be fascicled or unfascicled. Methods of branching vary. An unusual method occurs in Corydendrium and Turritopsis, where there is a simple division of the stem into two, the perisarc of the two limbs remaining adnate for a short distance, then gradually diverging, so that the branches always arise at a very acute angle.

The hydranth is of simple construction, tubular or spindle-shaped, with filiform tentacles which are normally irregularly scattered over the body. Occasionally there is an indication of irregular whorling, but there are never
clear and definite whorls with regular arrangement. The hydranth may be sessile in some stolonical forms, but is usually pedicellate but there is then no clear demarcation between the hydranth body and the coenosarc of the pedicel (hydrocaulus).

Perisarc is present at least as a thin membrane clothing the hydorhiza. On the rest of the body the development is variable. The body may be completely naked as in Clava, or the hydrocaulus may be covered with perisarc up to the base of the hydranth, as in Tubiclava. In Merona the hydranth emerges from a firm tube of perisarc into which it can be withdrawn on contraction.

Nematophores occur in Merona, where they arise separately from the hydorhiza and are enclosed in nematothecae.

In the majority of genera reproduction is by means of fixed sporo-sacs, in which indications of medusoid structures, such as radial canals or subumbrella cavity, may sometimes be seen. The sporosacs may be borne direct on the hydorhiza, on the hydrocaulus, or on the hydranth. In Corydendrium the sporosacs are retained within the perisarc of the hydrocaulus and never become visible externally.

Occasionally the hydranth bearing the sporosacs shows signs of reduction to a blastostyle and in Merona this differentiation is fully achieved, for the sporosacs are borne on separate individuals without mouth or tentacles. Such polymorphism is, however, rare in the family.

Among the South African representatives only Turritopsis produces free medusae; but there are probably other medusa genera whose hydranth stage has not yet been discovered.

Most authorities (e.g. Naumov, Thiel) consider that the family Clavidae, with the scattered hydranth tentacles, is a primitive family and has led to several more advanced ones by the concentration of the tentacles into one whorl. This may have occurred along three separate lines:

(i) From stolonal colonies to the Hydactiniidae, with the development of polymorphism. Here it might be noted that in Merona (Clavidae) polymorphism has already been achieved, for there are gastrozoooids, gonozoooids and dacty-lozoooids. Among the Hydactiniidae, Clavactinia is a primitive member, in which the hydranth tentacles, although concentrated at the distal end, have not yet been reduced to one whorl.

(ii) From erect and at least slightly branched stems to the Bougainvilliidae. Thiel's family (1962), the Clavopselliidae, represents an intermediate stage, for the hydranth tentacles are concentrated into definite whorls, which in Clavopsella and Silhouetta are restricted to the distal end (but not in Balella). In this work these three genera are included in the Bougainvilliidae because of the medusa structure of Silhouetta. Balella's medusa has four marginal tentacles, but is otherwise imperfectly known. Clavopsella has sporosacs.

(iii) From erect and slightly branched stems to the Eudendriidae, with the development of a trumpet-shaped hypostome and the characteristic gonophores. In this case Myrionema (Eudendriidae) shows primitive characters in its elongated hydranth and several whorls of tentacles concentrated at the distal end.
It thus may be difficult to draw a dividing line between the four families Clavidae, Hydractiniidae, Bougainvilliiidae, and Eudendriidae, and in doubtful cases medusa structure should be the guide.

KEY TO GENERA
[Genera not represented in South Africa are bracketed]

1. Colony erect and freely branched .......................... 2
   Colony stolonal, polyps at most slightly branched. Gonophores in the form of fixed sporosacs ................. 4
   Colony stolonal (hydranth). Gonophores in the form of fixed sporosacs
   [Cordylophora]
   2. Branches adnate to stem. Gonophores in the form of fixed sporosacs
   3. Gonophores forming free medusae .......................... 3
   4. Gonophores in the form of fixed sporosacs contained in perisarc of stem

Genus Clava Gmelin, 1791

Diagnosis. Colony stolonal. Hydrorhiza giving rise directly to sessile hydranths which are naked except for a low perisarcal collar round base. Hydranth with scattered filiform tentacles. Gonophores in the form of fixed sporosacs, borne by the hydranth below the tentacles.

Type species: Hydra multicornis Forskål, 1755.

One species only from South Africa.

Clava sp.

Fig. 24A

Diagnosis. Hydrorhiza reticulate, clothed in thin perisarc which forms a low collar round the base of the hydranth. Hydranth unbranched, with 21–30 scattered filiform tentacles, reaching a maximum height of 7 mm.

Gonophores unknown.

Nematocysts of two types:
(i) Microbasic euryteles, 0,67 × 0,22 − 0,72 × 0,22 μ.
(ii) Desmonemes, 0,45 × 0,32 μ.

Colour: creamy pink.

Remarks. This species still awaits the discovery of gonophores for final diagnosis.

Distribution in South Africa. Cape Peninsula: Melkbosstrand, Bakoven and Oudekraal, littoral. 33°18 (1)
Genus *Corydendrium* van Beneden, 1844

*Syn.* *Soleniopsis* Ritchie, 1907.

*Diagnosis.* Colony with erect and branching stem. Stem with firm perisarc, branches adnate to stem for some distance after origin. Hydranth with scattered filiform tentacles. Gonophores in the form of fixed sporosacs contained wholly within perisarc of stem.

Type species: *Sertularia parasitica* Linnaeus, 1767.

One species only from South Africa.

*Corydendrium parasiticum* (Linnaeus, 1767)

*Fig. 24B–D*

*Sertularia parasitica* Linnaeus, 1767: 1315.
*Soleniopsis dendriformis* Ritchie, 1907a: 495, figs 142–143, pl. 26 (fig. 1).

*Diagnosis.* Stem thick, fascicled and branching, reaching 72 mm; perisarc stiff, not annulated, terminating abruptly below tentacles of hydranth. Branching by simple division of the coenosarc and surrounding perisarc into two, the two tubes running parallel and adnate to one another for a short distance, then diverging at an acute angle and free from one another to a varying degree. Branches commonly, but not always, in one plane. Hydranths emerging from the open ends of the tubes, which are 0.3–0.6 mm in diameter.

Hydranth elongated, 1–2 mm in length when extended, with 22–44 scattered filiform tentacles, the distal four or five arranged in a whorl. Hypostome prominent and club-shaped. Coenosarc swollen within terminal part of perisarc.

Gonophores (not recorded in South Africa) in the form of fixed sporosacs, wholly contained within perisarcal tube, arising from coenosarc and lying parallel to it, in the form of long, slender cylinders without spadix. Female containing about 13 eggs.

Nematocysts of two kinds:

(i) *Heteronemes*, 7.0 × 4.0 μ.

(ii) *Desmonemes*, 5.0 × 3.5 μ.

*Distribution outside South Africa.* Mediterranean, Cape Verde, Seychelles, East Indies, India, Indo-China, Japan.

*Distribution in South Africa.* Durban Bay and Inhaca. 29/31 (s, h), 26/32 (s)

Genus *Merona* Norman, 1865

*Diagnosis.* Colony stolonial and polymorphic. Gastrozoooid unbranched, with hydrocaulus enclosed in a firm perisarcal tube into which it can be withdrawn. Hydranth with scattered, filiform tentacles. Gonozoooid (blastostyle) borne on
Fig. 24.

Ciava sp. A, hydranths.
Corydendrium parasiticum. B, stem; C, part of stem with hydnanths; D, a single hydanth.
Rhizogeton nudum. E, hydanth and male gonophore.
Turritopsis nutricula. F, hydanth; G, stem with hydnanthsh and medusa-buds.

Scale: B in cm, A and C in mm, the rest in mm/10.
hydrorhiza, producing fixed sporosacs. Nematophores borne on hydrorhiza, enclosed in firm perisarcal tube.

Type species: *Tubiclava cornucopiae* Norman, 1864.

One species only from South Africa.

*Merona cornucopiae* (Norman, 1864)

Fig. 25

*Tubiclava cornucopiae* Norman, 1864: 82, pl. 9 (figs 4–5).

**Diagnosis.** Colony epizootic on the bivalve *Crassatella capensis* Lamy. Hydrorhiza reticulate, with tubes coalesced into mat in denser regions. Gastrozooids consisting of a perisarc-covered stem and a terminal hydranth. Perisarc forming a firm tube expanding distally and often curved, reaching 4.3 mm in height. Hydranth with 16–20 scattered filiform tentacles.

Blastostyle arising separately from hydrorhiza, surrounded by a low flaring collar of perisarc, without mouth or tentacles, bearing a cluster of gonophores, reaching a height of 1.4 mm. Gonophores in the form of fixed sporosacs, male and female on separate colonies.

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**Fig. 25.**

*Merona cornucopiae*. A, part of colony growing on bivalve showing gastrozooids, one gonozooid and nematophores; B, nematothecae.

Scale in mm/10.
Nematophores usually present, borne on hydrorhiza, 0.3–0.6 mm in height, completely enclosed in a slender perisarcal tube which expands distally into a funnel-shaped nematotheca.

Nematoctys of two kinds:

(i) Microbasic eurytels, 16,2 × 4,5 µ. Capsule elongated.
(ii) Desmonemes, 7,2 × 2,7 – 3,6 µ. Capsule ovoid.

Variation. Outside South Africa M. cornucopiae has been reported on a variety of different molluscs and on a gorgonian. The presence or absence of nematotheca in South African material is variable and one colony has been found with none at all. Since nematotheca have now been recorded in the type material (Cabiocch 1965), they can be included in the diagnosis.

Distribution outside South Africa. North Atlantic from the Shetland Islands (type locality) to the Mediterranean, Pacific and Atlantic coasts of North America, Seychelles.

Distribution in South Africa. Agulhas Bank, from Still Bay to Algoa Bay, 39–76 m. 34/21 (s), 34/25 (s)

Genus Rhizogeton L. Agassiz, 1862

Diagnosis. Colony stolonial. Hydrorhiza giving rise directly to naked and sessile hydranths. Hydranth with scattered filiform tentacles. Gonophores in the form of fixed sporosacs, borne directly on hydrorhiza.

Type species: Rhizogeton fusiforme L. Agassiz, 1862.

One species only from South Africa.

Rhizogeton nudum Broch, 1909

Fig. 24E


Diagnosis. Hydrorhiza creeping and reticular, coated with transparent perisarc. Hydranth reaching 2 mm in height, sessile, naked except for a low perisarcal collar around base, with 16–26 filiform tentacles irregularly scattered over distal two-thirds, the proximal tentacles shorter than the distal.

Gonophores in the form of fixed sporosacs, borne directly on hydrorhiza, completely enveloped in thin perisarc. Male gonophore oval, reaching 0.3 mm in height. Female unknown.

Distribution outside South Africa. Arctic (type locality: Spitzbergen, 35 m), Pacific (Christmas Is.), India.

Distribution in South Africa. Moçambique, Inhaca to Santa Carolina. 26/32 (s), 25/32, 21/35
Genus *Turritopsis* McCrady, 1856


**Diagnosis.** Colony with erect and branching stem. Stem with firm perisarc, branches adnate to stem for some distance after origin. Hydranth naked, not retractable into perisarc. Gonophores borne on stem, developing into free medusae.

Medusa with eight or more simple marginal tentacles; stomach with an apical mass of vacuolated endoderm cells; with ocelli.

Type species: *Oceania (Turritopsis) nutricula* McCrady, 1856.

One species only from South Africa.

*Turritopsis nutricula* McCrady, 1856

Fig. 24F–G

*Oceania (Turritopsis) nutricula* McCrady, 1856: 55; pls 4–5.


*Turritopsis dorhni*: Mammen 1963: 35, fig. 4.

**Diagnosis.** Stem reaching 5 mm in height, branching irregularly, increasing in diameter from base to distal end, covered with firm perisarc, branches adnate and parallel to stem for a short distance, then diverging at an acute angle, perisarc terminating below hydranth. Hydranth terminal, with 12–38 filiform tentacles irregularly scattered over distal part, proximal ones shorter than distal.

Medusa-buds arising below hydranths, pear-shaped, enclosed in perisarc, with eight marginal tentacles at liberation. Adult medusa (not known from South Africa) deep bell-shaped; stomach large, cross-shaped, brilliant red; mouth with four large lips and a row of nematocyst knobs on edge; 80–90 marginal tentacles in a single row.

Nematocysts (medusa): microbasic euryteles and desmonemes.

**Variation.** Only small unfascicled colonies have so far been found in South Africa. Mature colonies have thick and fascicled stems and reach about 20 mm in height. The perisarc of the stem is often in two layers: an inner firm layer, usually corrugated, and an outer thinner layer, which may have adhering silt. In newly settled colonies the stem is unbranched and bears a single terminal hydranth.

**Distribution outside South Africa.** Circumglobal, mainly in tropical waters but spreading into temperate waters too. Medusa more widely known and reported in North Sea, Japan and New Zealand.

Type locality: Charleston Harbour, S. Carolina.

**Distribution in South Africa.** Moçambique, Inhaca to Santa Carolina. 26/32 (s), 23/35, 21/35
Family *Eudendriidae*

*Diagnosis.* Colonial hydroids with an erect, usually branched stem enclosed in firm perisarc up to the base of the hydranth body. Hydranth large, radially symmetrical, with trumpet-shaped hypostome and one or more whorls of filiform tentacles immediately below it. Reproduction by fixed sporoacs borne on the hydranth body below the tentacles; reproductive hydranth often reduced to a blastostyle. Male gonophore usually with several chambers in linear series. Young female gonophore with a single egg encircled by a spadix.

*Introduction.* Members of the Eudendriidae are comparatively easy to recognize, but identification within the family, particularly in the genus *Eudendrium*, is not at all easy, since most of the macroscopic features vary with age and habitat.

The stem may be branched or unbranched, fascicled or unfascicled. It is always covered with firm perisarc which terminates on or below the base of the hydranth. The perisarc is usually smooth or wrinkled with characteristic groups of annulations on the origins of the branches and at other strategic positions.

The hydranth is large and distinguished from all other families of the Athecata by the wide, trumpet-shaped hypostome which usually gapes open even in preserved material. Broch (1916) was the first to point out that the endoderm of the hydranth has become differentiated, the cells of the oral part of the hypostome being small and ‘indifferent’, and the mucous and digestive cells being limited to the lower part of the hypostome and the gastral cavity. The ectoderm is thin over most of the hydranth, but usually there is a shallow groove round the base of the body where the perisarc of the stem terminates and where its growth occurs. The ectoderm below this level is thicker, with a circle of characteristic large cells just below the groove. Mammen (1963)

![Diagram of hydranth and gonophore](image)

Fig. 26. *Eudendrium*, parts of the hydranth and types of female gonophore.
maintains that the groove is only visible in the contracted hydranth and that it therefore cannot be used as a diagnostic character as has been done in the past. Immediately above the groove there is, in some species, a nettle ring, or circle of large nematocysts. Similar large nematocysts may occur on the hypostome as well, and they then belong to a different category to the small microbasic euryteles which are always present on the tentacles. The presence or absence, and the category, of these large nematocysts provide a useful diagnostic character.

Reproduction is by fixed sporosacs which develop in a whorl round the base of the hydranth. Male and female are normally borne on separate colonies, but there are rare cases of hermaphroditism (E. motzkossowskiae). The hydranth bearing the gonophores is usually atrophied to some extent, but the degree varies from species to species and sometimes within one species. Thus, the hydranth may retain its tentacles and continue to function as a normal feeding individual, or the tentacles may be progressively resorbed as the gonophores mature to form a blastostyle. Sometimes the tentacles are absent and the mouth closed from the earliest stage.

Male gonophores typically consist of several bulbous chambers containing the spermatogenic cells and arranged in linear series. In the earliest stage there is only one chamber, but as development proceeds additional chambers are added from below. Thus the number of chambers cannot be used as a diagnostic character although the maximum number may be characteristic of a species.

The female gonophore consists of a spadix arching round a single large egg. The spadix may be simple or branched. It provides a reliable diagnostic character, although it must be borne in mind that there are several species with an unbranched spadix and several with a bifid spadix. As the egg matures the spadix straightens out and arches away from the egg, eventually becoming shed or resorbed. The egg is left in a perisarcal capsule where it is fertilized and develops into a planula. As development proceeds the female gonophores lose their whorled arrangement and, due to lengthening of the blastostyle, become irregularly distributed along it.

Due to the fact that the earlier systematists based their descriptions on characters which have since proved to be unreliable, many of the records are of dubious validity and the distribution of the species uncertain. A new school of systematists has recently been growing in Europe, including Picard and Bouillon, in which the nematocysts are being increasingly used for species diagnosis. These, together with the nature of the female gonophores, and sometimes other specific characters, such as the presence of special nematocyst-bearing processes, or cnidophores, in E. racemosum, make certain diagnosis possible. The presence of the large nematocysts can easily be determined even with a low-powered microscope, and with practice their type can often be recognized in the undischarged state.

In view of these points, the South African material of Eudendrium has been re-examined and revised. Only that material in which the diagnosis is certain

irregular intervals. Hydranth with 25–30 tentacles, with mouth and hypostome blocked by a plug of elongated endoderm cells continuous with the digestive endoderm at base of hydranth.

Gonophores unknown.

Nematocysts of two types.

(i) Large, 23.3 x 10.4 μ, on hypostome and body of hydranth.
(ii) Small, 5.0 x 2.2 μ, chiefly on tentacles.

Remarks. This species has not been rediscovered in South Africa, although it has been reported, but not described, from Madagascar by Gravier (1970a). Its reproduction and nematocyst types remain unknown.

It might be noted that the blockage of the hypostome by endoderm, the feature on which the species was founded, may be a transitory phase, for cells are known to move through the coelenteron in certain species of Hydrozoa (Braverman 1973).

The large nematocysts in Warren’s diagram could be either macrobasic euryteles or isorhizas. They are not microbasic euryteles. This would suggest either E. motzkossowskai or E. carneum.

Distribution outside South Africa. South-east Madagascar.

Distribution in South Africa. Algoa Bay only; 73 m (type locality). 33/25 (s)

Eudendrium ?antarcticum Stechow, 1921

Fig. 27C–D


Diagnosis. Small colonies reaching a maximum height of 3 mm. Stem unfascicled, unbranched or sparingly branched, smooth for the most part but annulated at base, on origins of branches and at other irregular intervals, very delicate, only 0.05–0.075 mm in diameter. Hydranth with 16–23 tentacles and very large hypostome.

Male gonophores borne on blastostyles in which the tentacles are completely atrophied, one-chambered with a terminal tubercle. Female gonophores (not recorded from South Africa) borne in pairs on tentacular hydranths, with curved and unbranched spadix, containing one egg (Stechow 1925a).

Only one type of nematocyst: small microbasic euryteles, present on tentacles, terminal tubercles of male gonophores and elsewhere, 7.2 x 2.7 μ. Butt with only a few spines on distal end.

Remarks. The position of this material and its identity with the true E. antarcticum remain uncertain. It differs from the other small species of Eudendrium in the slender stem and the structure of the microbasic euryteles which are different to any in the northern hemisphere (Picard: personal communication).

Distribution outside South Africa. Bouvet Island, Antarctic (type locality).
Fig. 27.

*Eudendrium angustum*. A and B, stems redrawn from Warren (1908).

*Eudendrium ?antarcticum*. C, hydranths; D, male blastostyles.

*Eudendrium capillare*. E, colony with female blastostyles; F, very young female blastostyle;
G, older female blastostyles; H, mature female blastostyle with spadices shed; J, male
blastostyles, one mature and one young.

Scale: A in cm, B in mm, the rest in mm/10.
**Distribution in South Africa.** Two records only: False Bay and Agulhas Bank, in 18 and 102 m respectively. 34/18 (s), 35/21 (d)

_Eudendrium capillare_ Alder, 1856

Fig. 27E–J


_Eudendrium parvum_ Warren, 1908: 272, fig. 1, pl. 45 (figs 1–4).

_Eudendrium ?parvum:_ Millard, 1959a: 305, fig. 1G–H.


**Diagnosis.** Small colonies common on other hyroids and on weed, reaching a maximum height of 14 mm. Stem unfascicled, unbranched or sparsely and irregularly branched, annulated or corrugated on origins of branches and at other irregular intervals, hydranth pedicels often annulated or corrugated throughout. Hydranth with 15–23 tentacles.

Male gonophores borne on blastostyles in which the tentacles are completely atrophied at all stages, one- to three-chambered, sometimes with a terminal tubercle. Female gonophores borne on hydranthas in which the tentacles are reduced in size, with curved and unbranched spadix, containing one egg. In older stages the hydranth tentacles completely atrophied, the spadices shed and the eggs in their transparent capsules distributed irregularly along the blastostyle pedicel.

Only one type of nematocyst: small microbasic euryteles, abundant on tentacles and also present in body, 4,8 × 2,1 – 8,0 × 3,0 μ.

Colour: hydranthas pale horn-colour (Warren), eggs orange, spadix white.

**Distribution outside South Africa.** Uncertain, since most of the records in the literature give insufficient information. Certainly from the North Atlantic and Mediterranean, and from India. Type locality: Northumberland, U.K.

**Distribution in South Africa.** Park Rynie in Natal to Santa Carolina in Moçambique, probably more widespread than this. 30/30 (1), 26/32, 25/32, 21/35

_Eudendrium carneum_ Clarke, 1882

Fig. 28


**Diagnosis.** Colonies tall, much-branched and shrub-like, reaching a height of 162 mm. Stem and larger branches fascicled. Branching irregular. Perisarc distinctly annulated on origins of branches and at other irregular intervals. Hydranth pedicels with scattered groups of annulations or completely annulated. Hydranth with 26–33 tentacles.

Male gonophores borne on blastostyles in which the tentacles are completely atrophied, three- or four-chambered. Female gonophores borne on
Fig. 28.

*Eudendrium carneum*. A, stem; B, part of stem with male blastostyles; C, large isorhiza; D, microbasic euryele, undischarged and discharged; E, mature male blastostyle; F and G, young female blastostyles with bifid spadices; H, old female blastostyle with spadices shed leaving basket-shaped capsules.

Scale: A in cm, B in mm, C and D in μm, the rest in mm/10.
hydranth in which the tentacles are reduced in size, with bifurcating spadix, containing one egg. In older stages the tentacles completely atrophied, the spadices shed and the developing embryos contained in basket-shaped capsules distributed irregularly along the pedicel.

Nematocysts of two types:
(i) Large atrichous isorhizas, present on hypostome and hydranth body, 24 × 11 μ. Capsule bean-shaped. Thread coiled in figure of eight in longitudinal axis.
(ii) Small microbasic euryteles, present on tentacles and elsewhere, 9 × 4 μ. Capsule ovoid. Butt with three large spines on distal end.

Distribution outside South Africa. Atlantic coast of North America, Brazil, St. Helena, Pacific coast of North America, east tropical Pacific. Type locality: Fort Wool, Virginia.

Distribution in South Africa. Durban and Inhambane. On ships’ hulls, littoral and in shallow water. 29/31 (l, s, h), 23/35 (s)

*Eudendrium deciduum* Millard, 1957

Fig. 29A–F


Male gonophores borne on hydranth in which the tentacles are completely atrophied, two- or three-chambered. Female gonophores borne on hydranth in which the tentacles are reduced in size, with spadix bearing three or four lateral branches on each side, containing one egg. In older stages the tentacles completely atrophied, the spadices shed and the developing embryos contained in warty capsules distributed irregularly along the pedicel.

Colour: larger stems dark brown, smaller ones clear brown to horn-colour, female gonophores bright orange.

Only one type of nematocyst: small ?microbasic euryteles on tentacles and body, 6,3 × 2,7 – 8,1 × 3,6 μ. Capsule ovoid.

Distribution. Endemic to South Africa. Type locality: False Bay.

Distribution in South Africa. Dassen Island on the west coast to Algoa Bay, in 4–18 m. 33/18 (s), 34/18 (s), 34/22 (s), 33/25 (s)

*Eudendrium motzkossowskae* Picard, 1951

Fig. 29G–H

*Eudendrium simplex*: Motz-Kossowska, 1905: 56, pl. 3 (figs 18–19).
Diagnosis. Small colonies reaching a maximum height of 12 mm. Stem unfascicled, unbranched or sparsely branched, smooth for the most part but annulated on origins of branches and at other irregular intervals, hydanth pedicels sometimes annulated or corrugated throughout. Hydanth with 16–27 tentacles.

Gonophores borne on hydanthrs in which the tentacles are not atrophied, male and female on separate colonies. Male gonophore one- or two-chambered. Female gonophore (not reported from South Africa) with curved and unbranched spadix, hermaphroditic, containing one egg within the curvature of the spadix and one or more masses of spermatogenic cells at summit between spadix and superficial ectoderm.

Nematocysts of two types:

(i) Large macrobasic euryteles, present on hypostome and lower part of hydanth body, 15.6 x 6.0 – 31.6 x 14.0 μ. Capsule bean-shaped. Butt 5–6 times length of capsule, in 3–4 obliquely longitudinal coils when undischarged, swollen distally to about double the width when discharged, armed with spirally arranged barbs.

(ii) Small microbasic euryteles, present on tentacles and elsewhere, 6.6 x 2.4 – 7.2 x 3.0 μ. Capsule ovoid.

Variation. Only small colonies have so far been found in South Africa. Neither Motz-Kossowska nor Picard gives any indication of the size and degree of branching attainable in the Mediterranean material.

Distribution outside South Africa. Mediterranean only (type locality).

Distribution in South Africa. Moçambique, from Inhaca to Santa Carolina, littoral to 3 m. 26/32, 24/35 (s), 21/35

Eudendrium ramosum (Linnaeus, 1758)

Fig. 31A–D

Tubularia ramosa Linnaeus, 1758: 804.

Diagnosis. Mature colonies tall, reaching a maximum height of 175 mm; main stem fascicled at base, sometimes slender and flexuous with roughly alternate branches, sometimes stiff and bushy with irregular branches; branches unfascicled. Small colonies commonly occurring on weed and other hydroids, reaching 10–20 mm, with unfascicled stems which may be unbranched or sparingly branched in a roughly alternate fashion. Perisarc smooth for the most part but with groups of a few distinct annulations above origins of branches and at other irregular intervals. Hydanth pedicels annulated in basal region. Hydanth with 14–29 tentacles.

Gonophores borne on hydanthrs in which the tentacles are atrophied to a varying degree. Male gonophores one- or two-chambered. Female gonophores
Fig. 29.

_Eudendrium deciduum_. A, stem; B–D, young female gonophores showing branching spadix; E, part of sterile stem; F, branch with two male blastostyles.

_Eudendrium motzkowskii_. G, mature male blastostyle; H, large macrobasic eurytele, discharged and undischarged.

Scale: A in cm, E and F in mm, H in mm/100, the rest in mm/10.
with curved and unbranched spadix which is shed later leaving a smooth transparent capsule, containing one egg.

Nematocysts of two types:

(i) Large microbasic euryteles, present on hypostome and lower part of hydranth body, on spadix of female gonophore and on distal end of male gonophore, rather variable in size, 18.0 × 7.2 – 28.8 × 13.8 μ. Capsule bean-shaped. Butt about ½ length of capsule, increasing in diameter distally but not coiled when undischarged, when discharged held at right angles to capsule and dilated distally to about double its width. Spines spirally arranged on butt and decreasing in length distally.

(ii) Small microbasic euryteles, present on tentacles and elsewhere, 5.8 × 2.7 – 8.4 × 4.2 μ. Capsule ovoid.

Colour: hydranth body yellowish to orange-pink, tentacles and hypostome white.

Variation. This species has a variable growth-form and can be distinguished with certainty only on the nematocysts. It is the only South African species with large microbasic euryteles.

The degree of atrophy of the blastostyle is variable. The female gonophores are borne on fully developed hydranth, and the tentacles are then gradually resorbed until by the time the spadix is shed there is no sign of them left. In the male, gonophores may be borne on hydranth with their tentacles in any stage from fully-formed to completely atrophied. The gonophores are one-chambered when young, becoming two- or three-chambered when ripe.

In some colonies the stem is almost completely annulated throughout.

Distribution outside South Africa. North Atlantic, from the Arctic to Cape Verde, Mediterranean, Seychelles. Further distribution doubtful. Type locality: Kentish shore, U.K.

Distribution in South Africa. From off Saldanha Bay to Inhaca, littoral to 84 m. Probably more abundant than records indicate. 33/17 (s), 33/18 (s), 34/18 (l, s), 34/25 (s), 33/27 (l), 31/29 (l), 26/32 (s), 25/32

_Eudendrium ritchiei_ sp. nov.

Fig. 30


Description of holotype. Colony stiff and spiky, reaching a maximum height of 28 mm. Stem fascicled, branching irregularly and in all planes; branches stiff and making an angle of about 45° with stem, often rebranching. Perisare strongly annulated almost throughout, but with occasional smooth areas on some of the youngest pedicels. Hydranth with 16–21 tentacles. No cnidophores.
Male and female blastostyles on separate stems. Male with no sign of tentacles at any stage; bearing a circle of gonophores which are one- or two-chambered. Female with a cluster of reduced tentacles which are completely resorbed later; bearing a circle of 4–6 gonophores which become irregularly distributed as they mature. Young female gonophore with a bifurcating spadix surrounding the single egg, but sometimes the two limbs unequally developed or one of them rudimentary. Old female gonophore oval, with a smooth transparent capsule surrounding the developing embryo.

Nematocysts of two types:

(i) Large macrobasic euryteles, present on hypostome and body of hydranth, on spadix of female gonophore and on terminal tubercle of male gonophore, $23.4 \times 8.4 - 27.6 \times 10.8 \mu$. Capsule bean-shaped. Butt coiled longitudinally in one and a half coils when undischarged, reaching a length of 74 $\mu$ when discharged and increasing in diameter smoothly from about 1,2 $\mu$ proximally to 2,7 $\mu$ distally, armed with spiral bands of spines.

(ii) Small microbasic euryteles, abundant on tentacles of hydranth and elsewhere on the body, $6.0 \times 3.6 - 9.6 \times 3.6 \mu$. Capsule bean-shaped. Butt about 6,3 $\mu$ in length when discharged, bearing spines distally.

Colour: stem pale horn-colour to dark brown; hydranth and female gonophores orange, male gonophores white.

Variation. From colonies other than the holotype, stems may reach 50 mm and hydranth may have 15–24 tentacles.

The annulation of the perisarc varies. It may be completely annulated throughout, or there may be smooth areas on the pedicels and the stem itself. The annulation is always more strongly developed than in any other South African species.

Remarks. This species is very close to *E. carneum* and *E. racemosum*, both of which have a bifurcating spadix in the female gonophore. It differs from both of these in the cnidome and in the annulated stem. It is to this species that Ritchie's material from South Africa, described as *E. annulatum*, must be ascribed.

Distribution. Endemic to South Africa.

Distribution in South Africa. Saldanha Bay to Oudekraal, littoral to 46 m. 33/17 (s), 33/18 (l, s)

Family Bougainvillidae

Diagnosis. Colonial (rarely stolonial) hydroids with an erect, often branched, stem enclosed in firm perisarc which may terminate below the hydranth body or continue over it as a pseudohydrotheca. Hydranth radially symmetrical, with conical hypostome and one or more definite whorls of filiform tentacles. Reproduction by fixed sporosacs or medusae.

Adult medusa, when present, with simple tubular mouth, with four or
Fig. 30.

*Eudendrium ritchiei*, sp. nov., all from holotype. A, stems; B, part of stem with hydænum and male blastostyle; C, male blastostyle; D, young female blastostyle; E, old female blastostyle with spadices shed; F, nematocysts, from left to right three macrobasic euryteles (two discharged, one undischarged), and two microbasic euryteles (one undischarged, one discharged).

Scale: A in cm, F in mm/100, the rest in mm/10.
eight usually branched oral tentacles inserted above mouth opening, four radial canals, solid marginal tentacles often in groups on marginal bulbs, with or without ocelli, with interradial gonads.

Introduction. The Bougainvilliidae is a fairly well-defined family and the medusae in particular are very distinctive.

The stem, which may be branched or unbranched, fascicled or unfascicled, is always coated in firm perisarc, and this perisarc may terminate below the hydranths as in *Clavopsella* and *Silhouetta* or it may extend over the body of the hydranth as a pseudohydrotheca. This structure, unlike the true hydrotheca of the Thecata, has little form; it adheres closely to the ectoderm of the hydranth and is often gelatinous with adhering silt granules. The hydranth on contraction may partially or completely withdraw into it, when it becomes broader and shorter and often wrinkled. In *Bougainvilia* (some species) and in *Rhizorhagium* the pseudohydrotheca invests only the lower part of the hydranth body, but in *Bimeria* it covers the bases of the tentacles as well, so that each tentacle has a sheath around its base. In *Bimeria rigida* the pseudohydrotheca covers the whole body as far as the mouth, and the tentacles almost to their tips. Since the perisarc below the tentacles is particularly firm the hydranth in this species has little motility and the tentacles are held out in a rigid flower-like crown.

The hydranth is of fairly simple construction, though there is a differentiation of the endoderm into an oral region rich in gland cells and a gastric region below the tentacles. Unlike the Eudendriidae the hyposome is conical. Most species have a single whorl of filiform tentacles, but there is more than one whorl in *Clavopsella, Silhouetta* and *Balella*. As mentioned on p. 70 these genera are considered to be primitive in that the tentacles have not yet settled down into a single whorl, and are included in the Bougainvilliidae on the strength of the medusa structure of *Silhouetta*. In *Bimeria rigida* the tentacles were described as capitate by Warren (1919a), but there is only an indistinct swelling of the tips where they escape from the constricting perisarcal sheath.

The gonophores are usually borne on the stem or hydranth pedicels, more rarely on the hydrorhiza. In *Dicoryne* they are borne on reduced hydranths, or blastostyles, which are without mouth or tentacles, but have a prominent hyposome armed with nematocysts.

The gonophores may be in the form of fixed sporosacs (*Bimeria, Rhizorhagium, Clavopsella, Garveia*) or may be released as free medusae. In *Dicoryne* the sporosacs are unusual. Although essentially styloid in structure they are released and free-swimming with the aid of a coating of cilia and two long tentacles. The tentacles are not comparable with the marginal tentacles of a medusa, for they arise from the proximal (attached) end of the sporosac.

Free-swimming medusae are released in *Bougainvillia, Balella, Silhouetta* and *Thamnostoma*. Bougainvilliid medusae are easily recognized, even in their

* For *Rhizorhagium* the conception and definition of Rees (1938) are adopted.
young stages, by the oral tentacles which do not arise from the rim of the mouth but just above, leaving the mouth free. However, at any rate in the genus *Bougainvillia*, identification to the species level is difficult for it depends largely on the structure of the adult medusa, the hydranth generation being very variable in growth-form and having few reliable diagnostic characters.

**KEY TO GENERA**

[Genera not represented in South Africa are bracketed]

1. Hydranth with more than one whorl of tentacles...
   - Hydranth with one whorl of tentacles...
     [Boletella] 2

2. Hydranth with two whorls of tentacles, one at proximal end and one round widest part. Gonophores producing free medusae...
   - Hydranth with 2–4 whorls of tentacles closely approximated around mouth...
     [Silhouetta] 3

3. Gonophores producing free medusae...
   - Gonophores in the form of fixed sporosacs...
     [Clavospella] p. 100

4. Perisarc not continued over tentacles...
   - Perisarc continued at least part-way over tentacles...
     Bougainvillia p. 95

5. Producing medusae. Medusa with groups of marginal tentacles...
   - Not producing medusae...
     [Dicoryne] p. 101

6. Producing swimming sporosacs...
   - Producing fixed sporosacs...
     [Garvetia] p. 103

7. Stem with one terminal hydranth and, rarely, one or two lateral ones...
   - Stem much-branched...
     [Thamnostoma] p. 91

8. Producing medusae. Medusa with solitary marginal tentacles...
   - Producing fixed sporosacs...
     Bimeria p. 91

**Genus Bimeria** Wright, 1859

*Diagnosis.* Colony stolonial or with erect, branching stem. Stem with firm perisarc which also extends over part or all of the hydranth as a pseudohydropotheca and sheaths the proximal parts of the tentacles. Hydranth with one whorl of tentacles. Gonophores in the form of fixed sporosacs, completely invested in perisarc.

Type species: *Bimeria vestita* Wright, 1859.

**KEY TO SPECIES**

1. Estuarine. Stem branching profusely and at least several cm in height...
   - Marine. Stem unbranched or slightly branched, under 2 cm in height...
     B. fluminalis 2

2. Gonophores normally borne on stem, stem normally branched...
   - Gonophores borne only on hydrorhiza, stem never branched...
     B. vestita

**Bimeria fluminalis** Annandale, 1915

Fig. 31E–K


*Diagnosis.* Hydrorhiza forming a matted feltwork. Stem unfascicled, flexuous to stiff, profusely branched in a roughly alternate fashion, reaching a maximum
Eudendrium ramosum. A and B, male blastostyles; C, young female blastostyles; D, nematocysts, from left to right large microbasic eurytele discharged and undischarged, a small microbasic eurytele.

Bimeria fluminalis. E, part of colony; F, t.s. female gonophore with egg; G, t.s. female gonophore with planula; H, t.s. male gonophore; J, hydranth and two young female gonophores, one with an egg; K, microbasic eurytele.

Abbreviations: e: egg; ect: ectoderm; m: male spermatogenic cells; p: perisarc; sp: spadix.

Scale: E in cm, D and K in mm/200, the rest in mm/10.
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height of 330 mm. Perisarc annulated on base of stem, origin of branches and hydranth pedicels, continued over base of hydranth body as a thick pseudohydrotheca, of which a very thin extension covers the bases of the tentacles, covered with adherent silt. Hydranth with 10–12 tentacles, partially retractable into pseudohydrotheca.

Gonophores borne singly or in clusters on hydranth pedicels, pedicellate, completely clothed in perisarc, with no radial canals or tentacle rudiments, male and female on separate stems. Male ovoid, reaching 0,5 mm in length. Female ovoid, containing a single egg on one side of the curved spadix, reaching 0,4 mm in length. Egg developing into a planula in situ.

Nematocysts of two types:
(i) Desmonemes, 3,5 × 2,5 μ.
(ii) Microbasic euryteles, 7,0 × 4,5 μ (maximum).

Variation. The stem is sometimes straight and sometimes geniculate in the distal region. The development of the perisarc covering the tentacle bases is variable; in the type material there is usually a distinct layer, but in the South African material this part is very poorly developed and usually only discernible in sections.

Distribution outside South Africa. Tropical Indo-Pacific including India, the Gulf of Siam and W. Borneo. Type locality: Chilka Lake, Calcutta.

Distribution in South Africa. Richard’s Bay and St. Lucia estuaries, on mangroves, logs, etc. 28/32 (l)

Bimeria rigida Warren, 1919

Fig. 32A–B

Bimeria rigida Warren, 1919a: 1, figs 1–2, pls 1–2.

Diagnosis. Colony growing on weed. Hydorhiza with clasping processes and with internal thickenings of perisarc in some areas. Stem unfascicled, unbranched, narrower at base than at distal end, bearing a single terminal hydranth, reaching a maximum height of 3 mm. Perisarc indistinctly annulated, especially at base and distal end, continued over body of hydranth as a well-developed pseudohydrotheca. Pseudohydrotheca in proximal region stiff, longitudinally ridged and continued along the tentacles almost to the tips; in distal region thick and soft, completely enveloping the conical hypostome, with adherent silt. Hydranth about 0,6 mm in height to tip of hypostome, with 16–33 stiff tentacles held alternately elevated and depressed and swollen at the tips where they emerge from the perisarc, with an ectoderm-lined chamber distal to the mouth, with four endodermal ridges in hypostome.

Gonophores borne on hydorhiza, pedicellate, completely enclosed in perisarc. Male oval to spherical, reaching 0,5 mm in length, with no radial canals or tentacle rudiments, with branching spadix. Female unknown.
Fig. 32.

*Bimeria rigida*, A, hydranth; B, l.s. male gonophore redrawn from Warren (1919a).

*Bimeria vestita*, C, fertile stems; D, contracted hydranth showing perisarcal sheaths round tentacles; E, F and G, stages in development of female gonophore, the last two drawn without the perisarcal coat; H, male gonophore.

Scale in mm/10.
Nematocysts: microbasic euryteles, 7.2 × 3.0 – 9.0 × 4.2 μ.
Colour: pale horn-colour.

Distribution. Endemic to South Africa. Type locality: Port St. Johns.

Distribution in South Africa. Transkei coast, in rock pools. 31/29 (l), 31/30 (l).

Bimeria vestita Wright, 1859

Fig. 32C–H

Bimeria vestita Wright, 1859: 109, pl. 8 (fig. 4). Allman, 1872: 297, pl. 12 (figs 1–3). Millard, 1966a: 449, fig. 5A–F.

Diagnosis. Colony usually epizootic on other hydroids. Stem unfascicled, delicate, either unbranched and with one terminal hydranth, or branching, and rarely rebranching, in a roughly alternate manner, reaching a maximum height of 18 mm but usually much less. Perisarc annulated on base of stem, origin of branches and at other irregular intervals, continued over hydranth body and base of hypostome and forming distinct sheaths over the basal parts of the tentacles, often covered with adherent silt. Hydranth with 10–20 tentacles.

Gonophores borne on stem and branches, rarely on hydrorhiza, pedicellate, invested in thick gelatinous perisarc, with no radial canals or tentacle rudiments, male and female on separate colonies. Male elongate-oval with branching spadix, reaching 0.3 mm in length (without perisarc). Female oval to spherical, containing one terminal ovum, reaching 0.2 mm in length (without perisarc). Egg developing into a planula in situ.

Variation. The South African material is not so richly branched as some of that described from other areas.

Distribution. Cosmopolitan. Type locality: Firth of Forth, U.K.

Distribution in South Africa. All round the coast from the Orange River on the west to Inhaca on the east, 5–88 m. 28/16 (s), 34/18 (s), 34/20 (s), 34/21 (s), 34/22 (s), 33/25, 33/26 (s), 33/27 (s), 26/32 (s).

Genus Bougainvillia Lesson, 1836

Diagnosis. Colony erect with branching stem, or (rarely) stolonial. Stem with firm or soft perisarc which often extends over the base of the hydranth as a pseudohydrotheca but never covers tentacle bases. Hydranth with one whorl of filiform tentacles. Gorophores developing into free medusae.

Medusa with four unbranched radial canals and a circular canal, four dichotomously branched, capitate oral tentacles inserted above mouth opening, marginal tentacles all alike, arising in groups from four marginal bulbs, with ocelli.

Type species: Bougainvillia macloviana Lesson, 1836.
KEY TO SPECIES

1. Perisarc strongly wrinkled throughout. Colony epizootic on parasitic isopods  
   \textit{B. meinertiae}  
   \textit{Perisarc smooth for the most part, but wrinkled or annulated in certain regions. Not}  
   \textit{epizootic on parasitic isopods}  
   \textbf{2}  

2. Stem low-lying, delicate, never fascicled, unbranched or sparsely branched. Mature  
   medusa with well-developed peduncle, oral tentacles branching about 8 times, marginal  
   bulbs with about 53 tentacles  
   \textit{B. macloviana}  
   \textit{Stem erect, stiff, fascicled in larger colonies, branching profusely. Mature medusa with}  
   \textit{very slight peduncle, oral tentacles branching 1–6 times, marginal bulbs with 3–9}  
   \textit{tentacles}  
   \textbf{B. ramosa} 

\textit{Bougainvillia macloviana} (Lesson, 1830)  

Fig. 33A–C

\textit{Cyanaea bougainvillii} Lesson 1830: 118, pl. 14 (fig. 3).  
fig. 3E.  
\textit{Perigonimus maclovianus}: Vanhöffen, 1910: 284, fig. 10.  

\textit{Diagnosis}. Hydrorhiza forming a branching network. Stem slender, unfascicled  
and low-lying, unbranched or branching irregularly, narrower at base than at  
summit, reaching a maximum height of 8 mm. Perisarc smooth or wrinkled,  
more deeply corrugated on base of stem and origins of branches, continued over  
base of contracted hydranth as a gelatinous pseudohydrotheca. Hydranth with  
8–12 tentacles.  

Medusa-buds arising singly from hydrorhiza, stem or branches, larger than  
hydranths, shortly stalked, spherical, enclosed in perisarc, reaching a diameter of  
0.4 mm (without perisarc), before liberation with four unbranched, capitate  
oral tentacles and four marginal bulbs, each of the latter with two ocelli and  
two marginal tentacles.  

Adult medusa globular, with moderately thick jelly. Outer surface of bell  
with interradial furrows. Stomach short with large peduncle and four perradial  
lobes along peduncle. Oral tentacles four, branching dichotomously about eight  
times. Marginal bulbs V-shaped, each bearing about 53 tentacles in a double  
row and as many ocelli. Gonads interradial, hanging in folded bands along the  
stomach lobes. Reaching 9.0 mm in depth and 8.2 mm in diameter. Colour:  
marginal bulbs, gonads and stomach reddish-brown, ocelli black, the rest  
transparent.  

Nematocysts of two kinds, present in hydranths and medusae:  

(i) Desmonemes. Capsule ovoid, thread in 1½ coils. Smaller in hydranth  
\((3.5 \times 2.0 - 4.0 \times 3.0 \mu)\) than in medusa \((6.3 \times 3.6 - 8.1 \times 4.1 \mu)\).  
(ii) Microbasic euryteles. Capsule bean-shaped, butt about \(\frac{2}{3}\) length of capsule.  
\(5.4 \times 2.7 - 7.2 \times 3.6 \mu\).  

\textit{Variation}. The measurements and tentacle numbers given above are from South  
African material only. In material from elsewhere, however, the hydranth may  
have as many as 16 tentacles and the medusa-buds may reach a diameter of
0.75 mm and have up to five marginal tentacles on each bulb at liberation. Similarly the adult medusa may reach a depth of 15 mm and may have up to 65 tentacles on each marginal bulb.

**Distribution outside South Africa.** Hydranth: Kerguelen, Seychelles. Medusa: Subantarctic, North Sea, Firth of Clyde. Type locality: Falkland Islands.

**Distribution in South Africa.** Hydranth: Saldanha Bay, Table Bay and off Still Bay, 15–73 m and on ships' hulls. Medusa: Saldanha Bay, Langebaan Lagoon. 33/18 (s, h), 34/21 (s)

*Bougainvillia meinertiae* Jäderholm, 1923

Fig. 33D


**Diagnosis.** Colony epizootic on the parasitic isopod *Codonophilus* (*Meinertia*) *imbricata* (Fabr.) which lives in the buccal cavity of fish. Stem erect, fascicled at base, branching freely, reaching a maximum height of 10 mm. Perisarc thick, especially near base, very strongly and irregularly wrinkled throughout, continued over base of hydranth body as a thin and smooth pseudohydrorhetheca into which the hydranth can be partially retracted. Hydranth with about 14 tentacles.

Medusa-buds arising from hydranth pedicels, smaller than hydranths, sessile or shortly stalked, pear-shaped to spherical, about 0.16 mm in diameter. Marginal tentacles probably eight.

**Remarks.** This material differs only from that assigned to *B. ramosa* in the more extensive wrinkling of the perisarc. In view of its unusual habitat it is retained as a separate species until more material is forthcoming.

**Distribution.** Endemic to South Africa.

**Distribution in South Africa.** Agulhas Bank east of Cape Agulhas in 73 m (type locality). 34/20 (s), 34/21

*Bougainvillia ramosa* (van Beneden, 1844)

Fig. 33E–H

*Eudendrium ramosum* van Beneden, 1844: 57, pl. 4 (figs 10–13).


*Bougainvillia fruticosa*: Allman, 1872: 314, pl. 9 (figs 1–4).

*Bougainvillia muscosus*: Allman, 1872: 317, pl. 10 (figs 1–3).

*Bougainvillia van Benedeni*: Jäderholm, 1909: 46, pl. 3 (fig. 5).


**Diagnosis.** Stem erect, unfascicled or weakly fascicled, branching profusely and irregularly, narrower at base than at summit, reaching a maximum height of 53 mm. Branches forming an acute angle with the stem. Perisarc smooth for
Fig. 33.

*Bougainvillia macloviana.* A, nematocysts from medusa: desmoneme and microbasic eurytele; B, fertile stem; C, adult medusa.

*Bougainvillia meinertiae.* D, part of fertile stem, redrawn from Jäderholm (1923a).

*Bougainvillia rhizoma.* E, fertile colony; F, hydranth showing stolonization; G, medusa-buds; H, newly liberated medusae.

Scale: C and E in mm, A in mm/100, the rest in mm/10.
the most part, wrinkled, corrugated or distinctly annulated on origins of branches and on part or all of final pedicels, continued over base of hydranth body as a pseudohydrotheca. Stolonization common on all parts of colony. Hydranth with 9–15 tentacles.

Medusa-buds arising in groups from hydranth pedicels and smaller branches, smaller than hydranths, shortly stalked, pear-shaped when young.

Medusa at liberation subglobular, about 0.4 mm in diameter, with four capitate, unbranched oral tentacles and four marginal bulbs, each of the latter with two marginal tentacles and two ocelli.

Adult medusa of *B. ramosa* (not recorded from South Africa) semiglobular, with thick jelly. Stomach short, sometimes with very slight peduncle. Oral tentacles four, branching dichotomously once or twice (rarely up to six times). Marginal bulbs small and oval, each bearing 3–9 tentacles (usually 4–5) and as many ocelli. Gonads interradial, extending adradially along radial canals to a slight extent. Reaching 3–4 mm in depth and diameter.

Nematocysts of two kinds:

(i) Desmonemes, 3.6 × 2.5 – 4.2 × 3.2 μ.
(ii) Microbasic euryteles, 5.9 × 2.7 – 8.1 × 3.6 μ. Capsule elongate bean-shaped.

Colour: hydranth creamy white with pink endoderm.

**Variation and remarks.** *B. ramosa* is very variable in its growth-form and the several European forms have been described under different specific names. In *f. musea* the stem is short, reaching about 15 mm, unfascicled and little branched. In *f. fruticosa* the stem is tall, reaching about 50 mm, fascicled and much-branched; the pseudohydrotheca covers about one-third of the hydranth and is membranous and corrugated when contracted. *F. ramosa* is similar but the pseudohydrotheca forms a thin but distinct cup into which the hydranth can be completely withdrawn. *F. vanbenedenii* is characterized by the abundant stolonization; the stem is fascicled or unfascicled and irregularly branched. The South African material covers most of these variations.

Although young medusae have been released in the laboratory, they have not been reared to a stage where it is possible to be certain of the identification. For this reason, and since no adult medusae of *B. ramosa* have as yet been recorded from the South African coast, the identification is provisional. There is a possibility of confusion with *B. fulva* which has been recorded from the East coast of Africa (Kramp 1965; Bouillon personal communication) and whose hydroid stage is as yet unknown.

**Distribution outside South Africa.** ‘Probably in all temperate and subtropical regions’ (Vannucci & Rees 1961). Type locality: Ostend.

**Distribution in South Africa.** Langebaan Lagoon to Port Elizabeth, littoral to 126 m and on ships' hulls. 33/18 (l, h), 34/18 (s, h), 35/19 (s), 34/20 (s), 35/20 (d), 34/21 (s), 34/22 (s), 34/23 (l, s, d), 33/25
Genus *Clavopsella* Stechow, 1919

*Diagnosis*. Stem erect, branched or unbranched, with firm perisarc terminating at base of hydranth. Hydranth with tentacles in two to four closely alternating verticils immediately below hypostome. Gonophores in the form of fixed sporosacs or degenerate medusae without marginal tentacles, radial canals, mouth or oral tentacles.

Type species: *Pachycordyte weismanni* Hargitt, 1904.

One species only from South Africa.

*Clavopsella navis* (Millard, 1959)

Fig. 34A−D

*Rhizorhagium navis* Millard, 1959b: 244, fig. 2.


*Diagnosis*. Hydrorhiza creeping. Stem unbranched (in South African material), bearing a single terminal hydranth, reaching a maximum height of 5 mm. Perisarc often wrinkled, especially near base, terminating below hydranth.

Hydranth with 8−16 tentacles arranged in 2−4 closely alternating verticils immediately below hypostome, 0.4−1.3 mm in length from perisarc.

Gonophores in the form of fixed sporosacs, borne in an irregular spiral on stem below hydranth, pedicellate, completely clothed in perisarc, without tentacle rudiments or radial canals. Female containing about eight eggs usually in one tier, which develop into planulae in situ.

Nematocysts of two types:

(i) Desmonemes, $3.5 \times 2.0 \mu$

(ii) Microbasic euryteles, $6.5 \times 3.0 \mu$. Capsule bean-shaped, butt about two-thirds length of capsule.

Colour: creamy white, with pink tinges in hypostome of hydranth and spadix of gonophore.

*Variation and remarks*. Re-examination of the type material of this species established the fact that in the larger hydranths the tentacles are arranged in as many as four alternating verticils, whereas in the smaller ones (which may be sexually mature) there are only two. It thus becomes necessary to transfer the species from *Rhizorhagium* to *Clavopsella*.

In 1962 Thiel published his excellent account of *Clavopsella quadrangularis* from the Kiel Canal. This species differs from *C. navis* in only a few points, mainly in the fact that in the centre region of well-established colonies the stem branches to produce lateral hydranths of the first and second order. In its maximum development, thus, the colony is a raceme and reaches a height of 30 mm. Other minor differences are the larger number of hydranth tentacles (14−24) and slightly larger desmoneme nematocysts (4−6 $\times$ 3−4 $\mu$). Thiel also discussed the systematic position of *Clavopsella* and the closely related *Balella* and established a new family, the Clavopsellidae, for their inclusion.
In 1972 Dr Thiel and the author had the opportunity of comparing material and we agreed that the species were synonymous, the South African material being a younger colony in its first phase of reproduction.

Later, Millard & Bouillon (1973) established the genus Silhouetta for a species with several whorls of tentacles and bougainviliid medusae, and expressed the opinion that all genera with more than one whorl of tentacles should be included in the Bougainvilliidae.

It is possible that C. navis has been transported from one to the other of its widely separated localities on ships' hulls. The variations described by Thiel can be expected to occur in South Africa when a well-established colony is discovered.

**Distribution outside South Africa.** Kiel Canal.

**Distribution in South Africa.** One record only, from a ship's hull in Table Bay (type locality). 33/18 (h)

Genus *Dicoryne* Allman, 1859

*Diagnosis.* Stem erect, branched or unbranched, with conspicuous perisarc terminating on or below hydranth body but never continued over tentacle bases. Hydranth with one whorl of filiform tentacles. Gonophores borne on reduced hydranths (blastostyles) and released as free-swimming, ciliated sporosacs.

Type species: *Eudendrium confertum* Alder, 1856.

One species only from South Africa.

*Dicoryne conferta* (Alder, 1856),

Fig. 34E–J

*Eudendrium confertum* Alder, 1856: 354, pl. 12 (figs 5–8).

*Dicoryne conferta:* Allman, 1872: 226, 293, pl. 8. Jäderholm, 1909: 47, pl. 3 (fig. 6).

*?Dicoryne* sp.: Vervoort, 1972: 16.

*Diagnosis.* Colonies reaching a height of 25 mm growing on gastropod shells occupied by hermits (including *?Anapagurus hendersoni* Barnard). Hydrorhiza reticulate, without spines, clothed with perisarc. Stem unbranched or branching irregularly, unfascicled, increasing in diameter from base to distal end, clothed with thick perisarc which terminates below hydranth. Branches leaving stem at an acute angle. Perisarc wrinkled, especially near base. Hydranth with one circle of 10–13 filiform tentacles.

Blastostyles borne on stem or direct from hydrorhiza, in the form of modified hydranths without mouth or tentacles but with a long and extensible hypostome armed with nematocysts, bearing gonophores in a dense cluster below hypostome, male and female on separate stems. Gonophores released as free-swimming, ciliated sporosacs with two tentacles arising from proximal (i.e. originally attached) end. Female containing two eggs.
Fig. 34.

Clavapsella navis. A, part of female colony; B, mature female gonophore; C, female gonophore after release of eggs, eggs segmenting; D, later stage with advanced planulae.

Dicoryne conferta. E, hydranth; F, female blastostyle; G, female gonophore in semi-diagrammatic half-section; H, male gonophore; J, stems.

Abbreviations: e: endoderm; g: germ cells; p: perisarc; s: spadix; sc: subumbrellar cavity; t: tentacle.

Scale: A and J in mm, the rest in mm/10.
Nematocysts of at least two kinds:
(i) Small ones on hydranth tentacles, \(4,8 \times 2,4 - 5,4 \times 2,7 \mu\).
(ii) Large ones on blastostyle, \(14,4 \times 4,8 \mu\).

**Variation.** When the hydranth is contracted the perisarc around its base becomes compressed and bulging, partly covering the hydranth body as a pseudo-hydrotheca.

Although each female gonophore normally contains two eggs of equal size placed in a plane at right angles to that of the tentacles, there may be only one terminal egg or two of very unequal size.

**Distribution outside South Africa.** North Atlantic from the Arctic to the Mediterranean. Type locality: Cullercoats, U.K.

**Distribution in South Africa.** Agulhas Bank, from False Bay to Mossel Bay, 80–100 m. 34/18 (s), 34/21 (s), 34/22 (d)

**Genus Rhizohagium** M. Sars, 1877

*Parawrightia* Warren, 1907.
*Gravelya* Totten, 1930.

**Diagnosis.** Stem erect, bearing a single terminal hydranth and, rarely, one or two lateral ones as well, with firm perisarc continued over the base of the hydranth body as a pseudo-hydrotheca but never investing the tentacle bases. Hydranth with one whorl of filiform tentacles. Gonophores in the form of fixed sporosacs, arising either from the hydrorhiza or from the stem.

Type species: *Rhizohagium roseum* M. Sars, 1877.
One species only from South Africa.

**Rhizohagium robustum** (Warren, 1907)

Fig. 35A–B

*Parawrightia robusta* Warren, 1907a: 187, figs 1, 2B, 3–4, pls 33–34.

**Diagnosis.** Hydrorhiza creeping on weeds and sponges, reticular, giving rise to erect stems reaching a maximum height of 12 mm, each bearing one terminal hydranth and sometimes one or two lateral ones. Perisarc irregularly annulated on stem, especially near base, continued over base of hydranth as a pseudo-hydrotheca and terminating in a shallow groove below the tentacles, usually with adherent silt. Hydranth with 13–22 tentacles, reaching a height of about 1,1 mm, not completely retractable into pseudo-hydrotheca.

Gonophores borne singly on stem below hydranth, pedicellate, completely clothed in perisarc, with radial canals but no tentacle rudiments, male and female on separate colonies. Male elongate-oval, female subspherical. Eggs developing into planulae *in situ*.

Nematocysts \(5,0 \times 2,9 - 5,6 \times 2,9 \mu\).
Colour: endoderm red, other living parts translucent white, perisarc pale to dark brown.

Distribution outside South Africa. South-east Madagascar. Type locality: Park Rynie, South Africa.

Distribution in South Africa. East London to Natal, littoral. 33/27 (l), 30/30 (l)

Family Hydractiniidae

Diagnosis. Colonial hydroids with a stolonal habit and polymorphic hydranths, typically with gastrozoooids, gonozoooids and dactylozooids. Skeleton of chitinous perisarc or calcium limited to hydrorhiza and often forming spines. Hydranths sessile and naked; with one or more whorls of filiform tentacles, if more than one then concentrated around hypostome. Reproduction by fixed sporo sacs or medusae.

Medusa, when present, with four or more solid marginal tentacles not in groups, mouth with four lips elongated to form four or eight simple or slightly branched oral arms with terminal clusters of nematocysts, four radial canals, with gonads on interradial walls of stomach or on proximal portions of radial canals as well.

Introduction. Among the Hydractiniidae the subdivision into genera has been the subject of much discussion. The arguments cannot be reproduced here, but the works of Stechow (1923c), Kramp (1932), Iwasa (1934), Rees (1962) and Bouillon (1971) may be consulted. In this paper the definitions of Bouillon (1971: 351) for the genera Hydractinia, Podocoryne and Stylactis are adopted. In addition the genera Clavactinia and Hydrocorella are represented in South Africa.

All the Hydractiniidae have stolonal colonies. They are also polymorphic, and there occur gastrozoooids, gonozoooids, usually smaller than the gastrozoooids and with fewer tentacles, and dactylozooids, often confined to the edge of the colony. Dactylozooids may take the form of spiral zoids or tentaculozooids.

The nature of the hydrorhiza has been the cause of most of the dissension on generic limits. It arises as a system of perisarc-covered stolons which anastomose to form a reticulum, and tend to coalesce with one another. In Stylactis the tubes are usually separate and are always covered with firm perisarc. In Hydractinia, Podocoryne and Clavactinia the superficial layer of perisarc over the coalesced tubes tends to disappear leaving a layer of naked ectoderm over the surface of the mat-like hydrorhiza. In young colonies, or at the edge of older ones, this process may be incomplete, so that there is then liable to be confusion with Stylactis, but as Kramp (1932) states, it is the potentiality for producing the layer of naked coenosarc which is important. Horny spines arising from the perisarc protrude through the coenosarc in many species.

In Hydrocorella the hydrorhiza secretes a calcareous skeleton which rises into a fantastic arrangement of spines and pillars, the whole covered by naked
Fig. 35.

*Rhizorhagium robustum*. A, stem with two hydranths; B, two hydranths, one with a sporo sac, redrawn from Warren (1907a, as *Parowrightia robusta*).

*Clavaectina multitentaculata*, sp. nov. C, colony with gastrozooids, male gonozooids and spines, from holotype; D, spiral zooids from holotype; E and F, l.s. and t.s. young female gonophore; G, t.s. male gonophore from holotype.

Scale: A, B and C in mm, the rest in mm/10.
coenosarc as in the above-mentioned genera. A calcareous skeleton is unusual among the hydroids and according to Stechow (1925a) provides a link with the Stylasteridae.

Most of the genera have a single whorl of tentacles on the hydranth but, among these, species with many tentacles may have alternate ones slightly displaced, giving the appearance of two closely alternating rows. In Clavactinia there are several such whorls and, as was mentioned on p. 70, this is probably a primitive condition for the family.

Reproduction is by fixed sporosacs or free medusae and all stages between these two extremes may occur. It has been claimed that because of intermediate conditions it is not possible to separate genera on this basis. However, it is felt that there is a big difference between the highly developed medusae of a typical Podocoryne and the degenerate medusae found in some species of Hydractinia. The intermediate stages are, as elsewhere in this work, classified as 'sporosacs'.

One of the most interesting features of the Hydractiniidae is the adoption of an epizootic life on the shells of hermits or gastropods. The advantage of this type of life appears to be the ability to inhabit niches otherwise not available, e.g. Hydractinia kaffiraria in the mud of estuaries and H. altispina in sandy tidal pools, where the hydranths are not only provided with transport but are held clear of the substratum. A list of hosts carrying epizoites will be found on p. 23.

KEY TO GENERA

[Genera not represented in South Africa are bracketed]

1. Hydrocoriza with calcareous skeleton .... Hydrocoriza p. 115
   - Hydrocoriza without calcium in the skeleton 2

2. Gastrozooids with several whorls of tentacles .... Clavactinia p. 106
   - Gastrozooids with only one whorl of tentacles, which may be displaced alternately to form two apparent whors 3

3. Gonoozooids producing free medusae .... [Podocoryne]
   - Gonoozooids producing fixed sporosacs 4

4. Hydrocoriza covered with a layer of naked coenosarc .... Hydractinia p. 108
   - Hydrocoriza reticular, the tubes covered with firm perisarc; no naked coenosarc Stylactis p. 118

Genus Clavactinia Thornely, 1904

Diagnosis. Hydrocoriza of anastomosing perisarc-covered tubes coalesced into a basal incrusting layer and covered by a layer of naked coenosarc, often bearing spines. Gastrozooids with several close-set whorls of tentacles. Gonophores in the form of fixed sporosacs.

Type species: Clavactinia gallensis Thornely, 1904.

One species only from South Africa.

Clavactinia multitentaculata sp. nov.

Fig. 35C–G


Holotype. A male colony growing on the shell of the gastropod Melapium
lineatum (Lamarck) occupied by a hermit, Dardanus arrosor (Herbst). Off Natal, approximately 29°54'S/31°11'E, 99 m. Cat. no. SAM–H389.

Description of holotype. Hydrorhiza a network of coalesced perisarcal tubes covered by a layer of free coenosarc, giving rise to numerous smooth, hollow spines 0.4–0.6 mm in length.

Gastrozoooids with many tentacles in several close-set verticils. The number of tentacles varies according to the size (and presumably the age) of the gastrozoooids. In the larger polyps they are almost impossible to count. Counts made by cutting off the tentacles and counting the tips yielded numbers of 65, 84 and 91. More approximate counts gave numbers ranging from 42+ to 73. The normal adult number is thus well over 40. Larger gastrozoooids are longitudinally marked, shown by sections to be due to ridging of the endoderm.

A few spiral zooids present in local areas around the opening of the host shell.

Male gonozooids smaller and more slender than gastrozoooids, with mouth and 7–13 tentacles, bearing 3–4 gonophores in the form of fixed sporosacces. Sections show no endodermal ridging. Sporosac spherical, reaching 0.66 mm in length and 0.68 mm in diameter, with four radial canals and a circular canal. Spadix central. Spermatogenic cells divided into four compartments alternating with the radial canals. Sections reveal the presence of a thickened and intumous 'umbrella' margin and a depressed velar plate. The largest sporosacs are so swollen with spermatogenic cells that the cavities of the spadix and the radial canals are not visible. These structures are, however, quite distinct in the younger ones.

Information from other specimens. Colonies other than the holotype have been found on the gastropods Astraea tayloriana (Smith) and Turbo sarmaticus Linnaeus.

Female gonozooids are similar to the male, though with only 5–8 tentacles. Each bears two sporosacs, one large and one small, at about two-thirds of its length. Sporosac spherical, the largest reaching 0.70 mm in length and 0.68 mm in diameter, though possibly not quite mature, with four radial canals and a circular canal and four minute tubercles at margin. Spadix central, with a quadrate lumen, bearing a single layer of eggs arranged in four compartments alternating with the radial canals. Eggs small and numerous, estimated to be about 300 in number (about 20 longitudinal rows with about 15 to a row). This colony with no tuberculate zooids, but with a few scattered tentaculozooids. Spines not so numerous as in the holotype.

A living male colony showed that mature gastrozoooids reach 8.0 mm when fully extended; young hydranths have only one whorl of tentacles but the number increases with age. Extended gonozooids reach a maximum length of 3.2 mm; those with young gonophores have as many as 16 tentacles, but those with mature gonophores often have only one or two or none at all, apparently due to reproductive exhaustion.
Nematocysts of two kinds:
(i) Desmonemes, $5.4 \times 3.0 - 7.2 \times 3.6 \mu$. Capsule oval; abundant on tentacles.
   Thread in four coils when discharged.
(ii) Microbasic eurytelas, $9.0 \times 2.4 - 13.8 \times 4.2 \mu$. Capsule banana-shaped;
   abundant on hypostome.

Colour: orange throughout.

Remarks. *C. multitentaculata* differs from *C. gallensis*, the type species of
*Clavactinia*, in the larger size of the gastrozooids and greater number of tentacles,
in the presence of radial canals in the sporosacs and in the greater number of
eggs in the female sporosac.

*Distribution*. Endemic to South Africa.

*Distribution in South Africa*. False Bay and Natal only with certainty, in 15–99 m,
but probably more widespread. 34/18 (s), 29/31 (s)

Genus *Hydractinia* van Beneden, 1841

*Diagnosis*. Hydrorhiza of anastomosing perisarc-covered tubes coalesced into a
basal incrusting layer and covered by a layer of naked coenosarc, often bearing
spines. Gastrozooids with tentacles in one whorl (or rarely two closely alternating
whorls). Gonophores in the form of fixed sporosacs.

Type species: *Hydractinia lāctea* van Beneden. 1844.

**KEY TO SPECIES**

(Doubtful species not included, for these see p. 115)

1. Spines present, smooth
   - Spines absent

2. On *Thais squamosa*. Spines reaching 1 mm. Sporosacs without tentacles, male divided
   into 4 compartments, female with about 32 eggs in about 4 tiers
   - On hermit shells. Spines reaching 0.6 mm. Sporosacs without tentacles, male not
     divided, female with 5–13 eggs in 2 tiers
   - On *Nassa speciosa*. Spines reaching 0.4 mm. Sporosacs with 4–8 marginal tentacles and
     external marsupium, male divided into 4 compartments, female with 20–40 eggs in
     3–6 tiers

3. On *Nassa kraussiana*. Gastrozooids normal. Female sporosacs with 21–32 eggs in about
   4 tiers
   - On weed. Gastrozooid mouth blocked by endoderm. Female sporosacs with over 50
     eggs in about 7 tiers

*Hydractinia altispina* Millard, 1955

Frontispiece; Fig. 36A–D

*Hydractinia* sp. Broch, 1914: 24 (material from South West Africa).

*Diagnosis*. Colonies epizootic on the gastropod *Thais squamosa* (Lamarck). Hydrorhiza
covered with a layer of naked coenosarc, bearing spines, gastrozooids and gonozoooids. Spines smooth, hollow and long, 0.4–1 mm. Gastro-
zoooids reaching 4 mm, with 5–12 tentacles, long and short alternating. Gono-
zooids much smaller than gastrozooids, reaching 0.8 mm, with 3–5 very short
tentacles, bearing several sporosacs usually on the basal region. No dactylo-
zooids.

Sporosacs with four radial canals and a circular canal, but no marginal
tentacles, bearing the sexual products around a central spadix, male and female
on separate colonies. Male spherical, reaching 0.4 mm in diameter, with sperma-
togenetic cells divided into four compartments separated by the radial canals.
Female oval, reaching 0.5 mm in diameter, containing about 32 eggs in about
four tiers.

Colour: Colony orange throughout, gastrozooids sometimes paler.

Nematocysts: desmonemes, 6.0 x 3.6 μ; microbasic euryteles, 8.4 x 2.4 —
13.8 x 5.4 μ.

Distribution. Endemic to South Africa. Type localities: False Bay and Lambert’s
Bay.

Distribution in South Africa. Lüderitz Bay to False Bay, littoral to 24 m. 26/15
(l), 28/16 (s), 32/18 (l, s), 33/18 (l), 34/18 (l, s)

Hydractinia canalisfera Millard, 1957

Fig. 36E–G

Hydractinia canalisfera Millard, 1957: 179, fig. 1.

Diagnosis. Colony growing on weed. Hydrorhiza covered with a layer of naked
coenosarc in centre of colony, of separate perisarc-covered tubes at periphery,
bearing gastrozooids, gonozooids and tentaculozooids, but no spines. Gastro-
zooid reaching 3.2 mm, with 10–14 tentacles, with mouth and hypostome plug-
ged with endodermal tissue; hydrocalus with a strongly marked, narrow,
central lumen. Gonozooid smaller than gastrozooid, reaching 1.3 mm, with
6–9 tentacles, bearing 4–5 sporosacs on upper half of hydrocalus. Tentaculo-
zooids sparse, scattered.

Female sporosac ovoid, reaching 0.5 mm in diameter, with four radial
canals and a circular canal (visible only when young), no tentacle rudiments,
containing over 50 eggs in about seven tiers around a central spadix. Male
sporosac unknown.

Distribution. Endemic to South Africa.

Distribution in South Africa. Known only from the type locality: Clovelly,
False Bay, littoral. 34/18 (l)

Hydractinia diogenes Millard, 1959

Fig. 37A–D


Diagnosis. Colonies epizoic on shells of the hermit, Diogenes costatus (Fabr.).
Hydrorhiza covered with a layer of naked coenosarc, bearing spines, gastro-
Fig. 36.

*Hydractinia altispina.* A, various zooids: two gastrozooids, two female gonozooids, one male gonozooid and two spines; B, microbasic eurytele and desmoneme; C, t.s. male sporosac; D, l.s. female sporosac.

*Hydractinia canalicera.* E, part of colony, with two gastrozooids, two female gonozooids and a tentaculozooid; F, l.s. young female sporosac showing radial and circular canals; G, l.s. mature female sporosac.

Scale: A in mm, B in mm/100, the rest in mm/10.
zoooids, gonozooids and spiral zoooids. Spines smooth, hollow and of medium length (0.5–0.6 mm). Gastrozooids 2–3 mm in length, with 10–26 tentacles. Gonozooids generally smaller than gastrozooids, with 5–15 tentacles often reduced to mere stumps, bearing a ring of up to six sporasacs. Spiral zoooids sometimes present, 2–3 mm in length, with terminal battery of nematocysts.

Sporasacs spherical, reaching 0.5 mm in length and breadth, male and female on different colonies, with four radial canals (but visible in female only) and a circular canal, bearing the sexual products around a central spadix. Female containing 5–13 eggs in two tiers. Male not divided into segments.

Nematocysts: desmonemes, 5,0 × 3,5 μ; microbasic euryteles, 9,0 × 4,0 μ.

**Distribution.** Endemic to South Africa.

**Distribution in South Africa.** East coast, Inhaca to Morrumbene (type locality), in shallow water. 26/32 (s), 23/35 (s)

**Hydractinia kaffraria** Millard, 1955

*Fig. 37E–G*


**Diagnosis.** Colonies epizootic on the gastropod *Nassa kraussiana* (Dunker). Hydrorhiza covered with a layer of naked coenosarc, bearing gastrozooids, gonozooids and tentaculozooids, but no spines. Gastrozooid reaching 2.0 mm, with 8–15 tentacles. Gonozooid smaller than gastrozooid, reaching 1.1 mm, with 5–12 tentacles, bearing sporasacs below the tentacles. Tentaculozooids sparse and scattered, reaching 3.0 mm.

Sporasacs subspherical, with four radial canals and a circular canal, with rudimentary marginal tentacles, bearing the sexual products around a central spadix, male and female on separate colonies. Male reaching 0.6 mm in diameter, spermatogenic cells not divided into compartments. Female reaching 0.9 mm in diameter, containing 21–32 eggs in about four tiers.

**Observations on living material.** Although the sporasacs have some medusoid structures, the sexual products are released while they are still attached and there is no free-swimming life. Powerful pulsations of the whole bell in the male, and of the area around the aperture in the female, expel the spermatozoa and eggs respectively. This species is easily kept in aquarium tanks.

**Distribution outside South Africa.** Red Sea. Type localities: Breede River and Keiskama River estuaries, South Africa.

**Distribution in South Africa.** In estuaries only, from the Breede River on the south coast to Durban Bay in Natal. 34/20 (s), 34/23 (s), 33/25 (s), 33/26 (s), 33/27 (s), 29/31 (s)
Hydractinia diagens. A, part of female colony; B, t.s. female sporosac showing radial canals; C, l.s. female sporosac showing circular canal; D, l.s. ripe male sporosac.

Hydractinia kaffiraria. E, l.s. young female sporosac; F, l.s. male sporosac; G, part of colony with gastrozoid, tentaculozooid and female gonozooid.

Scale in mm/10.
**Hydractinia marsupialia** sp. nov.

Fig. 38


**Holotype.** A female colony on *Nassa speciosa* from Table Bay. Cat. no. SAM–H1854.

**Paratypes.** Nine other colonies, including both male and female, on the same host and from the same locality. Cat. no. SAM–H1855.

**Description of type series.** Colonies epizootic on the gastropod *Nassa speciosa* Adams. Hydrorhiza a network of perisarc-covered tubes which is open in young colonies but in older ones is coalesced to form an incrustation covered with a layer of naked coenosarc; bearing spines, gastrozooids and gonozooids.

- Spines smooth and short, reaching a maximum height of 0.4 mm, but more often only 0.2 mm or less; occasionally absent, especially in young colonies.
- Gastrozooids reaching a maximum height of 1.9 mm (preserved), with 8–16 tentacles, with no perisarcal collar.
- Gonozooids smaller than gastrozooids, reaching a maximum height of 0.8 mm (preserved), with 5–9 tentacles, bearing a circle of up to six gonophores. Gonophores round or oval, reaching a maximum length of 0.7 mm and a maximum diameter of 0.6 mm, with 4–8 marginal tentacles reaching 0.18 mm in length, each with a pigmented spot at base, with four radial canals and a circular canal. Sexual products discharged into, and retained for a while within, a marsupium formed by the perisarcal coating of the gonophore. Medusoid remaining attached after evacuation of sexual products from marsupium. Female with 20–40 eggs arranged in 3–6 tiers. Male with four groups of spermatogenic cells alternating with the radial canals.
- Colour: creamy white, marginal bulbs of medusoids dark red.
- Nematocysts of two kinds:
  - (i) Long-oval capsules, 7.2 × 2.7 – 10.2 × 3.6 μ.
  - (ii) Short-oval capsules, 5.4 × 3.0 μ.

**Histology.** Sections through a mature male medusoid with the spermatogenic cells extruded into the marsupium show several interesting features. The ectoderm lining the subumbrellar cavity (entocodon) is thickened and contains branching mesogloea lamellae bearing muscle fibres. The latter are presumably used to expel the sexual products and are similar to those found in the Myriothelidae. This whole layer is much thinner before extrusion when it is stretched by the bulging gonads and the lamellae are then scarcely recognizable. The stomach is well developed and quadrangular; during extrusion the tip of the hypostome is squeezed out into the marsupium and its cavity closed by pressure in the region of the bell margin. Remains of the ruptured velum are clearly visible.
Fig. 38.

*Hydractinia marsupialia* sp. nov. A, Male colony from holotype; B, l.s. ripe male sporosac compiled from sections and whole mounts and passing through a radial canal on left; C, ripe male sporosac; D, ripe male sporosac with spermatogenic cells extruding into marsupium; E, spent male sporosac; F, ripe female sporosac from paratype.

Abbreviations: c: capsule; cc: circular canal; ec: ectoderm with muscle layer; en: endoderm; g: gonad; m: marsupium; rc: radial canal; t: tentacle; v: remains of velum.

Scale in mm/10.
The structure of the female gonophore is similar, but no stages with eggs extruded into the marsupium occur. In the oldest specimens the velum is ruptured and the tentacles extended into the marsupial cavity. The eggs are arranged in four groups although these are not so clearly demarcated as in the male. The muscle layer of the entocodon is clearly visible in young gonophores but stretched and thin in older ones.

**Remarks.** This species was previously ascribed to *Podocoryne carnea* (Millard 1957, 1966a) when gonophores full of sexual products and young medusae without gonads were found on the same colony. From a further study it is now clear that the medusoids with free tentacles are individuals which have released their sexual products but have remained attached to the gonozooid. There is thus no evidence that the medusae are freed, and the material must be removed from the genus *Podocoryne*.

The condition is similar to that described for *Hydractinia proboscidea* (Hincks 1868) where also the sexual products are extruded and held temporarily within the perisarcal covering. *H. proboscidea* differs in the absence of spines and lack of differentiation between gonozooids and gastrozooids.

**Distribution.** Endemic to South Africa.

**Distribution in South Africa.** Saldanha Bay to Algoa Bay, 4–82 m. ?Inhaca. Type locality: Table Bay. 33/17 (s), 33/18 (s), 34/18 (s), 34/21 (s), 34/22 (s), 34/23 (s), 33/25 (s), 33/26 (s), 34/25 (s), ?26/32 (s)

Doubtful species

*Hydractinia pacifica* Hartlaub, 1905

*Hydractinia pacifica*: Stechow, 1925a: 408.

**Remarks.** Stechow records this species from Algoa Bay. However, his colony was male, and the distinctive features of *H. pacifica* rest in the female sporosac, which has only one egg surrounded by a branching spadix. No *Hydractinia* with such female sporosacs has been recorded from South Africa and Stechow’s record should be dropped from the literature.

The host snail (*Phos plicosus*—*Nassa speciosa*) and the number of tentacles in gastrozooid and gonozooid suggest that Stechow’s material was a spineless variety of *Hydractinia marsupialis*.

Genus *Hydrocorella* Stechow, 1921

*Diagnosis.*** Hydrorhiza with a calcareous skeleton developing small spines and large pillar-shaped processes, covered by a layer of naked coenosarc. Gastrozooids with one whorl of tentacles. Gonophores in the form of fixed sporosacs.

Type species: *Hydrocorella africana* Stechow, 1921.

One species only from South Africa.
Hydrocorella africana Stechow, 1921

Frontispiece; Fig. 39


*Diagnosis.* Colonies epizootic on shells of gastropods and hermits. Hydrorhiza secreting a calcareous skeleton which is covered by a layer of naked coenosarc bearing gastrozooids, gonozooids and tentaculozooids. Skeleton produced into conspicuous longitudinally ridged processes of two grades: the larger reaching 5 mm or more and bearing hydranths on the surface, the smaller 0.5–1.0 mm.

Gastrozooids reaching 3 mm in length when expanded, with 5–12 tentacles, of which one or two are usually much longer than the others. Tentaculozooids situated round shell aperture, with terminal battery of nematocysts, not always present. Gonozooids reduced, about 0.5 mm in length, with about six rudimentary tentacles, bearing several sporosacs.

Sporosacs spherical, with no radial or circular canals and no tentacles, male and female on separate colonies. Male reaching 0.3 mm in diameter, bearing the sexual products around a central spadix. Female reaching 0.6 mm in diameter, bearing a single egg which is later surrounded by hollow outgrowths from the short, basal spadix. Planula gourd-shaped, developing *in situ*.

Colour: skeleton chalky white, hydранths creamy white to pale orange, sporosacs orange.

Nematocysts of two kinds:

(i) Microbasic euryteles, $7.2 \times 2.7 - 11.4 \times 4.8 \mu$.

(ii) Desmonemes, $4.5 \times 2.4 - 6.6 \times 3.0 \mu$.

Variation. Although there is much variation in the shape and size of the skeletal processes, the species is easily recognized by the chalky white skeleton. In young colonies only the small processes are present and the colony is low, spreading and *Hydractinia*-like in appearance. Later the skeleton becomes thicker and the larger processes develop, giving a grotesque appearance to the whole. There may be as many as six large processes on one host, and they often show a tendency to project forwards over the mouth of the shell in the line of movement of the host. The processes are usually longitudinally ridged and star-shaped in section, but there may be fusion between two or more, compression in one plane or other irregularities. In old colonies the smaller processes may form compressed and curved plate-like structures arching over the gonozooids and the developing planulae. The latter are thus imprisoned until they become free from the gonozooids and able to escape by amoeboid movements.

The presence of one or two extra long tentacles on the gastrozooid is very typical. The tentacles usually arise in one whorl, but sometimes one or more appear to arise at a lower level than the rest.

There seems to be no specificity in the choice of host, and a considerable number of host gastropods and hermits has been recorded (see p. 23). Often the host is so overgrown that it is impossible to identify it.
**Hydrocorrella africana.** A, colony completely covering shell of hermit; B, section through colony and host shell showing calcareous processes and contracted hydranths; C, gastrozooids; D, gonozoooids, two female and one male; E, planula; F, t.s. female sporoascs of different ages; G, l.s. female gonozoooid and sporoascs; H, nematocysts, from left to right: microbasic euptyele discharged and undischarged, desmoneme.

Scale: A, B and C in mm, H in mm/100, the rest in mm/10.
Distribution. Endemic to South Africa. Type locality: 'South Africa'.

Distribution in South Africa. Orange River mouth to Durban, littoral to 500 m. Common in shallow dredgings round the south-west Cape. 28/16 (s), 30/17 (l), 32/17 (s), 33/17 (s), 33/18 (l, s), 34/18 (s), 34/19 (s), 35/19 (s), 34/20 (s), 35/20 (s), 34/21 (s), 34/22 (d), 34/23 (d), 35/23 (vd), 34/24 (d), 29/31 (s)

Genus *Stylactis* Allman, 1864


Diagnosis. Hydrorhiza of anastomosing perisarc-covered tubes which may bear spines. No superficial layer of naked coenosarc. Gastrozooids with tentacles in one whorl (or rarely two closely alternating whorls). Gonophores in the form of fixed sporosacs, borne on blastostyles.

Type species: *Stylactis inermis* Allman, 1872.

One doubtful species from South Africa

Doubtful species

*?Stylactis siphonis* (Stechow, 1921)

*Stylactella siphonis* Stechow, 1921b: 224.

*Halerella siphonis*: Stechow, 1925a: 407, fig. 2.

Diagnosis. Colonies epizootic in the siphon of a gastropod. No spines. Gastrozooids reaching 0.8 mm, with a broad base and 8–10 tentacles. Reproduction unknown.

Remarks. Stechow reported this species from 500 m, south of Plettenberg Bay. It has not been rediscovered, and Stechow's description is so brief that the systematic position is in doubt. Examination of a whole mount from Stechow's collection has added nothing further to our knowledge. Stechow records the host gastropod as *Sipho islandicus*, but this species is not known in South African waters.

Family *Cytaeidae*

Diagnosis. Colonial hydroids with a stolonic habit but no polymorphism. Hydrorhiza of anastomosing perisarc-covered stolons which are not incrusted and are without spines. Hydranth sessile and naked, but often with a cup-shaped collar of perisarc around base, with one whorl of filiform tentacles and a conical hypostome. Gonophores borne directly on the hydrorhiza, in the form of fixed sporosacs or medusae.

Medusa, when present, deep bell-shaped, with simple mouth, four solid marginal tentacles, unbranched oral tentacles on mouth-rim and four unbranched radial canals; without ocelli; gonads interradial or forming a continuous ring.

Introduction. This is a small family created originally for the medusa genus *Cytaeois*. The hydranth generation was unknown until 1931, but since then several life histories have been worked out. The family has been revised and/or discussed by Kramp (1932), Rees (1956b, 1962) and Uchida (1964).
The hydranth generation is very similar to that of the Hydractiniidae and, as in this family, shows a preference for an epizootic life on gastropod shells. However, unlike the Hydractiniidae, the hydrorhizal tubes do not coalesce and become incrusted, spines never occur and there is no polymorphism. A collar or vase-like tube of perisarc typically surrounds the base of the otherwise naked hydranth, and this does not occur in the Hydractiniidae. As in some species of Hydractinia alternate tentacles of the hydranth may be displaced, giving the appearance of two closely alternating whorls.

One of the most distinctive features of the family is the fact that the gonophores are borne direct on the hydrorhiza and not on hydranths or on gonozooids. These may develop into free-swimming medusae in Cytaeis or may remain attached as sporosacs or degenerate medusae in Perarella, a genus which was re-established by Rees (1956b).

The adult medusa is of simple construction and shows resemblances to that of the Hydractiniidae and the Bougainvilliidae. It differs from the Hydractiniidae in the better defined oral tentacles, and from the Bougainvilliidae by the insertion of the oral tentacles on the mouth-rim rather than just above it. Uchida (1964) considers that the Bougainvilliidae could have arisen from the Cytaeidae by the branching of the oral tentacles and the increase in number and clustering of the marginal tentacles.

In the type species of Cytaeis, C. tetrastylo, Kramp (1959) has reported the budding-off of hydranths from the stomach wall of the medusa. The further history of these buds is unknown, nor is it established whether there is any fixed hydranth stage.

KEY TO GENERA

[Genera not represented in South Africa are bracketed]

1. Producing free medusae
   - Producing fixed sporosacs

   Cytaeis p. 119
   [Perarella]

Genus Cytaeis Eschscholtz, 1829

Diagnosis. Gonophores developing into free medusae. Adult medusa with characters of family.

Type species: Cytaeis tetrastylo Eschscholtz, 1829.

One hydranth species only from South Africa.

Cytaeis nassa (Millard, 1959)

Fig. 40

Podocoryne nassa Millard, 1959a: 307, fig. 3.

Diagnosis. Colony epizootic on shells of gastropods of the genus Nassa. Hydrorhiza reticular, following the grooves of the host shell. Hydranths columnar,
Cystaeis nassa. A, colony on host shell; B–D, stages in development of medusa-bud.
Scale in mm/10.
widest near base but narrowed at origin from hydrorhiza, reaching a maximum height of 2.5 mm, with conical hypostome and 8–16 tentacles in two closely alternating whorls, often surrounded at base by a cup-like expansion of perisarc.

Gonophore arising separately from hydrorhiza on slender pedicel, pear-shaped when young, globular when mature, completely enveloped by membranous perisarc. Medusa at liberation deep bell-shaped, reaching 0.5 mm in depth, with four radial canals, four perradial marginal bulbs bearing tentacles, tubular hypostome with four oral tentacles armed with distal nematocyst clusters. Adult medusa unknown.

Nematocysts of two types: heteronemes, 8,1 × 3,1 μ, and ?desmonemes, 6,3 × 3,6 μ.

Distribution outside South Africa. Red Sea (on Nassa arcularia and N. fenestrata), Madagascar (on N. arcularia and N. albscens), Seychelles, Mauritius.

Distribution in South Africa. Inhaca Island, Moçambique (type locality), littoral, on N. fenestrata and N. coronata. 26/32 (I), 25/32

Family Pandeidae

Diagnosis. Colonial hydroids with a stolonial habit. Hydranths with one whorl of filiform tentacles or with tentacles absent. Perisarc of variable development or completely absent. Producing free medusae.

Adult medusa without oral tentacles but with four simple or crenulated oral lips, four radial canals, hollow marginal tentacles, with or without ocelli.

Introduction. The Pandeidae is an important medusa family in which the hydranth generation is usually inconspicuous, has little to distinguish it from several other families and has practically no diagnostic characters. In many species the hydranth is still unknown. Among those which are known Leuckartiara and Hydrichtythus are fairly easily recognized; others must be reared to the medusa stage for identification to genus or even family level.

So far as is known the hydroid generation is always stolonial, with hydranths rarely branching once or twice only.

The hydrorhiza is usually reticular and covered by perisarc, but in the aberrant parasitic genus Hydrichtythus the hydrorhiza is expanded and plate-like, capable of eroding the flesh of the host, and is reminiscent of the naked coenosarc encountered in the Hydractiniiidae.

The degree of development of perisarc varies considerably. It is entirely absent in Hydrichtythus, and limited to the hydrorhizal tubes in Pandeia conica. In both these genera the hydranth is sessile. In Amphinema and Leuckartiara the hydranth is borne on the summit of a distinct hydrocaulus. In Amphinema the perisarc continues on to the hydrocaulus and terminates below the hydranth body. In Leuckartiara it continues over the base of the hydranth as well, where it forms a swollen and gelatinous pseudohydrotheca similar to that found in
some Bougainvilliiidae. In *Hydrichthys* the hydranths are devoid of tentacles, apparently a secondary condition associated with the parasitic mode of life.

The adult medusa is characterized by its four-lipped mouth without oral tentacles but usually with elaborately folded margins, and by its large and usually laterally compressed marginal bulbs. Unlike the Bougainvilliiidae the marginal tentacles are hollow.

Both medusa and hydranth generations show much diversity and, as suggested by Uchida (1964), the family will undoubtedly need subdivision once the life-histories are better known.

**KEY TO GENERA**

[Genera in which the hydranth generation is unknown in South Africa are bracketed.]

1. Hydranth generation parasitic on fish, without tentacles  .... *Hydrichthys* p. 122
   - Hydranth generation not parasitic, but often epizootic on gastropods and other hosts. Tentacles present ............ 2
   - Perisarc continued over base of hydranth as a pseudohydrotheca  *Leuckartiara* p. 123
   - Perisarc not covering hydranth  ....... ....... ....... 3
2. Hydranths sessile, with no distinct hydrocaulus ....... ....... ....... .......  *Pandea*
   - Hydrocaulus well developed, longer than hydranth ....... ....... ....... ....... *Amphinema*

**Genus Hydrichthys** Fewkes, 1888

*Diagnosis.* Colony parasitic on fish. Hydrorhiza expanding to form a plate-like layer without covering perisarc and, in at least some species, capable of eroding the underlying fish tissue. Hydranths without tentacles. Gonophores developing into free medusae with two opposite marginal tentacles at liberation, two or four at a later stage. Adult medusa unknown.

Type species: *Hydrichthys mirus* Fewkes, 1888.

One species only from South Africa

*Hydrichthys boycei* Warren, 1916

Fig. 41E–H


*Diagnosis.* Colony parasitic on fish of the species *Ambassis safgha* (Forskål) (syn. *A. natalensis*), *Chaetodon lunula* (Lacépède), and *Mugil* sp.

Hydranth without tentacles, naked, reaching 2.5 mm in height, with a band of nematocysts around mouth. Medusa-buds borne on hydrorhiza and on hydranth in clusters, the hydranth when fully developed becoming very large and often branched.

Medusa at liberation with four radial canals and a circular canal, a quadrirhedral mouth and two massive and opposite marginal bulbs. No ocelli. Slightly older medusa with two very long marginal tentacles.

Colour: reddish.

Nematocysts of one type only, possibly stenoteles, 9.1 × 3.6 μ.
Remarks. In this species the lower surface of the hydrorhiza is capable of eroding the tissues of the host and can send haustorium-like outgrowths into the flesh. The hydranths can then apply their open mouths to the damaged surface and tap the blood vessels.

Warren distinguished between normal feeding hydranths and ‘gonostyles’ bearing medusae, some of the gonostyles being very large and fleshy and apparently without a hypostome. In my material there is no essential difference between the infertile and fertile hydranths. The medusa-buds develop on the body of the hydranth and gradually increase in number, the attachments of the clusters becoming drawn out as lateral branches. At the same time the hydranth increases in size and girth. In this sample at any rate the hypostome is always retained though often obscured by the wealth of medusa-buds. It is possible that it may atrophy in older individuals.

The genus *Hydrichthys* is included in the Pandeidae on the structure of the young medusa, although no adult medusae with ripe gonads are known.

**Distribution.** Endemic to South Africa. Type locality: Durban Bay.

**Distribution in South Africa.** Durban area only. 29/31

Genus *Leuckartiara* Hartlaub, 1914

**Diagnosis.** Colony stolonial. Hydrorhiza reticular. Stem unbranched or sparingly branched, unfascicled, covered with perisarc which extends as a gelatinous pseudohydrotheca over the base of the hydranth, but does not invest the bases of the tentacles. Hydranth with one whorl of filiform tentacles and a conical hypostome. Gonophores borne on stem or hydrorhiza, completely invested in perisarc, developing into free medusae.

Medusa with apical process; with large stomach attached to radial canals by ‘mesenteries’; mouth with much-folded or crenulated lips; gonads interradial, horseshoe-shaped, with folds directed perradially; radial canals broad and ribbon-like, often with jagged edges; with numerous marginal tentacles with elongated laterally compressed marginal bulbs; often with rudimentary tentacles.

Type species: *Geryonia octona* Fleming, 1823.

One hydranth species only from South Africa.

*Leuckartiara octona* (Fleming, 1823)

**Fig. 41A–D**

*Geryonia octona* Fleming, 1823: 298.

*Perigonimus vestitus* f. *radiens* Vanhöffen, 1910: 286, fig. 11.


**Diagnosis.** Colonies epizootic on the shells of gastropods, reaching a maximum height of 5 mm. Stem increasing in diameter from base to distal end, bearing a terminal hydranth and occasionally 1–3 lateral ones as well. Perisarc firm.
**Fig. 41.**

*Leuckartiara octona.* A, hydramths bearing medusa-buds; B–D, medusa-buds of different ages.  
*Hydrichthys boycei.* E and F, medusa-buds at liberation, redrawn from Warren (1916)  
G, various zooids from colony; H, older medusa, redrawn from Warren (1916).  
Scale in mm/10.
often annulated or wrinkled, especially at base, expanding to form a gelatinous pseudohydrotheca over base of hydranth, usually covered with adherent silt. Hydranth with 6–12 tentacles.

Medusa-buds pedicellate, completely invested in perisarc, oval, reaching a diameter of 0.45 mm. Newly released medusa with two opposite marginal tentacles.

Adult medusa reaching 20 mm in depth, with conical or spherical apical process, ‘mesenteries’ extending about halfway along stomach, 12–24 marginal tentacles, each with abaxial spur, 16 or more club-shaped rudimentary tentacles. Ocelli present.

Variation. The usual host for this species is Bullia annulata (Lamarck), but it also occurs on Nassia speciosa Adams and N. analogica Sowerby and probably on other gastropods as well. Vanhöffen reports it (as Perigonimus vestitus) from a crab, Halicarcinus sp.

The form of the colony varies according to the position on the host shell and the amount of friction to which it is subject. On the underside hydranths are small and the stems low (about 1 mm) and thus protected to some extent in the grooves of the shell. In this position the colony seldom produces gonophores and sometimes only the hydrorhiza occurs. On the upper surface of the shell and round the tip of the spire hydranths are larger and stems taller and often branched, reaching 5 mm. Here abundant medusa-buds are produced on the stem, several to each, and rarely on the hydrorhiza.

Distribution. Cosmopolitan. Type locality: Bell Rock, Scotland.

Distribution in South Africa. False Bay to Algoa Bay in 3–82 m. Medusae from Natal and Moçambique in 100–300 m. Hydranths: 34/18 (s), 34/23 (s), 34/25 (s), 33/25 (s), 33/26 (s). Medusae: 31/30 (d), 29/32 (d), 25/36 (d).

SUBORDER THECATA

Diagnosis. Hydranth with a definite hydrotheca of definite shape; with one whorl of filiform tentacles. Gonophores enclosed in gonothece; in the form of fixed sporosacs or free medusae. Medusa usually flattened or hemispherical; with gonads on radial canals but sometimes contiguous with stomach; marginal sense organs usually present, in the form of cordyli, ectodermal statocysts or, occasionally, ocelli.

KEY TO FAMILIES

1. Hydrotheca with operculum
   - Hydrotheca without operculum

2. Hydrotheca bilaterally symmetrical, usually with marginal teeth. Gastral endoderm differentiated .......................... Sertulariidae .......................... p. 239
   - Hydrotheca radially symmetrical, never with true marginal teeth. Gastral endoderm undifferentiated .......................... Campanulinidae .......................... p. 126
3. Hydrotheca saucer- or basin-shaped, usually too small to contain contracted hydranth.  
   - Hydrotheca usually deep enough to contain contracted hydranth.  
   HALECIDAE  
   p. 141  
4. Hydrotheca always restricted to one side of stem or branches. Nematophores 
   present and with regular arrangement, usually 3 or 5 to each hydrotheca.  
   PLUMULARIIDAE  
   p. 325  
   - Hydrotheca on two or more sides of stem or branches. Nematophores, if 
   present, seldom regularly arranged  
   5  
5. Hypostome trumpet-shaped. Hydrotheca always pedicellate, usually campanu-
   late and radially symmetrical. Margin toothed or untoothed CAMPANULARIIDAE  
   p. 200  
   - Hypostome conical. Hydrotheca pedicellate or sessile, of varying shape, radially 
   or bilaterally symmetrical. Margin always untoothed  
   6  
6. Hydrotheca with a definite floor, always sessile and bilaterally symmetrical.  
   No nematothecae  
   SYNTHECIDAE  
   p. 230  
   - Hydrotheca with no definite floor, with or without diaphragm, diaphragm 
   when present always delicate. Hydrotheca pedicellate or sessile, bilaterally or 
   radially symmetrical. Nematothecae present or absent  
   LAFOIDEA  
   p. 166  

Family Campanulinidae

*Diagnosis.* Small thecate hydroids with stolonal colonies or sympodially 
branched stems. Hydrotheca deep and usually cylindrical, with untoothed 
margin, with a conical or roof-shaped operculum of converging segments which 
may or may not be sharply demarcated from margin, with or without a dia-
phragm. Hydranth slender and extensile, completely retractable into hydrotheca, 
with conical hypostome, with or without an intertentacular web. Nematophores 
present or absent. Gonophores in the form of fixed sporosacs or free medusae.

*Introduction.* With the exception of a few authors in recent years polyp systema-
tists have grouped together all operculate hydroids other than the Sertulariidae 
in the family Campanulinidae. These forms are mostly minute and inconspicuous 
and show a certain uniformity in structure. Some of them produce fixed sporo-
sacs and others medusae, and in the latter the medusa is obviously the dominant 
generation and its evolution has outpaced that of the polyp.

Medusa systematists, on the other hand, have independently grouped the 
medusae among several different families, so that two completely different 
systems of classification have arisen. Attempts to combine the two classifica-
tions into one have not so far been successful, due to the fact that the polyp 
generation is still unknown for the majority of medusa species. Recent work on 
life-histories has produced anomalous situations; for instance, two very similar 
polyp species may produce medusae belonging to different families, e.g. *Cuspi-
della* produces medusae of the families Laodiceidae and Mitrocomidae; or polyps 
of one medusa family may differ in structure, e.g. *Euchelota* and *Lovenella* in the 
Lovenellidae.

Rees (1939) felt that the medusa families should be used where possible, 
transferring the polyps to them as the life-histories become known. However, 
it is evident that the medusa families may also need revision. For instance, the 
Lovenellidae are distinguished from the Phialellidae mainly by the presence of cirri 
in the former, and Uchida (1964), in discussing the relationships of the polyp genus
Eugynnanthea, where some species produce Lovenellid medusae and another a Phialellid medusa, remarked that 'the cirri seem not to be very important'.

For a polyp systematist the only practical solution is to retain the family Campanuliniidae until such time that a better knowledge of both generations will permit a critical reassessment of the whole group. A key to the currently used medusa families based on the works of Kramp and Russell is, however, appended to this section.

At the generic level, genera must be diagnosed primarily on the characters of the type species, and where this is known for one generation only, the generic name may have to be changed in the future. At present the medusa cannot be deduced from the polyp or the polyp from the medusa.

Rees (1939) revised the genus Campanulina, retaining it solely for the type species C. tenuis.

The polyp generation is generally minute and, unless specially reared, is often encountered only in an epizootic or epiphytic habitat. The colony may be stolonial, or it may produce upright stems which branch sympodially a few times. Very rarely the stem is fascicled, when the sympodial character may be largely obscured. The perisarc of the stem is usually firm, and annulated to a varying degree.

The hydrotheca may be sessile, as in Lafaecina, but is more often pedicellate, with a distinct, though sometimes very short, pedicel. The hydrotheca may merge gradually into the pedicel, or be clearly demarcated from it by a well-marked floor. In the aberrant genus Lineolaria the hydrothecae are adherent to the algal substratum for almost the entire length.

The hydrotheca is typically cylindrical, but may be turbinate, deep bell-shaped or deep ovate. It is always deeper than wide. Normally it is radially symmetrical, but in Lineolaria it is bent up from the substratum and in Modeeria the distal end is produced on two sides to support the operculum. There are never true marginal teeth. A diaphragm occurs in some species and is always extremely thin and delicate.

The operculum consists of a number of converging segments which close over the retracted hydranth. There appear to be three main types:

(i) The segments are few (4–10) and distinct, seated in embayments of the thecal margin and clearly demarcated from it. According to Kramp (1932) this type of operculum is formed from the original roof of the growing hydrotheca, e.g. Calicella, Lovenella and Tetrapoma, a small central part being discarded in the first two. He includes these three genera in the polyp subfamily Calicellinae.

(ii) There are only two pleated membranes which meet one another like the roof of a gable and impart a bilateral symmetry to the distal part of the hydrotheca, e.g. Modeeria.

(iii) The distal part of the hydrotheca wall is longitudinally creased or split to form an irregular number of delicate valves which fold inwards in an untidy manner to close the aperture. The valves are not clearly demarcated from the hydrotheca, e.g. Euchelotia, Phialella, Aeociorea, Lafaecina, Cuspidella, Opercularella.
According to Kramp (1932) the operculum in Stegopoma (= Modeeria), Lofoeina and Cuspidella is formed from the distal part of the hydrothecal wall, the original roof being discarded. He included these three genera in the polyp subfamily Cuspidellinae. He used a separate subfamily, Campanulininae, for Opercularella, Campanulina, Oplorhiza and Egmundella, where the operculum develops like that of the Calicellinae but the appearance is like that of the Cuspidellinae.

The type of opercular development, though obviously important, cannot be used to distinguish families as they stand at present, since, for instance, two completely different types occur in the Lovenellidae (Lovenella and Eucheilota).

The hydranth is usually long and slender and very extensile. It often reaches several times the length of the hydrotheca when fully extended and can be completely withdrawn into the hydrotheca. The tentacles are equally extensile and bear clusters or rings of nematocysts. In many species an intertenticular web connects the bases of the tentacles and may contain accumulations of large nematocysts (Fig. 43C). The endoderm of the hydranth is undifferentiated.

Nematophores are present in the genera Lofoeina, Oplorhiza, Egmundella and in at least one species of Lineolaria. They are contained in nematothecae which are round or tubular in shape.

Gonothece may be borne directly from the hydororhiza or from the stem. Fixed sporosacs are diagnostic of the genera Calicella, Opercularella, Tetrapoma and Lineolaria.

In conclusion it should be mentioned that there are certain species of the medusa families Eutimidae and Eirenidae which produce polyps without hydrothecae. Russell (1953) has assumed that the hydrothecae are reduced. Brinckmann-Voss (1973) has proposed unifying these two families under the name Eirenidae. Since no hydranth of this type are as yet known from South Africa the problem can conveniently be postponed, and such polyps have not been allowed for in the diagnosis of the Campanulinidae or in the keys.

KEY TO MEDUSA FAMILIES RELATED TO THE CAMPANULINIDAE

1. Producing fixed sporosacs
   - Producing free medusae
     2
2. Medusa with marginal cordonli ... ... ... ... LAODICEIDAE
   - Medusa without cordonli, with statocysts ... ... ... ... ... 3
3. Statocysts open ... ... ... ... ... MITROCOMIDAE
   - Statocysts closed ... ... ... ... ... ... ... ... ... ... EIRENIDAE (including EUTIMIDAE)
   - Medusa without peduncle ... ... ... ... ... PHIALUCIDAE
   - No cirri ... ... ... ... ... PHIALELLIDAE

5. Stomach very broad; many radial canals; with excretory pores AEOHOREIDAE
   - Stomach narrow; usually with 4 or 8 radial canals; with or without excretory pores PHIALUCIDAE
   - With excretory pores; 4-8 radial canals PHIALUCIDAE
   - Without excretory pores; 4 radial canals PHIALUCIDAE
7. Lateral or marginal cirri present ... ... ... ... LOVENELLIDAE
   - No cirri ... ... ... ... PHIALELLIDAE

KEY TO GENERA

[Genera not represented in South Africa are bracketed]

1. Hydrotheca adherent to substratum ... ... ... ... Lineolaria p. 133
   - Hydrotheca erect and free ... ... ... ... ... ... ... ... ... ... ... 2
2. Operculum of two pleated membranes meeting one another like the roof of a gable ... ... ... ... ... ... ... ... ... ... Modeeria p. 137
   - Operculum pyramidal, of more than two valves ... ... ... ... ... ... ... ... ... ... 3
3. Operculum of 4 valves ... ... ... ... ... ... ... ... ... ... ... 4
   - Operculum of more than 4 valves ... ... ... ... ... ... ... ... ... ... ... 5
4. Opercular valves sharply demarcated from hydrothecal wall ... [Tetrapoma]
   - Opercular valves not sharply demarcated from hydrothecal wall [Stegella]
5. Opercular valves seated in distinct embayments of thecal margin and sharply demarcated from it ... ... ... ... ... ... ... ... ... ... ... 6
   - Opercular valves not sharply demarcated ... ... ... ... ... ... ... ... ... ... ... 7
6. Producing free medusae with lateral cirri ... ... ... ... Lovenella p. 134
   - Producing fixed sporosacs ... ... ... ... ... ... ... ... ... ... Calicella p. 132
7. Nematophores present ... ... ... ... ... ... ... ... ... ... ... 8
   - Nematophores absent ... ... ... ... ... ... ... ... ... ... ... 10
8. Hydrotheca sessile and tubular; nematotheca tubular; gonophores, where known, producing free medusae ... ... ... ... [Lafocina]
   - Hydrotheca pedicellate; nematotheca not tubular ... ... ... ... ... ... ... ... ... ... ... 9
9. Hydrotheca widest at distal end, tubular to top-shaped; gonophores, where known, producing free medusae ... ... ... ... Egmundella p. 132
   - Hydrotheca widest in middle, narrowing at base and distal end; gonophores unknown ... ... ... ... ... ... ... ... ... ... [Opiorhiza]
10. Producing fixed sporosacs ... ... ... ... ... Opercularella p. 138
    - Producing free medusae ... ... ... ... ... ... ... ... ... ... ... 11
11. Hydrotheca sessile, long and tubular ... ... ... ... [Cuspidella]
    - Hydrotheca pedicellate ... ... ... ... ... ... ... ... ... ... ... 12
12. Hydranth without intertentacular web. Medusa without excretory pores or cirri ... ... ... ... ... Phialella p. 140
    - Hydranth with intertentacular web ... ... ... ... ... ... ... ... ... ... ... 13
13. Medusa with excretory pores, without cirri ... ... ... ... Aequorea p. 129
    - Medusa without excretory pores, with lateral cirri ... ... ... ... [Euchelolota]

Genus Aequorea Péron & Lesueur, 1809

Diagnosis. Colony stolonial or producing sparsely branched sympodial stems. Hydrotheca minute, pedicellate and free, radially symmetrical, with an oper-

Medusa with broad stomach; with many unbranched radial canals; with hollow marginal tentacles; with excretory pores; without cirri; with closed statocysts; without ocelli. (Medusa family: Aequoreidae.)

Type species: *Aequorea forskalea* Péron & Lesueur, 1809.

One polyp species only from South Africa.

*Aequorea africana* Millard, 1966

Fig. 43A–E

*Aequorea africana* Millard, 1966a: 461, fig. 8.

*Diagnosis.* Hydrorhiza creeping, giving rise to short stems which either bear a single terminal hydrotheca or branch sympodially up to three times, each limb terminating in a hydrotheca.

Stem reaching 2 mm, annulated or corrugated throughout, increasing in diameter from base to distal end, not sharply demarcated externally from hydrotheca.

Hydrotheca deep, tubular, very thin and membranous, with distal region creased longitudinally to close the aperture, 0.3–0.6 mm in depth and 0.11–0.18 mm in maximum diameter. Hydranth with 11–17 tentacles with a web between the bases. Extended tentacles moniliform.

Gonotheca arising from hydrorhiza or stem on short, annulated pedicel; pear-shaped, containing one medusa-bud.

Medusa structure unknown.

*Variation.* The length of the stem varies from 0.2 to 2.1 mm. Short stems are closely and distinctly annulated, but the longer ones are closely annulated in the basal part only and irregularly corrugated for the rest.

The base of the hydrotheca appears to be somewhat stouter than the rest, and in dead or damaged specimens it is the only part which persists, forming a saucer-shaped structure reminiscent of *Haleciun.* Successive regeneration after damage may result in tiers of saucer-shaped structures.

*Remarks.* This species shows strong resemblances to *Eucheilota maculata* as described by Werner (1968), to *Camponoma hineksi* as illustrated by Leloup (1952), and to *Campanulina paraceminata* Rees, 1938, which is possibly the polyp generation of *Aequorea forskalea.* The genus name is thus provisional pending further knowledge of the life-history. Several *Aequorea* medusae have been reported from South Africa (see p. 482).

*Distribution.* Endemic to South Africa.

*Distribution in South Africa.* Mossel Bay (type locality), Inhaca, in 18 m. 34/22 (s), 25/32
Aequorea africana. A, hydrotheca and extended hydranth; B, hydrotheca and contracted hydranth with gonophore; C, expanded hydranth showing intertentacular web; D, empty stem surmounted by saucer-shaped structure which is all that remains of the hydrotheca; E, gonotheca containing medusa-bud and arising from hydrorhiza.

Callicella oligista. F, hydrothecae redrawn from Stechow (1925a).

Egmundella amirantensis. G, hydrothecae and nematothecae.

Lineolaria graviera sp. nov. H, surface view of colony growing on weed.

Scale in mm/10.
Genus *Calicella* Hincks, 1861

*Diagnosis.* Colony stolonial. Hydrotheca pedicellate and free, deep and tubular. Margin crenulated. Operculum of many converging segments, which do not quite meet in the centre and which are clearly demarcated from the hydrothecal wall by a sharp and sometimes raised edge. No nematothecae. Hydranth with no intertentacular web.

Gonophores in the form of fixed sporosacs.

Type species: *Sertularia syringa* Linnaeus, 1767.

One species from South Africa.

*Calicella oligista* Ritchie, 1910

Fig. 43F


*Calicella oligista*: Stechow, 1925a: 440, fig. 15.

*Diagnosis.* Hydrorhiza creeping, epizootic on other hydroids, giving rise to solitary hydrotheca on short pedicels. Pedicel usually very short, always less than half height of hydrotheca, smooth or irregularly twisted.

Hydrotheca deep-campanulate, smooth, delicate, minute, 0,12–0,14 mm in depth and 0,05–0,07 mm in maximum diameter. Operculum of 12–14 converging segments seated in wide bays of the margin. Diaphragm distinct, delicate. Hydranth with 7–10 tentacles.

Gonotheca unknown.

*Remarks.* This species has not been reported since Stechow's record. Its allocation to the genus *Calicella* is provisional pending the discovery of gonophores.

*Distribution outside South Africa.* Mergui Archipelago (type locality), Red Sea.

*Distribution in South Africa.* Plettenberg Bay, in 100 m. 34°23’ (d)

Genus *Egmundella* Stechow, 1921

*Diagnosis.* Colony usually stolonial (but with branching fascicled stem in *E. fasciculata*). Hydrotheca pedicellate, not sharply demarcated from pedicel, turbinate or cylindrical, usually widest at level of opercular origin. Operculum of triangular segments and (except in *E. grandis*) not sharply demarcated from hydrotheca, and not seated in embayments of margin. Rarely a basal perisarcal thickening. Nematotheca pedicellate, oval or spherical, borne on thecal pedicel or on hydrorhiza.

Gonotheca, where known, cylindrical, arising from hydrorhiza, with an operculum very like that of the hydrotheca, releasing free medusae.

Remarks. Gonophores are unknown in the type species of *Egmundella*, but have been reported from *E. polynema* Fraser. *E. amirantensis* definitely produces medusae, but the adult medusa is unknown. See discussion by Vervoort (1966b:
109). *Eg mundella* differs from the closely related *Oplorhiza* only in the shape of the hydrotheca.

Type species: *Eg mundella gracilis* Stechow, 1921.

One species only from South Africa.

**Eg mundella amirantensis** Millard & Bouillon, 1973

Fig. 43G

*Eg mundella amirantensis* Millard & Bouillon, 1973: 40, fig. 5A–D

**Diagnosis.** Colony stolonial. Hydrothecal pedicel very short or absent. Hydrotheca cylindrical, rounded at base, generally widest at level of opercular origin, often slightly narrowed below this, 0.2–0.5 mm in depth and 0.08–0.11 mm in marginal diameter. Operculum of about 11 fragile segments not clearly demarcated from one another or from thecal wall. Hydranth very extensile, with 9–13 tentacles and no intertentacular web.

Nematostele arising from hydrorhiza, deep-oval, with slender pedicel, containing a cluster of large, elongate nematocysts.

Gonotheca (not reported from South Africa) arising from hydrorhiza, deep, irregular in outline, generally widening distally, containing one or two medusa-buds, with faintly demarcated opercular segments.

Medusa with at least two marginal tentacles at release. Adult medusa unknown.

**Variation.** The thecal pedicel is always very short, but may be quite absent so that the hydrotheca is sessile. The hydrotheca is variable in length, and extra long ones are possibly the result of regeneration though the perisarc is so delicate that growth-lines are not visible. A perisarcal thickening may be visible in the base. Occasionally a faint line may demarcate the opercular segments from the hydrotheca.

**Distribution outside South Africa.** Seychelles: Amirante (type locality), Praslin and Mahé.

**Distribution in South Africa.** Moçambique, Inhaca to Santa Carolina. 26/32, 25/32, 21/35

**Genus Lineolaria** Hincks, 1861

**Diagnosis.** Colony stolonial and epizootic on weeds. Hydrotheca sessile or nearly so, tubular or sac-shaped, adherent to weed for part or all its length, then bent up. No diaphragm. Operculum present or absent, when present membranous or of very delicate converging segments distinctly demarcated from hydrothecal wall. Nematosteleae present or absent.

Gonotheca adherent, where known containing fixed sporosacs.

Type species: *Lineolaria spinulosa* Hincks, 1861.

One species only from South Africa.
Lineolaria graviera sp. nov.

Fig. 43H


Holotype. An infertile colony growing on Cymodocea from Barreira Vermelha on the west coast of Inhaca Island, Mozambique. Part of colony mounted or slide in South African Museum (Cat. no. SAM–H1955) and part in Musée Royal de l’Afrique Centrale, Bruxelles.

Diagnosis. Hydorhiza generally running parallel to the long axis of the weed substratum, in single, double or triple strands, each coated with a thin layer of perisarc; giving rise to hydrothecae on both sides and to transverse strands which usually form loops around the hydrothecae. Hydrothecae opposite, alternate or irregular.

Hydrotheca tubular, adherent to weed for most of length, then bent upwards, 0.4–0.6 mm in length and 0.16–0.2 mm in marginal diameter. Perisarc thick near base, becoming thin distally. No pedicel, hydropore either open for the full width of the hydrotheca or constricted to about one quarter of width. Margin facing obliquely upwards, circular, untoothed, with an operculum of many delicate converging segments. Hydranth with about 14 tentacles and a conical hypostome.

Nematothecae borne on hydorhiza on the transverse strands flanking the hydrothecae, erect, not adherent, tubular, containing a group of large nematocysts, reaching 0.2 mm in height.

Gonothecae (not reported from South Africa) adherent, obovate, smooth, larger than hydrothecae, not bent up, with terminal aperture. Gonophores in the form of fixed sporo sacs. (From Gravier 1970a.)

Distribution outside South Africa. Madagascar.

Distribution in South Africa. Inhaca, Mozambique, only, on Cymodocea. 26/32

Genus Lovenella Hincks, 1868

Diagnosis. Colony stolonal or producing sparsely branched sympodial stems. Hydrotheca minute, deep-campanulate, pedicellate and free, with a conical operculum of about eight distinct converging segments seated in embayments of the margin and sharply demarcated from the wall. Hydranth without intertentacular web. Nematophores absent. Gonophores producing free medusae.

Medusa with small stomach; without peduncle; with four unbranched radial canals; with hollow marginal tentacles; without excretory pores; with lateral cirri; with an indefinite number (16 or more) of closed marginal vesicles; without ocelli.

Remarks. The above diagnosis is based on the type species where the medusa has been reared from the polyp (Russell 1953).
Type species: *Campanularia clausa* Lovén, 1836.

One polyp species only from South Africa.

*Lovenella chiquitita* Millard, 1957

Fig. 44


**Diagnosis.** Hydrorhiza creeping, often epizootic on other hydroids, giving rise to short stems which either bear a single terminal hydrotheca or branch sympodially up to nine times, each limb terminating in a hydrotheca. Stem reaching 1.9 mm, annulated throughout, increasing in diameter from base to distal end, not sharply demarcated externally from hydrotheca.

Hydrotheca deep-campanulate, smooth, minute, 0.13–0.3 mm in depth and 0.09–0.16 mm in marginal diameter. Margin with 8–10 wide and shallow bays. Operculum of 8–10 converging segments with a gap between their central points. Diaphragm delicate. Hydranth with over 12 tentacles.

Gonotheca arising from hydrorhiza on short, annulated pedicel; smooth, elongated, tapering below, truncated above, containing two medusa-buds.

Medusa at liberation with eight unbranched, marginal tentacles, without cirri, with eight closed adradial marginal vesicles each containing two concretions, with a short stomach and a simple, quadrangular mouth; 0.3 mm in depth and 0.4 mm in diameter. (Medusa family: Phialellidae.)

**Variation.** The proportions of the hydrotheca are variable; in some the diameter is almost equal to the depth and in others the depth is almost three times the diameter. The perisarc of the hydrotheca is usually very delicate, but sometimes thicker and in this case there may be an annular thickening just below the diaphragm.

**Observations on living material.** Living hydranthas are long, slender and very extensible, the tentacles being held alternately elevated and depressed. Gonophores have released medusae in the laboratory, but the latter have not been reared to maturity. The young medusae have four of the eight marginal tentacles slightly longer than the others.

Colour: hydranthas transparent; medusae transparent, with brown patches on tentacle-bases and in stomach.

**Remarks.** The polyp generation of this species closely resembles that of the type species of *Lovenella*, hence its inclusion in this genus. The newly released medusa, however, differs from that of *Lovenella* in the absence of cirri.

**Distribution.** Endemic to South Africa. Type locality: False Bay.

**Distribution in South Africa.** Lüderitz Bay to False Bay, littoral to 40 m. 26/15 (s), 33/18 (h, l); 34/18 (h, l, s)
Fig. 44.

*Lovenella chiquitita*. A, branching stem and gonotheca; B–D, hydrothecae, D with partly extended hydranth; E, young medusa escaping from gonotheca; F, newly liberated medusa, preserved and somewhat contracted.

Scale in mm/10.
Genus *Modeeria* Forbes, 1846


*Diagnosis.* Colony stolonial. Hydrotheca pedicellate, deep and tubular, with margin produced on two sides. Operculum of two longitudinally pleated membranes seated in the embayments of the margin and meeting one another like a gable. No diaphragm. No nematothecae. No intertentacular web. Gonotheca similar to hydrotheca. Producing free medusae.

Medusa with thick jelly; with large quadrangular stomach attached to subumbrella along margins of four cruciform per radial furrows; mouth with four well-developed folded lips; with four simple radial canals; gonads in sinuous folds along sides of per radial furrows; with numerous hollow marginal tentacles with conical basal bulbs; with cordyli; without ocelli; without statecysts. (Medusa family: Laodiceidae.)

*Type species:* *Dianaea rotunda* Quoy & Gaimard, 1827.

*Remarks.* Edwards (1973) traced the development of the well-known *Stegopoma fastigiatum* (Alder) and linked it to the medusa *Modeeria rotunda* (Quoy & Gaimard). This is the only member of the genus *Modeeria* in which the hydranth is known, and on it is based the diagnosis given above. Further knowledge of the life-history of other species of *Stegopoma* (including the type species, *S. plicatile*) is required in order to decide whether they also should be included in *Modeeria* or whether the genus *Stegopoma* should be retained. Edwards transferred the genus *Modeeria* from the Tiarannidae to the Laodiceidae.

One species only from South Africa.

*Modeeria rotunda* (Quoy & Gaimard, 1827)

*Fig. 45A*

*Figured in:* *Dianaea rotunda* Quoy & Gaimard, 1827: 181, pl. 6A (figs 1–2).

*Campanularia fastigiata* Alder, 1860: 73, pl. 5 (fig. 1).


*Diagnosis.* Colony epizootic on other hydroids. Hydrorhiza creeping, giving rise to solitary, pedicellate hydrothecae and gonothecae.

Hydrotheca 0.4–1.8 mm in length and 0.2–0.4 mm in maximum diameter, not sharply demarcated from pedicel, which is smooth, and 0.1–1.2 times length of hydrotheca. Hydranth with about 13 tentacles. Operculum as for genus.

Gonotheca similar to hydrotheca but wider, with very short, smooth pedicel, containing a series of medusa-buds.

Medusa (not recorded from South Africa) at liberation deep and somewhat conical, with umbilical canal, four oral lips, four per radial marginal bulbs with well-developed tentacles, four inter radial and four or eight adradial marginal bulbs which may bear rudimentary tentacles, about 2 mm in diameter.
and 1.5 mm in height. Adult medusa as for genus, reaching 22 mm in diameter, with up to 28 marginal tentacles.

Variation. The size of the hydrotheca and length of its pedicel are notoriously variable in this species.

Distribution. Cosmopolitan. Type locality: Straits of Gibraltar (medusa).

Distribution in South Africa. East coast, from Natal to Moçambique, in 70 to 347 m. 30/31 (d), 29/31 (s, d), 26/33 (d), 24/35 (d)

Genus Opercularella Hincks, 1868

Diagnosis. Colony stolonial or sympodially branched. Hydrotheca pedicellate and free, deep and tubular. Operculum of many converging segments, which do not quite meet in the centre, and which are not sharply demarcated from the hydrothecal wall. No nematothecae. Hydranth with no intertentacular web, or if present, not well developed.

Gonophores in the form of fixed sporosacs.

Remarks. Rees (1939) advocated the retention of the genus Opercularella for species previously assigned to Campanulina and which produce fixed sporosacs, and also (provisionally) those species in which the gonosome is unknown. The only South African species falls in the latter category.

Type species: Campanularia lacerata Johnston, 1847.

Opercularella sp.

Fig. 45C–D


Diagnosis. Colony erect and branching sympodially, reaching 22 mm. Stem fascicled in lower regions, straight, giving rise to branches and more-or-less alternate hydrothecae, with occasional nodes immediately above origins of hydrothecae. Branches similar to stem.

Hydrotheca pedicellate. Pedicel shorter than hydrotheca and not sharply demarcated from it, more-or-less distinctly ringed or indistinctly wrinkled. Hydrotheca tumbler-shaped, sometimes slightly swollen near base, with flaring margin, 0.3–0.4 mm in depth from diaphragm and 0.16–0.19 mm in maximum diameter. Operculum formed from distal part of hydrotheca which folds longitudinally along 10–12 longitudinal striae. A thin diaphragm present.

Gonotheca unknown.

Distribution. Endemic to South Africa.

Distribution in South Africa. Type locality and only record: off Durban in 430 m. 29/31 (d)
Fig. 45.

*Modeeria rotunda*. A, hydrothecae from different colonies, and gonotheca on extreme right. *Phialella turrita*. B, hydrothecae and gonotheca, redrawn from Vanhöffen (1910, as *Campanulina turrita*).

*Opercularella* sp. C and D, redrawn from Vervoort (1966b).

Scale: D in mm, the rest in mm/10.
Genus Phialella Browne, 1902

*Diagnosis*. Colony stolonial or producing sympodially branched stems. Hydrotheca minute, deep and conical, pedicellate and free, with an operculum of many acute converging segments not sharply demarcated from hydrothecal wall. Hydranth without intertentacular web. Nematophores absent. Gonophores producing free medusae.

Medusa with small stomach, without peduncle, with four unbranched radial canals, without excretory pores, with many hollow marginal tentacles, without cirri, with eight closed statoecysts, without ocelli. Newly hatched medusa with four marginal tentacles. (Medusa family: Phialellidae.)

*Remarks*. The polyp generation is not known in the type species. The above diagnosis is based on the polyp of *P. quadrata* (Forbes). This species was reported by Allman (1864) to have a very shallow intertentacular web, but Russell (1953) says this is not confirmed, and Huvé (1952) illustrates the tentacle bases without a web.

Type species: *Phialella falklandica* Browne, 1902.

One polyp species only from South Africa.

*Phialella turrita* (Hincks, 1868)

*Fig. 45B*

_Campanulina turrita* Hincks, 1868: 190, pl. 36 (fig. 2). Vanhöffen, 1910: 309, fig. 29.

*Diagnosis*. Stem bearing a single terminal hydrotheca or several hydrothecae in a sympodial manner, two or three at a time; occasionally branching sympodially; distinctly annulated throughout.

Hydrotheca deep, widening gradually upwards, 0.2–0.4 mm in depth and 0.10 mm in diameter. Operculum of short converging segments, about $\frac{1}{4}$ depth of hydrotheca. No diaphragm.

Gonotheca arising from hydrorhiza or stem, pear-shaped, containing one medusa-bud.

*Remarks*. Vanhöffen identified his material from South Africa as _Campanulina turrita_ Hincks. This species has been ascribed to _Aequorea_ by Rees (1939) and to _Phialella_ (_Hypsorophus_) _quadrata_ by Huvé (1952). Huvé's identification was queried by Rees & Thurstield (1965).

Vanhöffen's material strongly resembles 'Campanulina' repens, the polyp generation of _Phialella quadrata_. I have therefore included the species in the genus _Phialella_, but have retained the specific name _turrita_ pending further information on the life-history.

_Distribution outside South Africa_. Great Britain (type locality), Mediterranean, Greenland, Denmark, Falklands, New Zealand. (*Phialella quadrata* is known
from the Atlantic, Pacific and Indian Oceans, though it has not as yet been reported from South Africa.)

*Distribution in South Africa.* Simonstown in False Bay. 34/18 (s)

**Family Haleciidae**

*Diagnosis.* Thecate hydroids with shallow, saucer- or basin-shaped hydrothecae. Hydrotheca radially symmetrical, without operculum, with untoothed margin, usually with diaphragm. Hydranth very large and usually not completely retractable into hydrotheca, with conical hypostome and one circle of filiform tentacles, endoderm differentiated into proximal digestive part and distal non-digestive part. Nematophores present or absent. Gonophores in the form of fixed sporosacs, or, rarely, freed as medusae.

*Introduction.* The majority of the Haleciidae have upright branching stems with sympodial growth. The stems and their branches are divided into internodes, each typically bearing a hydrotheca on an apophysis near its distal end. The apophyses occur alternately on the right and on the left, so that the hydrothecae form two longitudinal rows. The stem may be fascicled or unfascicled, but the final branches are always unfascicled.

In the genera *Hydranthea* Hincks (1868) and *Campalecium* Torrey (1902), which do not occur in South Africa, and in *Hydrodendron cornucopia*, which does, the colony is stolonial. A stolonial form may also occur in normally erect species.

The hydranths are always large. In *Halecium* they cannot be contained in the shallow hydrothecae; in *Hydrodendron*, where the hydrothecae are a little deeper, they can be almost or entirely contained. The base of the hydrotheca generally contains a diaphragm on which the hydranth rests. The hydranth is fastened to the wall of the hydrotheca above the level of the diaphragm by coenosarcal strands, whose position is normally marked in the empty hydrotheca by a ring of refringent nodules. The gastric cavity of the living hydranth is usually (and possibly always) divided by a transverse constriction into two distinct regions, the oral and the aboral or digestive. In some species of *Hydrodendron*, *Hydranthea* and *Campalecium* the bases of the tentacles may be attached to one another by an intertentacular web. The web is absent in *Halecium*.

The hydrotheca may be sessile, with its base resting directly on the apophysis and its addauline wall usually adnate to the stem, or pedicellate. The pedicel is normally of the same diameter as the hydrotheca and is not externally demarcated from it. Regeneration is very common, resulting in tiers of hydrothecae arising one within the other. The secondary hydrothecae may differ from the primary one in the presence of a pedicel; for instance in *Halecium beanii* the primary hydrotheca is sessile and the secondary hydrothecae have pedicels of a characteristic shape. In the literature the hydrotheca plus its pedicel are often referred to as a HYDROPHORE. In the diagnoses of species which follow,
Haleciidae: parts of the skeleton. On the left a sessile hydrotheca with straight walls, on the right a pedicellate and regenerated hydrotheca with everted walls.

the depth of the hydrotheca is measured from the diaphragm to the margin. In some species a thickened shelf of perisarc may occur below the base of the hydrotheca in the pedicel and is usually better developed on one side than the other. This is termed a PSEUDODIAPHRAGM, e.g. Halecium delicatum, Halecium ?muricatum.

Nematophores are present in the genus Hydrodendron. The nematothecae are one-chambered, minute, cup-like or tubular, often without any regular arrangement.

In the genus Hydranthea the gonophores are naked. Generally, however, they are enclosed in gonothecae, which are generally dioecious. In some species of Halecium the female gonophores are very obviously modified hydranths. In H. beanii and H. dichotomum two well-developed hydranths protrude through the opening of the gonotheca. In H. delicatum a hydranth is recognizable, through completely contained within the gonotheca and without mouth and tentacles. In other species, e.g. H. tenellum, and in the males of all species the resemblance to a hydranth is lost.

In most genera the gonophores take the form of fixed sporosacs. In Campalecium, however, the gonophores release free medusae, and in the only species of the genus, C. microtheca (= C. medusiferum), the medusa was shown by Brinckmann (1959) to be Eucheilotta (Lovenella) cirrata, a member of the Campanuliniidae. This suggests a relationship between the Campanuliniidae and the Haleciidae and it is possible that the latter arose from the former by the loss of the operculum and distal part of the hydrotheca in the polypl generation. This is supported by the fact that in certain campanuliniids, e.g. Eucheilotta maculata, Eutonina indicans and Aequorea africana (Werner 1968; Millard 1966a) the distal part of the hydrotheca may be sloughed off in older colonies leaving a shallow, basin-shaped structure similar to the hydrotheca of the Haleciidae and complete with diaphragm and refringent nodules. The relationship between
these two families is further supported by the presence of an intertentacular web in certain members of both and by some similarities in the enidome.

In some of the species of Hydrodendron with deeper hydrotheca and with nematothecae, e.g. H. gracilis and H. cornucopia, the structure of the colony approaches very closely that in some Plumulariidae and Lafoeidae and it may be difficult to draw a dividing line between these families.

KEY TO GENERA

[Genera not represented in South Africa are bracketed]

1. Nematophores present
   - Nematophores absent
   2. Colony stolonial
      - Colony with erect stem
      3. Producing medusae
         - Producing fixed sporosaces
         4. Hydrothecae borne on stem and branches
            - Hydrothecae borne on branches only

Hydrodendron p. 157
[Campalecium]
[Hydranthea]
Halecium p. 143
[Hemitheca]

Genus Halecium Oken, 1815

Diagnosis. Colonies generally upright with sympodial growth. Stem (and branches when present) bearing two rows of alternate hydrothecae, divided into internodes, each internode with a hydrotheca-bearing apophysis near distal end. Hydrotheca sessile or pedicellate, shallow, basin- or saucer-shaped, with delicate diaphragm and generally a ring of refringent nodules above it. Regeneration common, resulting in tiers of secondary hydrothecae growing from within the primary. Hydranth large, without intertentacular web. Nematophores absent. Gonophores in the form of fixed sporosaces contained in gonothecae. Gonothecae solitary, not aggregated, male and female usually dissimilar and on separate colonies.

Type species: Sertularia halecina Linnaeus, 1758.

KEY TO SPECIES

1. Hydrothecal wall straight, usually widening to margin but never everted
   - Hydrothecal wall everted
   2. Hydrotheca deep (depth 1/2-3 marginal diameter)
      - Hydrotheca shallow (depth less than 1/2 marginal diameter)
      3. Female gonotheca with lateral opening containing two hydranth
         - Female gonotheca with terminal opening
      4. Hydrotheca not widening to margin. Female gonotheca with lateral-facing aperture
         on concave side
         - Hydrotheca widening to margin. Female gonotheca with distal-facing aperture on concave side
      5. Stem fascicled, normally straight, with hydrothecae offset alternately to right and left, not narrowed or corrugated at nodes
         - Stem unfascicled, geniculate and bent alternately to left and right below each node, with hydrothecae not offset, constricted at nodes and immediately above them

H. sessile
H. dyssymetrum
H. beanti
H. lankesteri
6. Female gonotheca slender, usually curved, containing several eggs in one row
   - Female gonotheca compressed, oval in side view, containing one egg
     \textit{H. halecinum}
   \textit{H. inhaecae}
   7. Stem unfascicled, short (under 7 mm). Hydrotheca with wall strongly everted throughout, small (diameter at margin under 0.18 mm). No pseudodiaphragm. Female gonotheca smooth, compressed-ovoid, with terminal aperture and no hydranths
     - Stem fascicled
     \textit{H. tenellum}
8. Hydrotheca deep (depth over \(\frac{1}{2}\) diameter). Primary hydrotheca pedicellate, pedicel separated from apophysis by node. Hydrothecal wall strongly everted in marginal region. Usually two pseudodiaphragmata. (Female gonotheca ridged and spiny)
     - Hydrotheca shallow (depth less than \(\frac{1}{2}\) diameter)
     \textit{H. ?muricatum}
9. Primary hydrotheca usually sessile. Hydrothecal wall usually everted only at margin. No pseudodiaphragm. Female gonotheca annulated, with lateral opening and two hydranths
   - Primary hydrotheca pedicellate, pedicel not separated from apophysis by node. Hydrothecal wall strongly everted throughout. Usually one pseudodiaphragm. Female gonotheca smooth, flat and eared, containing one reduced hydranth without tentacles
     \textit{H. dichotomum}  \textit{H. delicatulum}

\textit{Halecium beanii} (Johnston, 1838)

Fig. 47A–E

\textit{Thoa beanii} Johnston, 1838: 120, pl. 7 (figs 1–2).

\textit{ Diagnosis}. Colonies shrubby and stiff in appearance, 10–70 mm in height. Stem fascicled, branching irregularly or in a roughly alternate manner, segmented, usually straight, each internode giving rise to a hydrotheca from an apophysis near the distal end, the two rows of hydrothecae in one plane or shifted onto the anterior surface of the stem. No annulation of internodes. Branches arising from below or within hydrothecae, often rebranching many times.

Primary hydrothecae sessile. Secondary hydrothecae pedicellate. Pedicel typically with a constriction immediately above origin, gibbous above this, then narrowed and then widening gradually to distal end. Hydrotheca shallow, with straight sides, widening to margin, which is not everted, 0.03–0.05 mm in depth and 0.13–0.17 mm in marginal diameter. Diaphragm delicate, with a ring of refringent nodules immediately above it.

Male gonotheca spindle-shaped, smooth, without hydranths. Female gonotheca 'mitten-shaped', elongated and curved, with distal-facing aperture in centre of concave side, smooth, with two fully-formed hydranths emerging from aperture, containing a single row of large eggs.

\textit{ Variation}. The stem is occasionally slightly geniculate and the nodes are very variable in length.

The secondary hydrothecae normally bend away from the stem, due to the asymmetrical development of that part of the pedicel below its constriction, which is longer on the adcauline side. That part above the constriction may be
symmetrical or asymmetrical, the latter condition due to unequal development of the bulge near the base or to curvature of the whole pedicel. Likewise, the hydrothecal margin may be perpendicular to the axis of the pedicel, though it is more often oblique and tilted towards the adcauline side.

The female gonothecae sometimes tend to be S-shaped, with the proximal end convex on the adcauline side.

Remarks. There is no certain way of distinguishing *H. beanii* from *H. halecinum* in the absence of female gonothecae. Both species occur in South Africa. In the distribution which follows, therefore, all records without female gonothecae, including those from the literature, have been disregarded. The species is certainly far more common than is indicated, and sterile material, probably of this species, has been found as far north as Inhambane on the east coast (23/35).


Distribution in South Africa. From Lüderitz Bay, South West Africa, on the west coast to the northern boundary of the Cape on the east coast, littoral to 157 m. 26/15 (s), 33/17 (s, d), 33/18 (l, s), 34/18 (s), 34/19, 34/22 (s), 33/25 (s); 34/25 (s), 33/26 (s), 33/27 (s), 32/28 (s), 31/29

*Halecium delicatulum* Coughtrey, 1876

Fig. 47F–L


*Halecium flexile* Allman, 1888: 11, pl. 5 (fig. 2).

*Halecium gracile* Bale, 1888: 759, pl. 14 (figs 1–3).


*Halecium parvulum*, var. *magnum* Millard, 1957: 190, fig. 4B–O.

Diagnosis. Colony stiff and bushy, reaching 190 mm in height. Stem usually fascicled, profusely and irregularly branched, segmented, each internode giving rise to a hydrotheca from an apophysis near the distal end, the two rows of hydrothecae usually in one plane. Branches arising from hydrothecal pedicels, smaller ones flexuus and graceful.

Primary hydrotheca pedicellate; pedicel variable in length, tubular, continuous with stem apophysis and not demarcated from it by a node. Secondary hydrotheca pedicellate; pedicel tubular, often constricted or annulated at base. Primary and secondary pedicels commonly with a pseudodiaphragm which is better developed on adcauline side. Hydrotheca shallow, with wall strongly everted, more so on adcauline side, 0.03–0.08 mm in depth and 0.13–0.4 mm in marginal diameter. Diaphragm delicate, with a ring of refringent nodules immediately above it. Margin usually perpendicular to axis of pedicel.

Gonothecae arising from stem or hydrorhiza. Male gonotheca compressed, elongate-oval in side view, smooth, without hydranth; when immature flattened and disc-shaped. Female gonotheca large, compressed, smooth, elongate-
Fig. 47.

*Haleci um bean ii*. A, stem with female gonothecae; B and C, regenerated hydrothecae; D, male gonophore; E, female gonophore.

*Haleci um delicatulum*. F and G, parts of stem from small form (F) and large form (G); H, male gonophore; J-L, female gonophores, the first two showing hydranths, the third containing planulae.

Scale: H–L in mm, the rest in mm/10.
oval in side view with two distal ‘ears’ and between them a small terminal aperture at the base of an inverted collar; when immature flattened-oval with rounded distal end. Female gonotheca containing a single reduced hydranth without mouth or tentacles and bearing eggs, three or four of which mature into planulae.

Variation. This species is capable of great variation in size and the following forms can be distinguished:

(i) Small form. Marginal diameter of hydrotheca under 0.25 mm. Mature female gonotheca under 1.5 mm in length.
(ii) Large form (var. magna Millard 1957). Marginal diameter of hydrotheca over 0.25 mm. Mature female gonotheca over 1.5 mm in length.

The growth-form also varies, from luxuriant heavily-fascicled colonies to small unfascicled ones. Sometimes interconnection of the superficial tubes of the stems results in a tangled formless mass. In all cases, however, the smaller branches have a more delicate and flexuous appearance than, for instance, in *H. beanii*. The stem may be straight or zigzag, the internodes long or short, and there is usually an indication of annulation or twisting in the neighbourhood of the nodes. Occasionally atecate internodes may occur.

The pedicels of the hydrothecae may be straight or curved, and the greater development of the pseudodiaphragm and curvature of the hydrothecal wall on the adcauline side may impose a bilateral symmetry.

Male and female gonothecae change in shape during development, and abnormalities sometimes occur, such as the presence of two apertures and two reduced hydranths in the female.

Distribution outside South Africa. Circumglobal in tropics and southern oceans, extending northwards to Japan in the Pacific and Morocco in the Atlantic, and southwards to the Antarctic. Type locality: Dunedin (New Zealand).

Distribution in South Africa. From the west coast of the Cape Province to Moçambique, very common in False Bay and on the Agulhas Bank, littoral to 219 m. 30/15 (d), 32/18 (s), 33/17 (s), 33/18 (l, s), 34/18 (l, s, d), 34/20 (s), 34/21 (d), 35/21 (d), 34/22 (s), 35/22 (d), 34/23 (d), 33/25 (s), 34/25 (s), 33/26 (s), 33/27 (s), 33/28 (s), 32/28 (s), 31/29 (s), 29/31 (d), 26/35 (d), 24/34 (s), 24/35 (s)

*Halecium dichotomum* Allman, 1888

Fig. 48A–G


Diagnosis. Colonies varying from tall and robust to low and scrubby. Stem fascicled, fairly stiff, though unable to support itself out of fluid, segmented, typically branching repeatedly in a dichotomous manner in which two, or occasionally three, equally developed limbs arise at the same level from curved
apophyses near the distal ends of the internodes. Hydrothecae terminating internodes. Smaller branches flexuous and usually geniculate.

Primary hydrothecae normally sessile. Secondary hydrothecae pedicellate. Pedicel more or less symmetrical, usually annulated in basal region and then widening to distal end. Hydrotheca shallow and wide, with wall usually straight and widening towards margin for most of its height, then sharply everted, 0,03–0,05 mm in depth and 0,18–0,3 mm in marginal diameter. Margin usually perpendicular to axis of internode or pedicel. Diaphragm delicate, with a ring of refringent nodules immediately above it.

Male gonotheca slender, tapering to distal aperture, sometimes curved, annulated for all or most of length. Female gonotheca mitten-shaped, with rounded distal end and distal-facing aperture on one side, closely annulated, with two fully-formed hydranthes emerging from aperture, containing two or three large eggs.

*Variation.* The hydorhiza is smooth, annulated or roughly corrugated, and in epizootic colonies is capable of putting out rootlike projections to anchor the colony.

The growth-form and general appearance of the colony is very variable and all grades between the following extremes may occur:

(i) Large upright colonies reaching 110–120 mm in height, with strongly fascicled stems and branching mainly in one plane. Main stem more or less straight and dichotomy not obvious, due to the fact that one limb is enveloped by the peripheral tubes and contributes to the axis of the stem, while the other is short and forms a branch. Larger stems and branches stiff in appearance and up to 2 mm thick, though unable to support themselves out of fluid. Smaller branches graceful and flexuous. Stem and branches with long internodes with no annulation other than a shallow constriction near base. Secondary hydrothecae scarce.

(ii) Low, scruffy colonies, often epizootic, reaching a height of 10–20 mm. Stem usually weakly fascicled and strongly geniculate. Branching profuse and in all planes, and stolonization common resulting in a tangle mat which may cover large areas of the substratum and is very easily recognized. Dichotomy very obvious. Internodes of stem and branches shorter and more annulated. Secondary hydrothecae abundant and pedicels often closely annulated in basal regions.

The shape of the hydrotheca is also variable. Typically the wall is straight until close to the margin where it suddenly flares out, but the flaring may be much more extensive resembling that in *H. delicatulum*, or the flared-out portion may be largely worn off in old colonies. Variations in the shape of the pedicels of secondary hydrothecae and in the angle of the margin may also occur. Primary hydrothecae often have quite long pedicels. The perisarc is typically thin and a pseudodiaphragm only rarely occurs.

Solitary, pedicellate hydrothecae may also arise separately from the hydorhiza.

*Distribution.* Endemic to South Africa. Type locality: Simon’s Bay, Cape.
Fig. 48.

*Halecium dichotomum.* A–C, regenerated hydrothecae; D, part of stem showing unilateral branching; E, part of stem showing dichotomous branching; F, female gonophore; G, male gonophore.

*Halecium dyssymetrium.* H, part of stem; J, hydrotheca.


Scale in mm/10.
Distribution in South Africa. All round the coast from Lüderitz Bay in South West Africa to Moçambique, in 11–200 m. 26/15, 32/18 (s), 33/17 (s), 34/18 (s), 34/20 (s), 34/21, 35/21 (d), 34/22 (s), 35/22 (d), 34/23 (s, d), 34/24 (d), 33/25 (s), 34/25 (s, d), 33/26 (s), 33/27 (s), 32/28 (s), 33/28 (s), 29/31 (s, d), 24/34 (s)

Halecium dyssytemum Billard, 1929

Fig. 48H, J

Halecium dyssytemum Billard, 1929: 307, fig. 1C. Leloup, 1935: 8, fig. 1.

Diagnosis. Stem under 10 mm in height, unfascieled, unbranched, segmented, slightly geniculate, each internode giving rise to a hydrotheca from an apophysis near the distal end, the two rows of hydrothecae in one plane. No annulation of internodes.

Primary hydrothecae sessile. Secondary hydrothecae with assymetrical pedicels widening distally and usually bent outwards. Hydrotheca deep, widening to margin, which is not everted, 0,13–0,17 mm in depth and 0,2–0,3 mm in marginal diameter. Diaphragm very thick and pronounced, more so on adcauline side. Base of hydranth attached above diaphragm and attachment marked by a ring of refringent nodules, each of the latter shaped like an Indian wigwam.

Gonothecae unknown.

Distribution outside South Africa. Dutch East Indies (type locality), West Indies.

Distribution in South Africa. One record only, from off Moçambique in 55 m. 24/34 (s)

Halecium halecinum (Linnaeus, 1758)

Fig. 49A–E

Sertularia halecina Linnaeus, 1758: 809.

Diagnosis. Stem under 10 mm in height (but see under ‘Variation’ below), fascieled or unfascieled, branched or unbranched, segmented or slightly geniculate, each internode giving rise to a hydrotheca from an apophysis near the distal end, the two rows of hydrothecae in one plane or shifted on to the anterior surface of the stem. No annulation of internodes.

Primary hydrothecae sessile. Secondary hydrothecae pedicellate. Pedicel typically with a constriction immediately above origin, gibbous above this and then widening gradually to distal end. Hydrotheca shallow, with straight sides, widening to margin, which is not everted, 0,03–0,05 mm in depth and 0,12–0,15 mm in marginal diameter. Diaphragm delicate, with a ring of refringent nodules immediately above it.

Male gonothecae (not recorded from South Africa) spindle-shaped, smooth, without hydranths. Female gonothecae elongate, usually curved, widening slightly to distal end, which is truncated and bears a terminal aperture
on the adcauline side, smooth, with two fully-formed hydranths emerging from aperture, containing a single row of 2–4 large eggs or planulae.

Variation. The only certain records from South Africa are stunted colonies, but tall, rigid and pinnately branched stems occur in the North Atlantic reaching 100–200 mm or more in height. The terminal branches are said to be stiffer than in H. beanii and the whole colony much more regularly branched and less 'bushy'.

The hydrothecae are indistinguishable from those of H. beanii, but secondary hydrothecae and their pedicels are always asymmetrical, due either to unequal development of the proximal part of the pedicel, or to curvature of the whole pedicel away from the stem. The margin of the secondary hydrotheca is usually oblique to the axis (tilted towards the adcauline side) and seldom perpendicular as is said to be the rule for the species.

Remarks. As in the case of H. beanii this species is probably more abundant than is indicated by the records, since samples without female gonothecae have been disregarded, including that of Ritchie (1907b) from South Africa, who had only male gonothecae which might easily be confused with H. beanii.

Distribution outside South Africa. Certainly from the North Sea, North Atlantic and Arctic, but probably much more widespread. Type locality: U.K.

Distribution in South Africa. Agulhas Bank in 27 m and Inhaca, 10–15 m. 33/27 (s), 26/32 (s)

Halecium inhacae Millard, 1958

Fig. 49F–H


Diagnosis. Colony small and inconspicuous, reaching 4 mm in height. Hydro-rhiza with internal thickenings of perisarc. Stem unfascicled, usually unbranched, with segmentation inconspicuous or absent, slightly geniculate. Hydrothecae arising from short apophyses of stem, one to an internode where these are evident, the two rows in one plane. Perisarc heavy, with thickened internal ridges giving a corrugated appearance.

Primary hydrothecae sessile. Secondary hydrothecae with asymmetrical pedicels which are curved or bent away from stem. Hydrotheca shallow, with straight sides, widening slightly to margin, which is not everted, 0.03–0.04 mm in depth and 0.13–0.17 mm in marginal diameter. Diaphragm delicate, with a ring of refringent nodules about midway between diaphragm and margin. Walls markedly thickened just below level of diaphragm, more so on adcauline side. Hydranth with about 19 tentacles.

Male gonotheca unknown. Female gonothecae borne generally on hydro-rhiza, occasionally on stem, in the latter case emerging from within the hydrothecae, laterally compressed, broadly oval in side view, smooth, with terminal
Fig. 49.

aperture on adcauline side through which two hydranths emerge, containing a
single egg or planula.

Distribution. Endemic to South Africa.

Distribution in South Africa. Type locality and only records: Inhaca Island,
littoral. 26/32 (l, s)

Halecium lankesteri (Bourne, 1890)

Fig. 50B–E

Haloikena lankesteri Bourne, 1890: 395, pl. 26 (figs 1–2).

Diagnosis. Colony erect or stolonial. Erect stem reaching 5 mm in height,
unfascicled, branching irregularly, segmented, each internode giving rise to a
hydrotheca from an apophysis near the distal end, the apophysis and hydrotheca
lying in the same axis as the proximal part of the internode and the rest of
the internode bent sharply outwards and upwards, the stem thus geniculate with
the elbows below the nodes. Stem constricted at each node and immediately
above. Stolonial form with hydrophores arising direct from hydorhiza, usually
regenerated many times.

Primary hydrothecae sessile. Secondary hydrothecae pedicellate. Pedicel
usually constricted immediately above origin, bulging above this, then widening
to distal end. Hydrotheca shallow, with straight sides, widening markedly to
margin, which is not everted, 0.02–0.04 mm in depth and 0.10–0.15 mm in
marginal diameter. Diaphragm delicate.

Gonothecae borne on stem or hydorhiza. Male sausage-shaped, some-
times curved, smooth. Female similar to that of H. beanii, but shorter and
broader, curved, with obliquely distal-facing aperture on concave side, smooth,
with two fully-formed hydranths emerging from aperture, containing two or
three large eggs in a row.

Variation. Branching is very irregular and not necessarily in one plane. Branches
usually arise from the distal end of an internode and curve outwards and
upwards from the base, sometimes giving a dichotomous effect. The length of the
internodes is very variable and many irregularities occur.

Distribution outside South Africa. Adriatic Sea, North Atlantic, Mediterranean,
tropical West Africa. Type locality: Plymouth, England.

Distribution in South Africa. Moçambique: Inhaca to Santa Carolina, inter-
tidal. 25/32 (l), 21/35

Halecium ?muricatum (Ellis & Solander, 1786)

Fig. 50A

Sertularia muricata Ellis & Solander, 1786: 59, pl. 7 (figs 3–4).
Halecium muricatum: Hincks, 1868: 223, pl. 43 (fig. 1). Jäderholm, 1909: 59, pl. 5 (figs 4–6).
Diagnosis. Stems reaching 47 mm in height, fairly stiff, fascicled in basal region, unbranched or branching in an irregularly pinnate fashion, segmented, usually straight though sometimes weakly geniculate in distal region, each internode giving rise to a hydrotheca from an apophysis near the distal end, the two rows of hydrothecae in one plane. No annulation of internodes.

Primary hydrotheca pedicellate. Pedicel long (at least three times the depth of the hydrotheca) and separated from the stem apophysis by a distinct node, usually asymmetrical and more convex on adcauline side, containing at least one and usually two pseudodiaphragmata. Secondary hydrotheca pedicellate, the pedicel similar to that of the primary though shorter and usually with only one pseudodiaphragm. Hydrotheca deep, widening to margin, which is strongly everted, more so on adcauline side, 0.08–0.14 mm in depth and 0.2–0.3 mm in marginal diameter. Diaphragm delicate, with a ring of refringent nodules immediately above it.

Gonothecae (not reported from South Africa) similar in the male and female, compressed-ovate, with radiating ridges bearing spines, without hydranths.

Variation and remarks. The identification of this species cannot be certain until confirmed by the gonothecae.

In the South African material the fascicled parts of the stems are matted together in the lower part of the colony by coalescence or crossing over of the superficial tubes. From this region graceful, unfascicled stems arise with regularly alternating hydrothecae. These stems are either unbranched or branch in a roughly pinnate manner. The branches may replace hydrothecae, but more usually arise from the anterior or posterior face of a hydrothecal pedicel, then curve to conform to the plane of the colony.

The node separating the primary hydrotheca from the stem apophysis is sometimes incomplete.

Distribution outside South Africa. Arctic (circumpolar), North Pacific, North Atlantic.

Distribution in South Africa. Rare on the south coast, from Table Bay to east of Port Elizabeth in 0–46 m. 33/18 (s), 34/18 (s), 33/26 (s)

Halecium sessile Norman, 1867

Fig. 48K–M


Diagnosis. Stem reaching 25 mm, fascicled in lower part, branching irregularly, segmented, geniculate, each internode giving rise to a hydrotheca from an apophysis near the distal end. No annulation of internodes. Branches arising from below hydrothecae.

Primary hydrotheca sessile, but with adcauline wall free from stem. Second-
Fig. 50

Halecium ?muralvum. A, part of stem.
Halecium lankesteri. B and C, parts of stem with hydrophores; D, stem with female gonophore; E, male gonophore
Halecium tenellum. F and G, female gonophores containing planulae; H, male gonophore; J–L, parts of stem.

Scale in mm/10.
ary hydrotheca pedicellate. Pedicel with one or two nodes near base, then widening gradually to distal end. Hydrotheca shallow, with straight sides, normally not widening to margin, which is not everted, 0.01–0.03 mm in depth and 0.12–0.14 mm in marginal diameter. Secondary hydrotheca shallower on adcauline than on abcauline side. A ring of refringent nodules about midway between diaphragm and margin.

Gonothecae not reported from South Africa. Male elongated, smooth, with rounded summit and no hydranths, bearing spermatogenic cells along one side of spadix. Female kidney-shaped, short, with laterally facing aperture on concave side, smooth, with two fully-formed hydranths emerging from aperture, containing a single row of eggs or planulae.


Distribution in South Africa. Off Durban, in 425–430 m. 29/31 (d)

*Halecium tenellum* Hincks, 1861

Fig. 50F–L


Diagnosis. Colonies small and usually epizootic on other hydroids, under 7 mm in height. Stem unfascicled, slender, unbranched or sparsely branching, segmented, geniculate. Hydrothecae arising from short apophyses of stem near the distal ends of the internodes. A constriction usually present above and below each node.

Primary hydrotheca sessile or with short pedicel. Secondary hydrotheca pedicellate. Pedicel symmetrical or asymmetrical, constricted near base and widening slightly to distal end. Hydrotheca shallow, with wall widening to margin and strongly everted, 0.02–0.05 mm in depth and 0.11–0.17 mm in marginal diameter. Diaphragm delicate, with a ring of refringent nodules immediately above it.

Male and female gonothecae on separate colonies, arising from stem or hydorhiza. Male gonotheca compressed, smooth, elongate-oval in side view, with pointed distal end, without hydranths. Female gonotheca compressed, smooth, pear-shaped in side view, with terminal aperture on a papilla seated in a circular depression, without hydranths, containing a cluster of 2–7 eggs or planulae.

Variation. This minute species is extremely variable in its growth-form, yet easily recognizable. The typical form has a regular geniculate stem with long, slender internodes, each bearing a hydrotheca on its summit. Some of the South African material is of this type, but more often the stem contains a number of intervening athecate internodes, often a whole series one after another. In small epizootic colonies a single hydrotheca often tops a stem made up solely of athecate internodes, of which the terminal one resembles a secondary pedicel,
Athecate internodes may be due to regeneration after injury and are especially characteristic of this species. Regeneration by the production of tiers of secondary hydrothecae is also very common.

Branches, when they occur, arise from below the hydrothecae and are often as long as the main stem, giving a subdichotomous effect with an acute angle between the limbs. Branches sometimes arise in pairs.

The hydrotheca is always small and delicate with the margin strongly everted. The everted part is very thin and may be held straight out, curled under, or is occasionally worn right off.

Distribution. Cosmopolitan. Type locality: Salcombe Bay, U.K.

Distribution in South Africa. Occurring irregularly along the south and east coasts from False Bay to Moçambique, littoral to 120 m, with one deeper record from Natal (495 m) by Vervoort (1966b). 34/18 (s), 35/19 (s), 34/22 (s), 34/23 (s), 33/25 (s), 33/26 (d), 33/27 (s), 32/28 (s), 31/29 (l, 29/31 (s, d), 28/32 (s), 25/32 (s), 26/32 (s)

Genus Hydrodendron Hincks, 1874

Syn. Ophiodes Hincks, 1866.
Diplocyathus Allman, 1888.
Phylactotheca Stechow, 1913.
Ophiodissa Stechow, 1919.

Diagnosis. Colony erect or stolonal. Erect stem usually bearing two rows of alternate hydrothecae; divided into internodes, each with a hydrotheca-bearing apophysis near distal end. Hydrotheca pedicellate, basin- or cup-shaped, with delicate diaphragm and usually a ring of refringent nodules above it. Hydranth constricted immediately below tentacles, with or without intertentacular web between tentacle bases. Nematophores present, enclosed in one-chambered nematothecae. Gonophores in the form of fixed sporosacs contained in gonothecae. Gonothecae solitary or, rarely (not in South African species), aggregated into a coppinia.

Type species: Halecium gorgonoide G. O. Sars, 1874

KEY TO SPECIES

1. Colony stolonal (hydrophores arising from hydrorhiza) ........................................ 2
   - Colony with erect stem bearing hydrophores .................................................. 3
2. Hydrophores cornucopia-shaped, each bearing one nematotheca
   - Hydrophores deep-campanulate, nematothecae on hydrorhiza only
     H. cornucopia
     H. caciformis

3. Diaphragm straight; hydrotheca shallow, with diameter at least twice depth ......... 4
   - Diaphragm oblique; hydrotheca deep, with diameter approximately equal to depth on deeper side ........................................................................................................ 5

4. Hydrotheca projecting obliquely from main sympodial axis of stem. Gonotheca smooth or lightly corrugated .............................................................. 6
   - Hydrotheca terminal, secondary hydrophore arising from lateral apophysis. Gonotheca deeply annulated ........................................................................ 6
8. Hydrodendron gracilis
8. Hydrodendron gardineri

5. Nematothecae curved, one on each hydrothecal pedicel ........................................ H. gracilis
   - Nematothecae goblet-shaped, never on primary pedicel (though may occur on regener- rated pedicel) ................................................................. H. gardineri
Hydrodendron cacifornitis (Ritchie, 1907)

Fig. 51

Ophiodes cacifornitis Ritchie, 1907a: 500, pl. 23 (figs 11–12), pl. 24 (fig. 1), pl. 25 (fig. 5).
Diplocytathus cacifornitis: Leloup, 1939: 4, fig. 3.
Ophodiassa cacifornitis: Vervoort, 1959: 218, figs 1–2.

Diagnosis. Colony erect or stolional, usually growing on weed. Hydrorhiza reticulate; perisarc with internal projections. Erect stem under 10 mm in height, unfascicled or weakly fascicled at base, occasionally branched, segmented, each internode giving rise to a hydrotheca from an apophysis near the distal end. The two rows of hydrothecae in one plane or shifted slightly onto anterior face. Stolional form with solitary hydrothecae arising directly from the hydrorhiza and supported by 1–3 short internodes.

Hydrotheca pedicellate, often with regeneration nodes between the stem apophysis and the pedicel. Pedicel deeper than hydrotheca, usually somewhat turgid near base and expanding slightly towards distal end. Hydrotheca with flaring wall and everted margin, 0.05–0.12 mm in depth and 0.14–0.2 mm in marginal diameter. Diaphragm very delicate, straight. A ring of refringent nodules usually about one third of the height above diaphragm. Hydranth with 19–23 tentacles.

Nematocetheae borne on hydrorhiza, stem internodes or hydrothecal pedicels, random in occurrence, sessile, goblet-shaped, with everted margin, sometimes bilaterally symmetrical.

Gonotheca borne on hydrorhiza, elongated, widening to just below truncated distal end, smooth or with rather indistinct transverse annulations, reaching 0.8 mm in length and 0.3 mm in diameter.

Variation. The perisarcal projections in the hydrorhiza are not regular and are more numerous in some regions than in others.

The erect form of the colony is more usual than the stolional form, though fair numbers of stolional hydrothecae are often encountered among the erect stems. Two entirely stolional colonies have been found. Stronger stems have been recorded from outside South Africa, and Ralph records strongly fascicled stems of 22 mm with regularly subalternate branches arising below every third and fourth hydrotheca from New Zealand. In some stems there is a suggestion of an annulation in the form of a constriction above and below each node.

Secondary hydrothecae may arise from primary ones, not from within them as in Haleciun, but from the sides of the pedicels or the regenerated internodes below them. This, indeed, is the way in which branches originate. Reduplicated margins are very rare.

Pseudodiaphragmata may occur, particularly in regeneration internodes and in the hydrothecal pedicels; they are usually better developed on the adcauline side.
Fig. 51.

*Hydrodendron caciniformis*. A, stem; B and C, parts of stem with hydrophores and nematothecae; D and E, male and female gonophores (material from Vema Seamount); F, living hydranths and nematophores.

Scale in mm/10.
Observations on living material. The hydranth when fully extended are long and tubular reaching 1,4 mm in length. The base is attached to the ring of refringent dots in the hydrotheca and narrows suddenly below to the coenosarc which passes through the opening in the diaphragm. There is always a distinct space between the hydranth base and the diaphragm. The body of the hydranth is narrowed distally immediately below the tentacles and this contracted ring is visible even at full extension. The tentacles are held alternately elevated and depressed and are connected to one another at the base by a web. They are very mobile and may contract individually or all together. The hypostome is conical, but very distensible. On contraction the tentacles close over the mouth and the hydranth body is reduced to about half its length. It cannot be withdrawn into the hydrotheca.

The nematophore reaches 2 mm in length when fully extended. It consists of a solid core of endoderm cells and a covering of thin ectoderm and has a terminal spherical knob well armed with nematocysts. The nematophores are very mobile and are continually twisting about as though exploring the surroundings.

As in many other hydroids the stem and hydrorhiza tend to produce abundant stoloniferous processes under laboratory conditions. These are completely enclosed in perisarc and well supplied with nematocysts. After four days in a tank they reached 18 mm in length and were profusely branched. Many of them arose from within dead hydrothecae.

Colour: transparent white.

Distribution outside South Africa. Cape Verde Islands (type locality), Mediterranean, Portugal, West Indies, tropical West Africa, Vema Seamount (S. Atlantic), Australia, New Zealand, India, Japan.

Distribution in South Africa. False Bay and Transkei coast, littoral to 17 m. 34/18 (l, s), 21/29 (l)

Hydrodendron cornucopia (Millard, 1955)

Fig. 52

Zygophylax cornucopia Millard, 1955: 219, fig. 3.
Hydrodendron cornucopia: Millard, 1973: 30, 33, fig. 6A-F

Diagnosis of typical form. Colony stolonial, epizooctic on various species of Antennella, Monostaechas and Corhiza (most common host: Antennella africana). Hydrorhiza giving rise directly to solitary hydrophores, each of which is seated on a short basal internode. Hydrothecae facing alternately to right and left, forming two rows more or less at right angles to one another and forming an angle of about 45° with hydrorhiza.

Hydrophore (hydrotheca plus pedicel) with a cornucopia shape and double curvature (first outwards, then upwards), widening gradually to margin, which faces upwards (i.e. towards distal end of host), 0,3-0,4 mm in abcauline length
and 0.10–0.15 mm in marginal diameter. Pedicel more than twice length of hydrotheca. Diaphragm oblique, with hydropore off-centre and closer to ‘upper’ side, a row of refringent nodules just above it. Hydranth just able to be contained in hydrotheca, with about 18 tentacles and a constriction between proximal digestive part and distal non-digestive part, no intertentacular web.

Nematootheca curved-barrel-shaped, one about halfway along ‘upper’ side of each pedicel.

Gonothecae borne on hydrothecal pedicels close to nematothecae, elon-

Fig. 52.

*Hydrodendron cornucopia*. A, colony growing on *Antennella africana*; B, hydropore with nematotheca and female gonophore; C and D, two forms of branching hydrophores. Scale in mm/10.
gated, widening to truncated distal end. Male and female on separate hosts, female larger than male and containing numerous eggs.

Variation. Although the hydrophores are normally solitary, branching individuals rarely occur. Branching occurs from the lateral surface of the pedicel, either on one side only or on both sides. Such secondary hydrophores are similar to the primary one, with basal segment and pedicel; they may branch again several times.

Distribution. Endemic to South Africa. Type locality: False Bay.

Distribution in South Africa. South and east coasts, from Table Bay in the west to Natal in the east, littoral to 86 m. 33/18 (s), 34/18 (l, s), 34/22 (s), 33/25 (s), 34/25 (s), 33/27 (s), 32/28 (l), 33/28 (s), 31/29 (s), 30/30 (s), 29/31 (s), 29/32 (s), 28/32 (s)

_Hydrodendron gardineri_ (Jarvis, 1922)

Fig. 53A–D


Diagnosis. Colony erect or stolonial. Hydrorhiza reticulate; perisarc with internal projections. Erect stem reaching 4 mm in height, unfascicled, unbranched, segmented, each internode giving rise to a hydrotheca from an apophysis arising near the centre or at about two-thirds of the length. The two rows of hydrothecae in one plane. Stolonial form with solitary hydrothecae arising directly from the hydrorhiza.

Hydrotheca pedicellate, often regenerated between the apophysis and the pedicel resulting in additional nodes or corrugations. Pedicel deeper than hydrotheca, slightly turgid near base, expanding evenly towards distal end to merge into hydrotheca. Solitary hydrotheca usually with longer pedicel and several regeneration nodes at base. Hydrotheca deep, widening to margin which is usually everted, 0,11–0,16 mm in depth (adcauline) and 0,13–0,17 mm in marginal diameter; diameter at margin approximately equal to adcauline depth. Diaphragm oblique, sloping downwards to adcauline edge. No refringent nodules. Hydranth just retractable into hydrotheca; with 18 tentacles and no intertentacular web.

Nematothecae borne on hydrorhiza, stem internodes or regenerated parts of thecal pedicels, irregular in occurrence, sessile, goblet-shaped, with everted margin. Nematophore with a solid core of endoderm cells and a terminal capitulum.

Gonotheca (not reported from South Africa) borne on hydrorhiza, male cylindrical, with truncated distal end. Female unknown.

Distribution outside South Africa. Type locality and only record: Salomon, Chagos, 109–220 m.

Distribution in South Africa. Moçambique: Inhaca to Inhambane, 2–3 m. 25/32, 24/35 (s)
Fig. 53.

*Hydrodendron gardineri*. A and B, parts of erect colony; C and D, solitary hydrophores. *Hydrodendron gracilis*. E, stem; F and G, hydrophores with nematothecae; H, female gonophore with planulae; J, female gonophore with eggs.

Scale in mm/10.
Hydrodendron gracilis (Fraser, 1914)

Fig. 53E–J

Ophiodes gracilis Fraser, 1914: 171, pl. 22 (fig. 82).
Diplocyathus gracilis: Leloup, 1935: 11, fig. 2. Leloup, 1937: 17, fig. 9.
Zygophyllax enigmatica Millard, 1964: 19, fig. 5A–F.
Hydrodendron gracilis: Millard, 1973: 33, fig. 6F–E.

Diagnosis. Colony minute, epizootic on Nemertesia ramosa, with erect stems reaching a height of 2–3 mm. Stem unfascicled, unbranched, segmented, each internode giving rise to a hydrotheca from an apophysis near the distal end. The two rows of hydrothecae in one plane. Each apophysis with a mamelon on upper surface.

Hydrotheca pedicellate, usually with one or more regeneration nodes between the stem apophysis and the pedicle. Pedicel 1,2–2,4 times length of hydrotheca, expanding distally, with adcauline wall slightly convex near base. Hydrotheca widening slightly to margin, 0,07–0,10 mm in height and 0,10–0,11 mm in marginal diameter. Margin not everted. Diaphragm oblique, with hydropore off-centre and closer to adcauline side. No refringent nodules.

Nematotheca curved, one about halfway along adcauline side of each pedicel, and usually one on the distal end of each stem internode or on its apophysis.

Gonothecae borne on the hydrocladal apophyses; female flattened, flask-shaped in lateral view with slender neck and terminal aperture, containing about nine eggs which develop into planulæ in situ; male unknown.

Variation. The stem internodes vary in length, particularly near the base of the stem where they tend to be much shorter. Weakly developed internodal septa occasionally occur, both in the stem internodes and in the hydrothecal pedicels.

Remarks. This species shows some resemblances to the epizootic form of Plumularia setacea. It can be distinguished from it by the fact that the hydrotheca terminates the pedicel and is not seated on its anterior face and by the absence of supracalycine nematothecae.

Distribution outside South Africa. West coast of North America (type locality), West Indies, French Indo-China.

Distribution in South Africa. Reported once only, off the west coast of the Cape Peninsula. 34/18 (s)

Hydrodendron sympodiformis Millard & Bouillon, 1974

Fig. 54

Hydrodendron sympodiformis Millard & Bouillon, 1974: 25, fig. 5.

Diagnosis. Colony erect or stolonial, growing on weed. Hydorhiza reticulate; perisarc with or without internal projections. Erect stem reaching a maximum height of 7 mm, unfascicled, consisting of a series of hydrophores arising one
from another by sympodial branching, each hydrophore with a terminal hydrotheca and a lateral apophysis which bears the next hydrophore, each hydrophore other than the first curved upwards to stand almost parallel to the preceding one; hydrothecae not in one plane. Stolonial form with solitary hydrohores arising directly from hydrorhiza.

Hydrothecal pedicel of variable length, often with regeneration nodes or corrugations immediately above origin of apophysis in erect stem or at base in solitary hydrophore. Hydrotheca with flaring wall, with margin sometimes

**Fig. 54.**  
*Hydrodendron sympodium.* A, stem; B, part of stem; C, gonotheca; D, solitary hydrophore and nematothecae; E, gonotheca.  
Scale in mm/10.
everted, 0.06–0.10 mm in depth and 0.17–0.2 mm in marginal diameter. Diaphragm straight. A ring of refringent nodules about midway between margin and diaphragm. Hydranth with about 22 tentacles.

Nematothecae borne on hydrorhiza and hydrophore pedicels, random in occurrence, sessile, goblet-shaped, with everted margin and perisarcal thickening below it. Nematophore with terminal capitulum containing large nematoceysts.

Gonotheca (only female known) borne on hydrorhiza, barrel-shaped with widest part below centre, with 6–7 deep transverse annulations, reaching 0.8 mm in depth and 0.4 mm in maximum diameter.

*Distribution.* Endemic to South Africa.

*Distribution in South Africa.* Type locality and only record: Inhaca, Moçambique. 26/32

**Family Lafoeidae**

*Diagnosis.* Thecate hydroids with campanulate to tubular, and often bilaterally symmetrical, hydrothecae, into which the hydranth can be completely withdrawn. Hydrotheca stalked or adherent, without operculum, with untoothed margin, with or without diaphragm. Hydranth with conical hypostome, one circle of filiform tentacles and undifferentiated endoderm. Nematophores present or absent. Gonophores enclosed in gonothecae, which are often aggregated into a coppinia; in the form of fixed sporo sacs or, rarely, producing free medusae.

*Introduction.* The most primitive genera of the Lafoeidae are probably those with stolonial colonies, as in *Hebella* and *Scandia*. *Filellum* also has stolonial colonies, but the hydrothecae are adherent to the hydrorhiza for their proximal part, then bend away from it. In all other species the mature colony consists of an erect stem bearing hydrothecae, yet in most of them, and especially in the genera *Lafoea*, *Acryptolaria* and *Cryptolaria*, a juvenile or epizootic form is known which retains the stolonial arrangement. To separate the stolonial genera into a separate family (the *‘Hebelloidae’*) which has been done by some systematists, is therefore inadvisable.

The erect stem varies in complexity. It may be fascicled and the hydrothecae partly immersed. It may branch and rebranch, and there is little difference between the orders of branches, since all bear hydrothecae, but for the sake of uniformity the final branches are here termed hydrocladia.

In most genera the hydrotheca is supported by a slender pedicel, but typically the two are not clearly demarcated externally. A diaphragm or an annular thickening of perisare may or may not separate them internally. In the branching genera *Acryptolaria* and *Cryptolaria* the pedicel and hydrotheca are partly adherent to the stem, but in young stolonial colonies the hydrothecae are quite free. In this character these genera resemble *Filellum*.

*Regeneration* is common and may result in apparent segments in the stem
or hydrocladia, or, more commonly, may produce new hydrothecae within the old ones, giving the appearance of a margin which is reduplicated, often many times (Fig. 56A). The measurements of hydrothecae which are given are always without such supplementary margins.

Nematophores and nematothecae are present in the genera Cryptolaria and Zygophylax. The nematothecae are usually minute tubular structures and do not attain the complexity characteristic of many Plumulariidae.

The reproductive structure, the coppinia, is characteristic of the Lafoeidae, and consists of a nest of closely packed gonothecae surrounding part of the stem (Fig. 56F). It is usually protected by special defensive structures formed from modified hydrothecae or nematothecae which project beyond the surface giving to the whole a bristly appearance. Yet the more primitive 'Hebellidae' and Cryptolarella have separate gonothecae. Hebella is the only genus known to produce medusae, but the adult medusa is imperfectly known and in no species has been reared to maturity.

Reproductive bodies are strangely scarce in the Lafoeidae and in some species have never been recorded in this country. Since the final identification often depends on these structures the specific name remains doubtful in such cases and awaits confirmation at a later stage.

**KEY TO GENERA**

1. Hydrotheca stalked, not adherent
   - Hydrotheca adherent
      2
      5
2. Mature colony with erect, branching stem bearing hydrothecae irregularly on all sides. Hydrotheca without diaphragm or annular thickening, not sharply demarcated from pedicel. No nematothecae. Gonothecae aggregated into coppinia.  
   - Colony erect or stolonial; erect stem bearing hydrothecae in two longitudinal rows. Hydrotheca usually with diaphragm or annular thickening (always in South African species).  
     Lafoea p. 184

     Zygophylax p. 188

4. Gonophores producing free medusae. Hydrotheca small, never over 1.2 mm in height, usually much less.  
   - Gonophores in the form of fixed sporo sacs. Hydrothecae larger, 1.1–2.1 mm in height.  
     Hebella p. 178

5. Colony stolonial. Hydrotheca adherent to hydrothiza.  
   - Mature colony with erect, branching stem. Hydrotheca adherent to stem or branch.  
     Filellum p. 175

6. Diaphragm present between hydrotheca and stem apophysis. Nematothecae present.  
   - Normally no diaphragm. No nematothecae.  
     Cryptolaria p. 174

   - Hydrothecae on all surfaces of stem, though they may be alternate in some regions. Gonothecae solitary, not aggregated.  
     Acryptolaria p. 168

Genus Acryptolaria Norman, 1875

Syn. Scapus Norman, 1875.  
Oswaldaria Stechow, 1923.

Diagnosis. Colony normally erect, stolonial in young stages. Erect stem fascicled and branched; branches alternate or subalternate; stem and branches bearing hydrothecia which are similar to the branches. Hydrothecae arising from stem, branches and hydrothecia alternately in two rows and from the axial tube when fascicled. Hydrotheca tubular, at least partly adnate, not demarcated from apophysis and normally without a diaphragm. No nematothecae, but reduced hydrothecae sometimes borne on accessory tubes (but not in South African species). Gonothecae aggregated to form a coppinia. Gonophores in the form of fixed sporo sacs.

Type species: Acryptolaria andersoni Totton, 1930.

KEY TO SPECIES

1. Hydrotheca bent sharply outwards at almost a right angle. Abcauline wall with distinct notch at level of bend. Hydrotheca curved smoothly outwards. No notch on abcauline wall.  
   - A. conferta
   - A. rectangularis
Acrphysalaria conferta (Allman, 1877)

Fig. 56

Cryptolaria conferta Allman, 1877: 17; pl. 12 (figs 6–10).
Cryptolaria conferta var. australis Ritchie, 1911: 826, pl. 84 (fig. 2), pl. 87 (fig. 1).
Acrphysalaria conferta conferta: Millard, 1964: 7, fig. 1A–C, E.

Diagnosis. Colony reaching a height of 110 mm. Stem of variable robustness, fascicled, unsegmented, giving rise to alternate hydrothecae and irregularly alternate branches or hydrocladia from the axial tube. Larger branches fascicled, generally lying in one plane, each arising on a level with the free part of a hydrotheca, giving rise to hydrothecae and hydrocladia in a similar manner. Hydrocladia unfascicled or lightly fascicled, unsegmented, typically one to every third hydrotheca. The two rows of hydrothecae in one plane.

Hydrotheca tubular, curved smoothly outwards, adnate for \(\frac{1}{2}\) to \(\frac{3}{4}\) height and rarely more, 0.5–1.3 mm in total adcauline length (adnate plus free part) and 0.13–0.3 mm in marginal diameter (which is \(1\frac{1}{2}–2\frac{1}{3}\) times the diameter at base). Margin very slightly everted.

Gonothecae aggregated into a coppinia, in contact with one another though rather loosely packed, flask-shaped with slender distal neck and small terminal orifice, producing acroysts. Coppinia not provided with modified hydrothecae or nematothecae.

Variation. Much variation in the growth-form occurs and colonies may vary from small and flexuous to large and stiff. Irregularities in the branching may produce shrubby growths often complicated by stolons which anastomose with other regions.

The first hydrotheca on a hydrocladium is sometimes seated on the front and thus in a plane at right angles to that of the stem, but after this the hydrocladium rotates until the original plane is restored.

Hydrothecae vary in size, though they never exceed a marginal diameter of 0.3 mm. Their spacing on the stem varies, and the base of the adcauline wall may be well above the axil of the previous hydrotheca, level with it, or below it, the last condition resulting in densely packed overlapping hydrothecae (Ritchie’s var. australis). All grades between the two extremes occur. The adcauline wall of the hydrotheca may be concave and evenly curved throughout, or may bulge slightly near the base, when there may be a slight indentation below the hydrotheca, giving the effect of a poorly developed node. Rejuvenations of the margin are common.

Solitary hydrothecae may arise separately from the hydorhiza in young or epizootic colonies. These are erect, not adnate, and symmetrical or irregular in shape.

Distribution. Cosmopolitan. Type locality: off Cuba.

Distribution in South Africa. Sparsely distributed from the west coast round the
Acryptolaria conferta. A, part of stem of ‘var. conferta’; B, part of stem to show branching, portions of peripheral tubes in position; C, solitary hydrotheca; D, young stem arising next to a solitary hydrotheca; E, stem, heavy form; F, t.s. coppinia with female gonothecae.

Scale: E in cm, the rest in mm/10.
Agulhas Bank into Natal and Moçambique, in 64 to 350 m. 30/15 (d), 35/19 (d), 35/22 (d), 34/23 (d), 34/24 (d), 33/27 (s), 30/31 (d), 29/31 (s, d), 24/35 (d)

*Acryptolaria rectangularis* (Jarvis, 1922)

Fig. 57A–D

*Cryptolaria rectangularis* Jarvis, 1922: 335, pl. 24 (fig. 3).
*Acryptolaria angulata*: Vervoort, 1966b: 116, fig. 16.

**Diagnosis.** Colony reaching a height of 70 mm. Stem flexuous (not able to support itself out of fluid), fascicled, unsegmented, giving rise to alternate hydrothecae and irregularly alternate or subalternate branches or hydrocladia from the axial tube. Branches fascicled, given off more or less in one plane, each one arising on a level with the top of a hydrotheca, giving rise to hydrothecae and hydrocladia in a similar manner, commonly anastomosing with other parts of the colony. Hydrocladia fascicled or unfascicled, unsegmented. The two rows of hydrothecae in one plane.

Hydrotheca tubular, adnate for $\frac{1}{4} - \frac{2}{3}$ length, then bent sharply outwards forming almost a right angle with stem; free adcauline wall straight or slightly concave; adcauline wall with distinct notch at point of divergence; 0.5–1.3 mm in total adcauline length (adnate plus free part) and 0.10–0.2 mm in marginal diameter. The base of one hydrotheca commencing immediately above axil of the one below. Margin slightly everted, directed outwards and upwards at an angle to stem.

Gonothecae aggregated into a coppinia, firmly adpressed for complete length, tubular, widening slightly to distal, wide, terminal aperture. Coppinia provided with modified tubular hydrothecae which project above surface.

**Variation.** The branching in this species does not show the regularity common to most of the family. Only rarely does any regularity occur, with two alternate branches arising close together, and then it is usually after every fifth and sixth hydrotheca. Also there are no axillary hydrothecae, a branch leaving the stem immediately above, or next to, the axil of a hydrotheca.

The hydrotheca sometimes has an internal ring of tubercles for the attachment of the base of the hydranth, which may be coalesced to form a diaphragm in older parts of the colony. This character relates the species to the genus *Cryptolaria*.

Solitary hydrothecae may arise separately from the hydrorhiza in young or epizooic colonies; these are erect and without the right-angle bend, symmetrical or irregular in shape.

**Distribution outside South Africa.** Providence, tropical Indian Ocean (type locality) and south west Indian Ocean.

**Distribution in South Africa.** Off the coasts of Natal and Moçambique in 110 to 495 m. 30/31 (d), 29/31 (d), 26/33 (d), 24/35 (d).
Genus Cryptolarella Stechow, 1913


Type species: Cryptolaria abyssicola Allman, 1888.

One species only from South Africa.

Cryptolarella abyssicola (Allman, 1888)

Fig. 57E–G

Cryptolaria abyssicola Allman, 1888: 40, pl. 18 (figs 2–2a).

Diagnosis. Colony reaching a height of 60 mm. Stem flexuous (not able to support itself out of fluid), fascicled, unsegmented, giving rise to hydrothecae on all surfaces from an axial tube and to roughly alternate branches from the peripheral tubes. Larger branches fascicled and similar to stem, often rebranching and reuniting by stolonic processes; smaller branches unfascicled. Branching in one plane. Hydrothecae often partly buried by peripheral tubes, the base of the adcauline wall usually below the axil of the preceding hydrotheca.

Hydrotheca tubular, adnate to stem for about half height, then curved smoothly outwards, 0.6–2.3 mm in total adcauline height (adnate plus free part) and 0.13–0.2 mm in marginal diameter.

Gonothecae (not reported from South Africa) borne singly on stem, flask-shaped, partly adnate, with a short curved neck.

Variation and remarks. This species has been found from two localities only, and the specimens differ from one another rather markedly in hydrothecal size and proportions but cannot be separated on any constant factor.

The colony with the large hydrothecae (1.8–2.3 mm in total adcauline height and 0.16–0.2 mm in marginal diameter) comes from a greater depth (2740 m).

The colony with the small hydrothecae (0.6–0.7 mm in total adcauline height and 0.13–0.16 mm in marginal diameter) comes from a lesser depth (200 m). The hydrothecae are more closely set on the stem and the proportion of marginal diameter to total adcauline length is greater (0.18–0.27 as against 0.07–0.09). However, since the material described by Vervoort and Kramp does, to a large extent, bridge the gap between the two samples, it is not justifiable to create a new species for the form with small hydrothecae.

In both colonies the shape of the hydrotheca is variable and the free part often abnormally elongated, possibly due to regeneration although no regeneration lines are visible.
*Acryptolaria rectangularis.* A, part of branch; B, stem; C, t.s. part of coppinia with gonothecae and modified hydrothecae; D, solitary hydrothecae.

*Cryptolarella abyssicola.* E, stem; F and G, parts of branches with small and large hydrothecae respectively.

Scale: B and E in cm, the rest in mm/10
Distribution outside South Africa. North Atlantic, East Indies, South Pacific. Type locality: south of Australia, 42°42'S/134°10'E, 4 740 m.

Distribution in South Africa. Off Saldanha Bay in 2 740 m and off Still Bay in 200 m. 33/16 (a), 35/22 (d)

Genus Cryptolaria Busk, 1857

Syn. Perisiphonia Allman, 1888.

Diagnosis. Colony normally erect, stolonial in young stages. Erect stem fascicled and branched; branches subalternate; stem and branches bearing hydrocladia which are similar to branches. Hydrothecae arising from stem, branches and hydrocladia alternately in two or four longitudinal rows and from the axial tube when fascicled. Hydrotheca tubular, at least partly adherent in at least some part of colony, separated from apophysis by distinct diaphragm. Nematotrichae present. Gonothecae aggregated to form a coppinia. Gono- phores in the form of fixed sporosacs.

Type species: Cryptolaria prima Busk, 1857 (syn. Perisiphonia quadrisediata Trebilcock, 1928).

One species only from South Africa.

Cryptolaria pectinata (Allman, 1888)

Fig. 58A–F

Perisiphonia pectinata Allman, 1888: 45, pl. 21 (fig. 2). Ritchie, 1911: 835, pl. 87 (fig. 2).
Acryptolaria pectinata: Stechow, 1925a: 448, figs 20–21.
Cryptolaria pectinata: Ralph, 1958: 320, figs 5g–j, 6g–j, 7c.

Diagnosis. Colony reaching a height of 40 mm. Stem stiff, heavily fascicled, branching in one plane, unsegmented, giving rise to alternate hydrothecae and subalternate branches or hydrocladia from the axial tube. Branches fascicled, similar to stem. Hydrocladia fascicled except at extremities, unsegmented, arising below every third and fourth hydrotheca. The two rows of hydrothecae in one plane.

Hydrotheca tubular; adnate for a variable proportion of length, usually over half, but axillary hydrothecae often completely free from axial tube, those of stem partly immersed in peripheral tubes; bent strongly outwards at beginning of free part; with margin parallel to axial tube or tilted downwards; 0.3–0.4 mm in total adcauline length (adnate plus free part) and 0.06–0.10 mm in marginal diameter. Diaphragm oblique, with abcauline edge higher than adcauline.

Nematotrichae tubular, scattered irregularly on peripheral and axial tubes, and usually one on each hydrothecal apophysis.

Gonothecae aggregated into a coppinia, flask-shaped, firmly adpressed for about two-thirds of length and with slender, free neck provided with one or
two lateral openings and one or two curved, distal horns. Coppinia provided with branched nematothecae which project above the surface.

*Variation.* Colonies of 130 mm have been reported from outside South Africa. The arrangement of the hydrocladia is very regular and few deviations occur. Although there is no segmentation, the hydrothecae, at any rate on young stems, are usually distinctly grouped, there being a larger gap after every fourth one, i.e. after every subalternate pair of hydrocladia.

The abcauline wall of the hydrotheca is thickened at the point of curvature in older parts of the colony. Rejuvenations of the margin are common.

Solitary hydrothecae may arise separately from the hydorhiza in young or epizootic colonies; these are erect, not adnate, with a slender pedicel and curved hydrotheca.

*Remarks.* The coppiniae in this species are dioecious. Stechow states that the one-horned gonothecae are male and the two-horned ones female (containing planulae). Yet Ralph has found eggs in one-horned gonothecae in New Zealand material (which I can confirm after examination). Only two-horned gonothecae have been found in South Africa and these contain bodies which resemble planulae. The question of the sex thus needs confirmation.

*Distribution outside South Africa.* New Zealand (type locality), North Atlantic, West Indies, ?Galapagos Islands.

*Distribution in South Africa.* East London to Natal in 49–90 m. 33/27 (s), 29/31 (s)

Genus *Filellum* Hincks, 1868

*Syn. Reticularia* Wyville Thompson, 1853

*Diagnosis.* Colony stolonial, with hydrothecae arising directly from a creeping hydorhiza. Hydrotheca tubular, adnate to hydorhiza for part of its length, then free, without diaphragm. Gonothecae aggregated to form a coppinia, which also contains modified protective hydrothecae. Gonophores in the form of fixed sporosacs. Generally no nematothecae.

Type species: *Campanularia serpens* Hassall, 1848

*Remarks.* The genus *Filellum* is common in South Africa, yet of the three reported species only *F. serratum* is identifiable in the absence of coppiniae, and coppiniae rarely occur.

**KEY TO SPECIES**

1. Adnate part of hydrotheca transversely ridged on outer surface. Coppinia with straight accessory tubes
   - Adnate part of hydrotheca smooth.
     - Coppinia with forked accessory tubes
       - Coppinia with simple, curved accessory tubes
         - *F. serratum* 2
     2. Coppinia with forked accessory tubes
       - *F. antarcticum* 2
     3. Coppinia with simple, curved accessory tubes
        - *F. serpens* 2
**Cryptolaria pectinata.** A, part of stem from distal region to show axillary hydrothecae and origin of hydrocladia (the axial tube has thicker perisarc than the peripheral tubes); B, t.s. part of coppinia showing female gonothecae and nematothecae; C, part of hydrocladium (only the axial tube shown); D, a young stem (the single peripheral tube not shown); E, solitary hydrothecae; F, stem with coppinia.

**Filellum antarcticum.** G, hydrothecae; H, forked accessory tubes from coppinia.

Scale: F in cm, the rest in mm/10.
Filellum antarcticum (Hartlaub, 1904)

Fig. 58G–H

Lafoula antarctica Hartlaub, 1904: 11, pl. 2 (fig. 2). Vanhöfen, 1910: 311, fig. 31a–c.
Reticularia antarctica: Totton, 1930: 160, fig. 17.

Diagnosis. Colony epizootic on other hydroids. Hydrotheca distinctly demarcated from hydrorhiza, adnate for \( \frac{1}{2} - \frac{3}{4} \) length, then free and bent outwards, smooth, margin slightly everted, 0.10–0.12 mm in diameter.

Gonothecae aggregated into a coppinia, firmly adpressed, cylindrical, with terminal apertures, discharging their contents into acrocysts. Coppinia provided with numerous forked accessory tubes (modified hydrothecae) which arch over and protect the gonothecae.

Variation and remarks. A few of the hydrothecae show very faint transverse striations on the outer surface of the adnate part. Reduplications of the margin are common. Occasionally a few of the hydrothecae are not adnate at all, but free for the entire length.

One example of a mutilated coppinia has been found, establishing for certain the presence of the species in the country. Only this sample was used for measurements. Infertile material of this species or F. serpens occurs quite commonly.

Distribution outside South Africa. Antarctic (type locality), Australia, Chile.

Distribution in South Africa. The only certain record is from Mossel Bay on the south coast in 13 m. Doubtful records from the Agulhas Bank and Natal. 34/22 (s)

Filellum ?serpens (Hassall, 1848)

Complanaria serpens Hassall, 1848: 2223.
Filellum serpens: Hinde, 1868: 214, pl. 41 (fig. 4).
Coppinia arctica: Hinde, 1868: 219, pl. 41 (fig. 5).
Grammara serpens: Vervoort, 1946a: 194, fig. 82.

Diagnosis. Colony generally epizootic on other hydroids. Hydrotheca tubular, distinctly demarcated from hydrorhiza, adnate for \( \frac{1}{2} - \frac{2}{3} \) length, then free and bent outwards, smooth, margin not or only slightly everted, about 0.1 mm in diameter.

Gonothecae (not reported from South Africa) aggregated into a coppinia, firmly adpressed, cylindrical, with terminal apertures. Coppinia provided with numerous simple accessory tubes (modified hydrothecae) which curve over the gonothecae. Coppinia hermaphroditic, containing male and female gonothecae. (From Hinde and Vervoort.)

Distribution. Cosmopolitan. Type locality: U.K.

Distribution in South Africa. Uncertain. All previous records from the country have been infertile, so there is a possibility of confusion with F. antarcticum.
Filellum serratum (Clarke, 1879)

Fig. 59A–C


Reticularia serrata: Ralph, 1958: 312, figs. 2j, 3a.

Diagnosis. Colony generally epizootic on other hyroides. Hydrotheca tubular, distinctly demarcated from hydrorhiza, adnate for \( \frac{1}{2} \)–\( \frac{2}{3} \) length, then free and bent outwards, adnate part transversely ridged on outer surface, margin slightly everted, 0,10–0,3 mm in diameter.

Gonothecae aggregated into a coppinia, firmly adpressed, cylindrical, with terminal apertures, releasing planula larvae. Accessory tubes present, at least double the length of the gonothecae, unbranched, of very irregular shape and usually curved or twisted.

Variation and remarks. Regenerations of the thecal margin are common. The size of the hydrotheca and the proportion of its wall adnate are notoriously variable. The striations also vary in number and distinctness (4–45 observed in South Africa). Hartlaub reports nematothecae arising from the hydrorhiza in material from South America. Occasionally a few of the hydrothecae rise erect from the substratum with no adnate part.

The only previous description of the coppinia of this species is that of Ritchie (1911), which unfortunately was not illustrated. Ritchie states that the accessory tubes either ‘stand out stiffly from the surface . . .’ or ‘. . . do not project, but instead lie closely apposed to each other, parallel to the surface of the coppinia’. The variability of the tubes can be confirmed.

The planulae appear to become trapped by the basket-work of the accessory tubes and pour out when the coppinia is cut.

Distribution. Cosmopolitan. Type locality: Cuba.

Distribution in South Africa. Scattered, from the south-west Cape round the Agulhas Bank to Natal and Moçambique, 24–347 m. 34/18 (d), 35/19 (d), 35/22 (d), 33/25 (s), 30/30 (s), 24/35 (d)

Genus Hebella Allman, 1888

Syn. Hebellopsis Hadzi, 1913.

Diagnosis. Colony stolonial, with stalked hydrothecae arising from a creeping hydrorhiza. Hydrotheca cylindrical or deeply campanulate, distinctly demarcated from pedicel, usually with annular perisarcal thickening around base (always in South African species), with or without a true diaphragm. Gonothecae arising singly from the hydrorhiza, producing free medusae. No nematophores.
Fig. 59.

*Filellum serratum.* A and B, hydrothecae illustrating extremes in size; C, t.s. part of coppinia, showing gonothecae and accessory tubes, from the same colony as the small hydrothecae. *Hebella parvula.* D, hydrothecae, redrawn from Stechow (1925a, as *Hebelopsis parvula*). *Hebella dispolians.* E, colony infesting *Amphisbetia maplesonei,* redrawn from Warren (1909 as *Laofea dispolians*).

Abbreviations: *ep* and *pa:* epizootic and parasitic parts of *Hebella; ho:* parts of host.

Scale in mm/10
Medusae imperfectly known, with at least two marginal tentacles and no cirri.

Type species: *Hebella striata* Allman, 1888.

**KEY TO SPECIES**

1. Hydrotheca very small (under 0.4 mm in height) ... ... ... ... ... 2
   - Hydrotheca larger (over 0.5 mm in height) ... ... ... ... ... 3

2. Colony with epizootic and parasitic forms, the latter invading the perisarce of the host and making use of its hydrothecae in place of its own. Epizootic form with cylindrical hydrothecae of about 0.4 mm in height ... ... ... ... ... *H. dispilans*
   - Colony with epizootic form only. Hydrotheca minute (under 0.2 mm in height), cylindrical ... ... ... ... ... ... ... ... ... *H. parvula*

3. Colony with epizootic and parasitic forms, the latter invading the perisarce of the host but producing its own hydrothecae. Hydrotheca expanding to margin, margin strongly everted ... ... ... ... ... ... ... ... ... *H. jurax*
   - Colony with epizootic form only. Hydrotheca cylindrical, not expanding to margin, margin not, or only very slightly, everted ... ... ... ... ... ... ... *H. scandens*

*Hebella dispilans* (Warren, 1909)

Fig. 59E


**Diagnosis.** Colony epizootic and parasitic on *Amphisbeta maplestonei*, with the hydroprhiza penetrating into the perisarce of the host or creeping over the surface.

Hydrotheca of epizootic form cylindrical, symmetrical or somewhat irregular; margin not everted and perpendicular to axis; 0.4 mm in length and 0.18 mm in marginal diameter. Annular thecal thickening present. Pedicel short, not annulated.

Hydrotheca of parasitic form giving rise to hydranths which either utilize the hydrothecae of the host or supplement them with short, terminal, perisarcal collars.

Hydranth with eight tentacles.

Gonophores unknown.

**Remarks.** The parasitic form of this unique species gains entry through the hydrothecae of the host, apparently killing the hydranths and replacing them with its own. The hydroprhiza may penetrate into the coenosarce of the host; it is normally without a perisarcal covering of its own, though the host tends to secrete perisarcal partitions or tubes to isolate it. The growing tips are in direct contact with the coenosarce of the host and can presumably obtain nourishment from it.

**Distribution.** Endemic to South Africa. Type locality: Isipingo, Natal.

**Distribution in South Africa.** Not reported since Warren’s original description.
Hebella furax Millard, 1957

Fig. 60A–C

Hebella furax Millard, 1957: 200, fig. 8. Millard, 1964: 10, fig. 2B–D.

Diagnosis. Colony epizootic on plumulariid hydroids of the subfamily Aglaopheninae, particularly Lytocarpus filamentosus, with the hydrorhiza sometimes penetrating into the perisarc of the host as a parasitic form.

Hydrotheca of epizootic form deep-campanulate and usually asymmetrical, smooth, with everted and slightly oblique margin, 0.6–1.2 mm in height and 0.4–0.6 mm in marginal diameter. Annular thecal thickening pronounced, usually better developed on one side than the other. Réduplications of margin common. Pedicel with 3–6 spiral annulations, 0.13–0.7 mm in length.

Hydrotheca of parasitic form emerging from hydrotheca or broken end of hydrocladium of host, similar to epizootic form though generally smaller, 0.6–0.9 mm in height and 0.3–0.5 mm in marginal diameter. Pedicel usually shorter than epizootic form, 0.03–0.17 mm in length, smooth or with one or two spiral annulations.

Hydranth with about 17 tentacles.

Female gonotheca usually curved, trumpet-shaped, widening gradually from a slender corrugated pedicel to a wide and everted margin, with smooth or slightly corrugated walls, with cap-shaped operculum, 1.6–2.5 mm in total height and 0.5–0.8 mm in marginal diameter. Containing several medusa-buds one above the other. Medusa with at least three long marginal tentacles and a four-lipped mouth.

Remarks. The species was named for the parasitic form, which was discovered first (furax = thievish), though later it was found to be less common than the epizootic form. The parasitic hydrorhiza apparently gains entry to the host through the mamelon or through a damaged part of the perisarc. It has no perisarcal covering of its own, making use instead of that of its host. The parasitic pedicels acquire their own perisarcal covering on emergence, but they appear to make use partly of the hydrothecae of the host, for they are usually shorter than in the epizootic form. The infected parts of the host are always dead. No gonophores have been observed to arise from parasitic hydrorhizae.

The parasitism in this species is not so extreme as in H. dispolians, for the hydrorhiza does not invade the coenosarc of the host but runs alongside it. Further the hydranths do not utilize the hydrothecae of the host to the same extent. See also remarks on Scandia mutabilis.

Distribution outside South Africa. Seychelles.

Distribution in South Africa. South coast, from False Bay to East London, in depths of 4 to 49 m. Off Natal and Moçambique, 2–42 m. Type locality: False Bay, 34/18 (s), 34/21 (s), 34/22 (s), 33/25 (s), 33/27 (s), 32/28 (s), 30/30 (s), 26/32, 25/32, 25/33 (s), 24/35 (s)
Hebella parvula (Hincks, 1853)

Fig. 59D

Lafoëa parvula: Hincks, 1868: 203, pl. 40 (fig. 1).
Hebellopsis parvula: Stechow, 1925a: 441, fig. 16.

Diagnosis. Hydrotheca minute, cylindrical, of equal diameter throughout, less than twice as deep as wide, smooth, symmetrical, margin not everted and perpendicular to axis, 0.16–0.19 mm in height and 0.08 mm in marginal diameter. Reduplications present. Annular thecal thickening present. Pedicel annulated, with about four rings, 0.07 mm in length.

Gonoophores unknown.

Distribution outside South Africa. Ireland (type locality), White Sea.

Distribution in South Africa. Reported once only by Stechow from the Agulhas Bank in 100 m. 35/20 (d)

Hebella scandens (Bale, 1888)

Fig. 60F–G

Hebella urceolata Millard, 1964: 12, fig. 2A.

Diagnosis. Colony epizootic on other hydroids. Hydrotheca cylindrical, of equal diameter or narrowing at or below margin, 2½–3½ times as deep as wide, smooth or lightly corrugated, usually asymmetrical and bent slightly to one side, margin not or only slightly everted and usually oblique, 0.5–1.0 mm in height and 0.19–0.3 mm in marginal diameter. Annular thecal thickening present and to it attached a thin diaphragm. Reduplications of margin common. Pedicel smooth or corrugated, 0.12–0.3 mm in length. Hydranth with about 13 tentacles.

Gonotheca widening gradually from a slender pedicel to a wide margin which is not everted, irregularly corrugated, with an operculum of four valves inserted in four bays in the margin, 1.1–1.4 mm in total height and 0.4–0.5 mm in marginal diameter. Containing up to four medusa-buds, one above the other. Medusa at liberation with a simple mouth, two long, opposite marginal tentacles, and rudiments of two other perradial tentacles and four interradial tentacles. Adult medusa unknown.

Remarks. This is a very common species, epizootic on many species of Sertulariidae, particularly Sertularella arbuscula, and also less commonly on Haleciidae, Syntheciidae and Plumulariidae. It grows profusely and often completely obscures the host.

One example has been seen in which the hydrorhiza penetrates the perisarc of the host, where it loses its own perisarcal covering and runs side by side with the coenosarc of the host, but this is apparently a rare condition.
Fig. 60.

*Hebella furax*. A, hydrotheca of epizootic form; B, hydrotheca of parasitic form infesting *Lytocarpus filamentosus*; C, gonotheca with medusa-buds.

*Scandia mutabilis*. D and E, hydrothecae.

*Hebella scandens*. F, hydrothecae; G, gonotheca with medusa-buds.

Scale in mm/10.
The name of *H. scandens* is used for this species in preference to *H. calcarata* for the reasons given by Rees & Thursfield (1965: 76).

In view of the discovery of intermediate forms *H. urceolata* has now been sunk in the synonymy of *H. scandens*.

**Distribution.** Cosmopolitan. Type locality: East Australia.

**Distribution in South Africa.** Common all round the coast from Lambert’s Bay on the west to Moçambique on the east, littoral and 0–164 m. 32/18 (s), 33/17 (s), 33/18 (l, s), 34/18 (l, s), 34/19 (s), 34/20 (s), 35/20 (d), 34/21 (s), 35/21 (d), 34/22 (s), 34/23 (s, d), 33/25 (s), 34/25 (s), 33/26 (s), 33/27 (s), 33/28 (s), 32/28 (s), 31/29 (s), 31/30 (l, s), 30/30 (l, s), 30/31 (s, d), 29/31 (s, d), 29/32 (s, d), 28/32 (s, d), 26/32 (s), 25/32, 25/33 (s), 24/35 (s), 23/35 (l), 21/35

**Genus Lafoea** Lamouroux, 1821

**Diagnosis.** Colony normally erect, rarely with stolonal form. Erect stem fascicled and branching; stem and branches bearing hydrothecae from all surfaces. Hydrotheca cylindrical to deep-campanulate, usually asymmetrical, free from stem, not distinctly demarcated from pedicel, with no diaphragm or annular perisarcal thickening, but with a ring of refringent dots marking the base of the hydranth. No nematothecae. Gonothecae aggregated to form a coppinia, which also contains modified protective hydrothecae. Gonophores in the form of fixed sporosacs.

Type species: *Sertularia dumosa* Fleming, 1820.

**Remarks.** The four South African species of this genus are extremely difficult to distinguish as they tend to grade into one another and combine features of the accepted European species. The most common form agrees best with *L. fruticosa*. *L. benthophila* was originally described as a large variety of *L. gracillima*. *L. gracillima* and *L. fruticosa* have been united by Naumov. Totton keeps them separate, although his figures of the hydrothecae of the two species appear identical. *L. dumosa* is perhaps the most easily distinguished, though it is possible that all the South African material should be included in one species. For the present they have been kept separate as recorded in the literature, with the hope that in time the problem will be clarified by the discovery of more reproductive bodies. So far only one coppinia has been discovered (assigned to *L. fruticosa*).

The key which follows is based mainly on the conception of Broch and Stechow, but is unsatisfactory in that it does not cover intergrading forms.

**KEY TO SPECIES**

1. Hydrotheca held perpendicular to stem or branch, with no distinct pedicel, but merely an indentation at base.
   - Hydrotheca held at an angle to stem or branch, with a distinct pedicel
2. Hydrotheca large, over 0,9 mm in height including pedicel
   - Hydrotheca small, under 0,9 mm in height including pedicel

   **L. dumosa**

   **L. benthophila**

   **L. fruticosa**
Lafoea benthophila Ritchie, 1909

Fig. 61G

Lafoea gracillima var. benthophila Ritchie, 1909: 76, fig. 2.
Lafoea benthophila: Stechow, 1925a: 455, fig. 24D. Vervoort, 1966b: 124, fig. 27.

Diagnosis. Colony small, reaching a height of 18 mm. Stem fascieled in lower parts, branching irregularly.

Hydrotheca pedicellate, forming an angle with stem, deep-conical and expanding slightly to margin, curved outwards, large (1.0 mm in height including pedicel, 0.2 mm in marginal diameter). Reduplications of margin common. Pedicel short (0.14–0.15 mm), without definite annulations, smooth or with 1–3 weak spiral twists.

Coppinia imperfectly known (not recorded from South Africa). Gonoophores producing acrocysts, protected by ‘spiral hydrothecae’ (Stechow).


Distribution in South Africa. Reported only once in 425–430 m off Natal by Vervoort (1966b). 29/31 (d)

Lafoea dumosa (Fleming, 1820)

Sertularia dumosa Fleming, 1820: 84.
Lafoea dumosa: Broch, 1909: 156, fig. 16. Stechow, 1925a: 455, fig. 24A. Fraser, 1944: 221, pl. 45 (fig. 205), pl. 46 (fig. 205).

Diagnosis. Colony stiff and bushy, reaching a height of 20 mm. Stem fascieled in lower parts, branching irregularly.

Hydrotheca without definite pedicel, separated from stem by indentation only and with only occasional indications of a spiral twisting, held more or less perpendicular to the stem, deeply conical and widening to margin, scarcely asymmetrical and curved only slightly outwards, 0.6–0.7 mm in height including pedicel and 0.14–0.16 mm in marginal diameter. Reduplications of margin occurring. Exists also in creeping form, with solitary hydrothecae arising direct from hydrohiza.

Coppinia (not recorded from South Africa) hermaphroditic, with closely packed gonothecae and long, tubular, curved hydrothecae projecting above them. Gonotheca hexagonal in section, with terminal aperture on short neck.


Distribution in South Africa. Reported only once in 106 m off Cape Town by Stechow (1925a). 33/18 (d)
Fig. 61.

*Lafoea fruticosa*. A, stem; B, part of fascicled stem to show branching; C, hydrothecae; D, surface view of part of coppinia; E, t.s. part of coppinia, with gonothecae (one with an acrozyst) and tubular hydrothecae; F, epizootic colony growing on an older colony.


Scale: A in cm, the rest in mm/10.
Lafoea fruticosa (M. Sars, 1851)

Fig. 61A–F

Campanularia fruticosa M. Sars, 1851: 138.
Campanularia gracillima Alder, 1856: 361, pl. 14 (figs 5–6).

Diagnosis. Colony usually shrubby in appearance, though not stiff, reaching a height of 90 mm. Stem and main branches fascicled, giving off branches irregularly from the accessory tubes.

Hydrotheca pedicellate, forming an angle of 40–60° with stem, usually deeply campanulate and asymmetrical due to a greater convexity on adcauline wall, 0.5–0.9 mm in height including pedicel and 0.11–0.19 mm in marginal diameter. Margin very slightly everted. Reduplications of margin common. Pedicel 0.09–0.3 mm in length, with one or more spiral twists. Exists also in stolonial form, with solitary hydrothecae arising directly from hydrothiza.

Coppinia with closely packed gonothecae and very long, tubular, coiled hydrothecae projecting above them. Gonothecae bottle-shaped with terminal aperture on short neck, more or less hexagonal in section, producing acrocysts, about 0.4 mm in height. Hydrothecae over 3 mm in length.

Variation. The branching follows no definite scheme, though in the distal regions of the colony the branches do tend to be in one plane and often unilateral. Stolons arising from the tips of the branches and anastomosing with other regions may result in a matted and shrubby effect.

The hydrothecae show much variation in shape, even within the same colony. Apart from the typical shape described above, some are very slender with almost parallel walls, and some are shorter and more obviously campanulate.

A pedicel is always distinct and is typically bent or twisted with two or three kinks, one adcauline, the second abcauline, and sometimes a third less-marked adcauline one.


Distribution in South Africa. Along the south and east coasts, from off Table Bay in the west into Moçambique on the east, in 64 to 430 m. 33/18 (s), 34/18 (s), 35/20 (d), 35/22 (d), 34/23 (d), 33/27 (s), 29/31 (s, d), 29/32 (s, d), 28/32 (s, d), 24/35 (d)

Genus Scandia Fraser, 1912

Diagnosis. Colony stolonial, with stalked hydrothecae arising directly from a creeping hydrothiza. Hydrothecae deeply campanulate, distinctly demarcated from pedicel, with an annular perisarcal thickening around base. Gonothecae
arising singly from the hydrorhiza, containing fixed sporosacs. No nemato-
phores.

Type species: *Campanularia mutabilis* Ritchie, 1907.

One species only in South Africa.

*Scandia mutabilis* (Ritchie, 1907)

Fig. 60D–E

*Campanularia mutabilis* Ritchie, 1907a: 504, pl. 23 (figs 3–5).
*Campanularia corrugata*: Billard, 1907a: 341, fig. 1. Jarvis, 1922: 337, pl. 24 (fig. 5).
*Lafoea magna* Warren, 1908: 342, fig. 22.
*Hebella corrugata*: Broch, 1914: 30, fig. 6.

**Diagnosis.** Colony growing on weed and other hydroids. Hydrotheca large, deep-campanulate and often asymmetrical, usually smooth, with strongly everted and frequently oblique margin, 1,1–3,9 mm in height and 0,6–2,2 mm in marginal diameter. Annular thecal thickening present. Pedicel with 3–11 spiral annulations, 0,2–4,2 mm in length. Hydranth with about 22 tentacles.

Gonotheca (not reported from South Africa) with short pedicel of one segment; male smooth and pear-shaped; female elongate-oval with truncated distal end, more or less corrugated, containing many eggs.

**Variation.** This species varies considerably in the size and shape of the hydrotheca. Rarely a few shallow transverse corrugations occur. Reduplications of the margin are sometimes present.

**Remarks.** The trophosome is very similar to that of *Hebella furax* and is distinguished only by the greater size of the hydrotheca. The dimensions in fact overlap, though the mean height of the hydrotheca in *H. furax* is 0,8 mm (68 measurements) and in *S. mutabilis* 1,7 mm (51 measurements). The pedicel length is so variable that it cannot be used as a distinguishing character, though it tends to reach greater lengths in *S. mutabilis*.

**Distribution outside South Africa.** Atlantic Ocean from the West Indies to tropical West Africa and Cape Verde. Indian Ocean from tropical East Africa to Ambon. Type locality: Cape Verde Is.

**Distribution in South Africa.** False Bay, Cape, to Moçambique, littoral to 44 m. 34/18 (s), 34/21 (s), 34/23 (l), 33/26 (l), 30/30 (s), 26/32 (s), 25/32, 24/35 (s), 23/35 (l).

**Genus Zygophylax** Quelch, 1885

*Brucella* Ritchie, 1907.

**Diagnosis.** Colony normally erect, rarely with stolonal form. Erect stem fascicled or unfascicled, branched or unbranched; when fascicled, branches arising from axial tube and usually subalternate. Stem (and branches when
present) bearing hydrocladia, which are often not distinguishable from branches. Hydrothecae arising from stem, branches and hydrocladia alternately in two rows and from the axial tube when fascicled. Hydrotheca free from stem or hydrocladium, pedicellate, not externally demarcated from its pedicel, but with it forming a bilaterally symmetrical figure whose shape is characteristic of the species, internally demarcated from pedicel by a diaphragm. Nematothecae usually present (always in South African species). Gonothecae usually aggregated to form a coppinia, which usually also contains modified protective hydrothecae or nematothecae. Gonophores in the form of fixed sporozae.

Type species: *Zygophylax profunda* Quelch, 1885.

**KEY TO SPECIES**

1. At least some of the hydrocladia forked ........................................ 2
   - Hydrocladia never forked. Gonothecae, where known, aggregated into coppinia 3

2. Pedicel less than \(\frac{1}{2}\) length of hydrotheca (usually \(\frac{1}{2}\)). Gonothecae in pairs, not forming coppinia ........................................ 4
   - Pedicel more than \(\frac{1}{2}\) length of hydrotheca (usually \(\frac{1}{2}\)). Gonothecae unknown Z. ?geniculata 5
3. Hydrotheca cornucopia-shaped, with plane of margin turned towards adcauline side 4
   - Hydrotheca deep-campanulate or tubular, with plane of margin at right angles to axis or turned towards adcauline side ........................................ 5

4. Hydrotheca and pedicel of about equal length ........................................ 6
   - Hydrotheca about twice as long as pedicel Z. infundibulum 7

5. Hydrotheca large (diameter at mouth over 0.16 mm). Nematothecae only rarely present on stem apophyses. Coppinia without nematothecae Z. antipathes 7
   - Hydrotheca smaller (diameter at mouth under 0.17 mm). Nematothecae regularly present on stem apophyses. Coppinia with modified nematothecae Z. africana 8

6. Hydrotheca tubular, strongly curved outwards, slender (length 2\(\frac{1}{2}\)-3\(\frac{1}{2}\) times diameter at mouth). Coppinia closed. Gonotheca with paired distal horns over-arching lateral orifices. One nematotheca on each apophysis Z. africana 7
   - Hydrotheca shorter and wider, asymmetrical but not markedly curved outwards (length 1\(\frac{1}{2}\)-3\(\frac{1}{2}\) times diameter at mouth). Two nematothecae on each apophysis Z. africana 8

7. Coppinia closed. Gonotheca with a single, short distal tube and terminal orifice Z. armata 7
   - Coppinia open. Gonotheca with two curved necks with terminal orifices Z. biarmata 8

*Zygophylax africana* Stechow, 1923

Fig. 62A-E

*Zygophylax africana*: Stechow, 1925a: 445, fig. 18. Millard, 1964: 15, fig. 4A-F. Millard, 1973: 28, fig. 4B.

**Diagnosis.** Colony erect and branching, reaching a height of 100 mm. Stem somewhat flexuous (not able to support itself out of fluid), fascicled, unsegmented, giving rise to alternate hydrothecae and subalternate branches or hydrocladia from the axial tube. Larger branches fascicled, given off in one plane and at a wide angle to the stem (70–90°), giving rise to hydrothecae and hydrocladia in a similar manner. Hydrocladia lightly fascicled or unfasicled, unsegmented, generally arising below every third and fourth hydrotheca. The two rows of hydrothecae in one plane.

Hydrotheca and pedicel seated on a short apophysis, slender at base, then
widening to a tubular structure which is curved definitely outwards, with slightly everted margin, 0.3–0.4 mm in total adcauline length and 0.07–0.10 mm in marginal diameter. Pedicel short, $\frac{3}{15}$–$\frac{3}{6}$ length of hydrotheca. Diaphragm oblique with adcauline edge higher than adcauline, with central hydropore.

Nematothecae tubular, normally one on each hydrothecal apophysis, and irregularly scattered on hydorhiza and peripheral tubes of stem.

Gonothecae aggregated into a coppinia, firmly adpressed to one another for about $\frac{3}{4}$ length, then free. Each gonotheca widening from base to top of contiguous portion, with free part slender and bearing two lateral orifices and two distal divergent horns. Coppinia provided with long, branching nematothecae, at least twice length of gonothecae, male and female similar.

Variation. The branching may show irregularities and occasionally an arrangement whereby branches arise below every third hydrotheca. Anastomoses between branches are common. Occasional transverse nodes may occur within branches and hydrocladia. Axillary hydrothecae are shifted onto the apophyses of the hydrocladia, as are their nematothecae. Reduplications of the thecal margin are common.

Solitary hydrothecae may arise from the hydorhiza or from young epizootic colonies; these are curved as in the adult or quite symmetrical and straight.

Distribution. Endemic to South Africa. Type locality: off Cape Town, 33°41' S/18°0' E

Distribution in South Africa. West coast to Agulhas Bank in 137–363 m. 29/14 (d), 30/15 (d), 33/18 (d), 34/18 (d), 35/22 (d), 34/24 (d)

Zygoephyllx ?antipathes (Lamarck, 1816)

Fig. 62F–G

Sertularia antipathes Lamarck, 1816: 115.
Lictorella halecioideus Allman, 1888: 35, pl. 17 (figs 1–2).
Lictorella cyathifera Allman, 1888: 36, pl. 11 (figs 3–3a).
Lictorella antipathes: Billard, 1910: 6, fig. 1. Totton, 1930: 166.

Diagnosis. Colony erect and branching, reaching a height of 47 mm. Stem moderately stiff, fascicled, unsegmented, giving rise to alternate hydrothecae and subalternate branches or hydrocladia from the axial tube. Larger branches fascicled at base, given off in one plane and at almost right angles to the stem, giving rise to hydrothecae and hydrocladia in a similar manner. Hydrocladia unfascicled; unsegmented; generally arising below every third and fourth hydrotheca. The two rows of hydrothecae in one plane or shifted slightly on to the anterior surface.

Hydrotheca and pedicel seated on a short apophysis, deep-campanulate, symmetrical or (more often) asymmetrical with the adcauline side more convex than the adcauline, with slightly everted margin, 0.4–0.6 mm in total length and 0.17–0.2 mm in marginal diameter. Pedicel $\frac{1}{6}$–$\frac{3}{10}$ length of hydrotheca.
Zygophylax africana. A, t.s. part of coppinia, with female gonothecae and branching nematothecae; B, surface view of coppinia; C, solitary hydrothecae; D, part of fascicled stem to show branching (branches cut off short); E, part of branch.

Zygophylax ?antipathes. F, basal part of hydrocladium with axillary and following two hydrothecae; G, stem.

Scale: D and G in mm, the rest in mm/10.
Diaphragm thick, straight and at right angles to hydrothecal axis, with central hydropore.

Nematothecae tubular, scarce, seated on hydrothecal apophyses, but only one or two to a branch.

Gonothecae (not reported from South Africa) aggregated into a coppinia, with hooded apertures and no protective nematothecae. (From Totton.)

*Variation.* Stems have been reported to reach as much as 120 mm outside South Africa. The usual irregularities occur in the method of branching, and occasional transverse nodes may occur in the stem and hydrocladia. Axillary hydrothecae are shifted on to the apophyses of the hydrocladia. The pedicel of the hydrotheca is usually separated from its apophysis by a distinct node, but the node is sometimes incomplete or absent altogether.

*Remarks.* The final identification of this species must await the discovery of gonophores. It is closely related to *Z. armata* and *Z. biarmata*, differing from them in the larger hydrothecae, stronger diaphragm and scarce nematothecae.

*Distribution outside South Africa.* Australasia (type locality: 'mers australies ou de la Nouvelle-Hollande'), East Indies, South Pacific (New Hebrides), ?Seychelles.

*Distribution in South Africa.* Off Natal and Moçambique in 6–110 m. 30/30 (s), 29/31 (s), 28/32 (s), 26/34 (s), 25/33 (s), 24/34 (s), 24/35 (d)

*Zygophylax armata* (Ritchie, 1907)

Fig. 63A–B

*Brucella armata* Ritchie, 1907b: 533, pl. 2 (fig. 2-2C).


*Diagnosis.* Colony erect and branching, reaching a height of 42 mm. Stem stiff and fascicled, unsegmented, giving rise to alternate hydrothecae and roughly alternate branches or hydrocladia from the axial tube. Main branches fascicled, given off in one plane and at an angle of 50–80° to stem, giving rise to hydrocladia in a similar manner. Hydrocladia unfascicled or lightly fascicled, unsegmented, each arising from immediately below a hydrotheca. The two rows of hydrothecae in one plane or shifted onto the anterior surface.

Hydrotheca and pedicel seated on a short apophysis, slender at base, then widening to an asymmetrical tubular structure with a convex adapaline wall and a straight or slightly concave adapaline wall, 0.19–0.4 mm in total adapaline length and 0.10–0.16 mm in marginal diameter. Pedicel short, $\frac{1}{3} - \frac{1}{4}$ length of hydrotheca. Diaphragm straight or slightly oblique, with central hydropore.

Nematothecae tubular, normally two on each hydrothecal apophysis (one anterior and one posterior) and irregularly scattered on peripheral tubes of stem.

Gonothecae (not reported from South Africa) aggregated into a coppinia,
flask-shaped with short and slender distal neck and terminal orifice. Coppinia provided with numerous long, branching nematothecae. (From Ritchie.)

Variation. The branching is much more irregular than in other closely related species of Zygophylax and only rarely does the subalternate arrangement typical of so many Ldaoidea occur. A height of 60 mm has been reported from outside South Africa. The margin of the hydrotheca is often slightly everted.

Solitary hydrothecae may arise separately from the hydrorhiza or from epizootic colonies. These tend to be less bilaterally symmetrical than in the adult, and are often quite irregular.

Remarks. Though the trophosome of this species agrees perfectly with the original description, the identity cannot be absolutely certain until fertile material is discovered.

Distribution outside South Africa. Off Gough Island in the South Atlantic (type locality).

Distribution in South Africa. From the south-east coast of the Cape Province northwards into Moçambique in 48–440 m. 33/27 (s), 33/28 (s), 30/31 (s), 29/31 (s, d), 29/32 (s), 28/32 (s, d), 24/35 (d)

Zygophylax ?biarmata Billard, 1905

Fig. 63C


Diagnosis. Trophosome as in Zygophylax armata.

Gonothecae (not recorded from South Africa) aggregated into a loose (or open) coppinia, ‘flattened-ovate, with an outward and downward curving neck distally on either side in the transversal plane’. Coppinia richly provided with nematothecae. (From Broch.)

Remarks. Z. biarmata is essentially a north Atlantic species. The coppinia was described by Broch, though unfortunately not illustrated, from material from Iceland. The coppinia is completely different from that of Z. armata, though there seems little to distinguish the trophosomes. Infertile material recorded as Z. biarmata from East Africa by Jarvis and from South Africa doubtfully by Millard possibly all belongs to Z. armata. Z. biarmata is included here since the possibility of its presence in the country cannot be disregarded. Only the discovery of fertile material can settle the question.

Distribution outside South Africa. Bay of Biscay and Straits of Gibraltar (type locality), North Atlantic (Iceland to north-west Africa), ?Japan, ?Tropical East Africa.

Distribution in South Africa. Dubious records from off Natal in 164–333 m. ?30/31 (d), ?29/31 (d)
Fig. 63.

*Zygophylax armata.* A, part of hydrocladium; B, stem.

*Zygophylax biarmata.* C, hydrothecae.

*Zygophylax gennocarpa.* D, part of hydrocladium; E, caulin hydrotheca with nematothecae; F, a pair of gonothecae; G, stem.

Scale: B, F and G in mm, the rest in mm/10.
Zygophylax geminocarpa Millard, 1958

Fig. 63D–G

*Zygophylax geminocarpa* Millard, 1958: 177, fig. 4D–G.

**Diagnosis.** Colony erect and branching, reaching 110 mm. Stem and main branches stiff, woody and heavily fascicled, giving rise to smaller, lightly fascicled branches and unfascicled hydrocladia subalternately and in one plane. Smaller branches giving off hydrocladia in a similar manner. Stem and branches bearing alternate hydrothecae from the axial tube, usually three and one alternately between consecutive branches of hydrocladia, those of the thicker parts buried by the peripheral tubes. Hydrocladia bearing alternate hydrothecae; either simple, with the two rows of hydrothecae in one plane; or forked at the base in a plane at right angles to the normal plane of branching, with the two rows of hydrothecae on each limb not in one plane but seated on the inner surface of the fork. Branches and hydrocladia with occasional transverse nodes at irregular intervals.

Hydrotheca seated on a short apophysis and a pedicel. Pedicel and hydrotheca together widening fairly rapidly to form a bilaterally symmetrical figure with a bulging adcauleine wall and a more or less straight adcauleine wall, and with margin everted, more so on adcauleine side; 0.4–0.5 mm in adcauleine length and 0.17–0.2 mm in marginal diameter. Pedicel about one quarter length of hydrotheca. Diaphragm thick, with central hydropore.

Nematotheca tubular, swollen at or below margin, two-chambered, with basal chamber very small; 1–4 (usually 2) on each hydrothecal apophysis, and irregularly scattered on peripheral tubes of stem.

Gonothecae not aggregated into coppinia, but attached in pairs (rarely single), these pairs occurring in dense clusters around certain areas of stem and main branches. Gonotheca elongated, tapering to tip, round in section, fused to its twin for about \(\frac{3}{4}\) length, then free, bearing scattered nematothecae on lower part.

**Distribution.** Endemic to South Africa. Type locality: off Port Shepstone, Natal.

**Distribution in South Africa.** Reported only once as above. 30/30 (s)

*Zygophylax ?genuculata* (Clarke, 1894)

Fig. 64

*Lictorella genuculata* Clarke, 1894: 74, pl. 3.

*Zygophylax genuculata*: Leloup, 1940: 13, pl. 1 (fig. 9).


**Diagnosis.** Colony erect and branching, reaching a height of 50 mm. Stem stiff, fascicled, unsegmented, giving rise to alternate hydrothecae and subalternate branches or hydrocladia from the axial tube. Branches fascicled, given off in one plane and almost at right angles to stem, giving rise to hydrocladia in a similar manner. Hydrocladia unfascicled or lightly fascicled at base; with distant
Fig. 64.

*Zygophylax* ?geniculata. A, part of stem and hydrocladia (some forked); B, hydrocladium; C–E, hydrothecae and nematothecae (the third hydrotheca is axillary).

Scale: A in mm, the rest in mm/10.
and irregular transverse nodes; generally arising below every third and fourth hydrotheca of stem; bearing alternate hydrothecae; often subdichotomously forked at the base in a plane at right angles to the normal plane of branching, the anterior limb of the fork being less well developed than the posterior. The two rows of hydrothecae in one plane or shifted towards the anterior surface, those of the anterior limb of a forked hydrocladium shifted towards the posterior surface.

Hydrotheca and pedicel seated on a short apophysis from which they are separated by at least one internode bounded by transverse nodes. Pedicel and hydrotheca slender proximally, widening just beyond diaphragm where the acauline wall is usually more convex than the acauline, slightly constricted just below margin: 0.4–0.5 mm in length and 0.11–0.15 mm in marginal diameter. Margin slightly everted and perpendicular to axis. Pedicel 3/5–1/5 length of hydrotheca and forming an angle of up to 70° with stem. Diaphragm delicate, straight or oblique, with central hydropore.

Nematothecae tubular, scarce, on peripheral tubes of stem, apophyses of hydrocladia and apophyses of hydrothecae.

Gonothecae unknown.

Remarks. The material assigned to this species shows certain differences from the type material, viz. the presence of a segment below the hydrothecal pedicel, the forking of some hydrocladia and the presence of nematothecae. It is close to Z. bifurcata Billard, 1942, from the Isle of Timor. This species has bifurcated hydrocladia throughout and very similar nematothecae, but the pedicel of the hydrotheca is much longer and the hydrotheca larger. Final identification must await further material and gonothecae.

Distribution outside South Africa. Gulf of Panama (type locality), Azores.

Distribution in South Africa. Reported only once from off the Cape Peninsula in 287 m. 34/18 (d)

Zygophy lax infundibulum Millard, 1958

Fig. 65D–E

Zygophy lax infundibulum Millard, 1958: 180, fig. 4B–C.

Diagnosis. Colony erect and branching, reaching a height of 60 mm. Stem moderately stiff, fascicled, unsegmented, giving rise to alternate hydrothecae and subalternate branches or hydrocladia from the axial tube. Branches fascicled, given off in one plane and at a wide angle to the stem (50–60°), giving rise to hydrothecae and hydrocladia in a similar manner. Hydrocladia unfascicled or lightly fascicled, unsegmented; generally arising below every third and fourth hydrotheca; bearing alternate hydrothecae. The two rows of hydrothecae not in one plane but on anterior surface, with an acute angle between them and with the members of one row rotated so that they face slightly away from those of the other row.
Hydrotheca and pedicel seated on a short apophysis; widening gradually to margin; together with a cornucopia shape and double curvature (first outwards, then upwards), 0.6-0.7 mm in total length and 0.11-0.14 mm in marginal diameter. Pedicel about half length of hydrotheca. Diaphragm well formed, markedly funnel-shaped, better developed on abcauline side and with hydropore slightly off-centre.

Nematothecae elongate-oval, one on each hydrothecal apophysis.
Gonothecae unknown.

Variation. Many irregularities occur in the method of branching and the intervals between consecutive hydrocladia. Rare transverse nodes occur in the hydrocladia, midway between two hydrothecae. The hydrotheca in the axil of a hydrocladium is shifted on to the apophysis of the latter, and its nematotheca is not on its own apophysis but on that of the hydrocladium. Regeneration is common, especially within the pedicel and lower part of the hydrotheca.

Distribution. Endemic to South Africa. Type locality: off Natal.

Distribution in South Africa. Reported twice off Natal in 155-219 m. 29/31 (d)

Zygophylax sibogae Billard, 1918

Fig. 65A–C


Diagnosis. Colony erect and branching, reaching a height of 30 mm. Stem stiff, fascicled, unsegmented, giving rise to alternate hydrothecae and subalternate branches or hydrocladia from the axial tube. Branches fascicled, given off in one plane and at a wide angle to the stem (50–70°), giving rise to hydrothecae and hydrocladia in a similar manner. Hydrocladia unfascicled or lightly fascicled, unsegmented; generally arising below every third and fourth hydrotheca; bearing alternate hydrothecae. The two rows of hydrothecae not in one plane but borne on anterior surface, with an acute angle between them and with the members of one row rotated so that they face slightly away from those of the other row.

Hydrotheca and pedicel seated on a short apophysis: slender and tubular for the proximal half, then widening and strongly recurved towards distal end of colony in the manner of a cobra's hood, 0.5-0.6 mm in total length and 0.11-0.13 mm in marginal diameter. Pedicel of approximately same length as hydrotheca. Diaphragm well formed, often funnel-shaped, with central hydropore.

Nematothecae tubular, on the peripheral tubes and one on each hydrothecal apophysis.

Gonothecae (not reported from South Africa) aggregated into a coppinia in which some are tightly packed and some quite free, the whole provided with modified protective nematothecae. Free gonotheca spherical, with two recurved
Fig. 65.

*Zygophyla* *x sibogae*. A, stem; B and C, part of hydrocladium in ventral and anterior view respectively.

*Zygophyllax infundibulum*. D, stem; E, hydrocladium.

Scale: A and D in mm, the rest in mm/10.
distal extensions with terminal apertures. Fused gonothecae more variable and irregular.

*Distribution outside South Africa.* Dutch East Indies (type locality), New Zealand.

*Distribution in South Africa.* Reported once only, from the Agulhas Bank off the south-east coast in 88 m. 33/27 (s)

Family *Campanulariidae*

*Diagnosis.* Thecate hydroids with campanulate or cup-shaped hydrothecae, which may be radially or bilaterally symmetrical and into which the hydranth may or may not be completely withdrawn. Hydrotheca stalked, without operculum, with toothed or untoothed margin, divided into a small proximal and a large distal hydranth-containing region by a diaphragm or annular thickening of the perisarcal wall. Hydranth with trumpet-shaped hypostome, one circle of filiform tentacles and homogeneous endoderm. Nematophores absent. Gonophores in the form of fixed sporosacs or free medusae.

Medusa when present, with small stomach, no peduncle, usually four simple radial canals, no excretory pores, hollow or, rarely, solid marginal tentacles, no cirri, closed statocysts (marginal vesicles), no ocelli. Gonads borne on radial canals separated from stomach.

*Introduction.* Among the Campanulariidae the colony may be stolonic or erect. The erect stem is in reality a symposium in which each hydrotheca arises, alternately on the right and the left, from the base of the one below it, and is characteristically geniculate or zigzag. Branching commonly occurs, branches usually arising next to the hydrothecal pedicels, and normally of much the same strength as the stem itself. This results in feathery colonies with no thick and obvious main stem. Fascicled stems are comparatively rare. The stem is usually divided into internodes, each bearing a hydrotheca.

The hydrothecae are pedicellate, and the pedicels may be smooth, roughly corrugated or distinctly annulated. In the genus *Campanularia* there is always one distinct ‘spherule’ at the distal end of the pedicel, usually of a smaller diameter.

The hydrotheca is typically campanulate, or inverted bell-shaped, though variations do occur, some being almost tubular, others cup-shaped, and some distinctly bilaterally symmetrical. The basal part of the cavity of the hydrotheca is separated from the distal part containing the hydranth by a diaphragm or analogous structure. In the genera *Clytia, Obelia, Gonothyraea* and *Lulaomedea* a true diaphragm is present in the form of a thin perisarcal shelf on which the base of the hydranth rests. This diaphragm is usually exceedingly delicate, but occasionally, as in *Obelia geniculata* and some species of *Clytia*, it may be thickened and almost triangular in section. In the genera *Campanularia* and *Silicularia* there is no true diaphragm, but instead an annular thickening of
the perisarcal wall, to the upper surface of which the base of the hydranth is attached. This thickening may be either very marked or inconspicuous.

In the genus *Silicularia* and in certain species of *Campanularia* (previously included in a separate genus *Orthopyxis*) the walls of the hydrotheca may be grossly thickened. This thickening typically occurs on two opposite sides imparting a bilateral symmetry to the hydrotheca and an oval rather than a circular cross-section. In the relevant *Campanularia* species this thickening is not sufficient to prevent the complete withdrawal of the hydranth into the cavity. The thickening appears to be a potentiality rather than an invariable rule, and thickened, bilaterally symmetrical hydrothecae may occur side-by-side with unthickened, radially symmetrical ones. For this reason it is not logical to retain a separate genus *Orthopyxis*. In *Silicularia* the thickening is always present and is developed to such an extent that the cavity can no longer contain the retracted hydranth. Furthermore the bilateral symmetry is more pronounced, one side of the thecal margin being higher than the other.

![Diagram](image)

*Fig. 66.*
Campanulariidae: structure and types of hydrothecae.

The reproduction in the Campanulariidae is very variable, and all grades of gonophore from fixed sporosacs to free-swimming medusae occur. This has been the cause of much disagreement on the limitation of genera, some authors basing the classification on the trophosome only and ignoring the reproductive bodies and others creating different genera for all different types of reproductive body. Following the practice in this monograph separate genera are retained for forms with fixed sporosacs and forms with free medusae, including for this purpose the various grades of degenerate medusae from the styloid to the eumedusoid type with the fixed sporosacs. The difficulty is that it may be necessary to have fertile material in order to delegate it to its genus and species. Infertile colonies of *Obelia, Gonothyraea* and *Eulaomedea*, for instance, are very similar in appearance.

The names of the various grades of degenerate medusae are defined on p. 18, and examples of all these types can be found among the Campanulariidae. Occasionally more than one type may occur within the same species. In *Campanularia integra*, for instance, it has long been known that the gonosome
may produce either fixed sporo sacs, in which the eggs and planulae are retained in the gonotheca, or eumedusae with a short free-living existence (Agastera). It was thought that the difference was dependent on the season of the year, yet in South Africa the two types have been found within a single colony and at the same time. The control of the process is clearly not yet understood. In some species there is a sexual difference in the type of reproductive body; thus in Eulaomedea flexuosa the male gonophores are styloid and the female heteromodusoid.

Two genera which produce fully-formed medusae, namely Clytia and Obelia, have very similar trophosomes, differing only in the stolonial colonies of the former and the erect stems of the latter. The medusae, however, are very different, those of Clytia being hemispherical with hollow marginal tentacles and a well developed velum, and those of Obelia shallow saucer-shaped, with solid marginal tentacles and a reduced velum. These two genera must thus remain separate.

The genus Gonothyraea is closely related to Eulaomedea, which has fixed sporo sacs, but can be retained as a separate genus on the grounds of its unusual reproductive bodies, which are of the eumedusoid type and are extruded through the opening of the gonotheca, where they hang in clusters until the planulae are released. These medusiform bodies, which have comparatively well developed marginal tentacles, are known as meconidia (Fig. 74C–F).

Two genera of doubtful affinities have been omitted from the following key; they are not known in South Africa. Billardia Totton, 1930, placed in the Campanulariidae by Totton and by Ralph (1957), shows relationships with the Lafoeidae (in the curved bilaterally symmetrical hydrothecae) and with the Synthecidiidae (hydrothecae sometimes slightly adnate). Tulpa Stechow, 1921 is distinguished from Campanularia only by the greater size and characteristic shape (tulip-shape) of the hydrotheca.

**KEY TO GENERA**

[Genera not represented in South Africa are bracketed]

1. Colony stolonial
   - Colony with an erect stem, bearing alternate hydrothecae. Hydrotheca with true diaphragm, which is distinctly demarcated from its wall

2. Hydrotheca with true diaphragm, which is distinctly demarcated from its wall. Producing free medusae
   - Hydrotheca without true diaphragm, but with an annular perisarcal thickening near base. Producing fixed sporo sacs, which may rarely take the form of degenerate, short-lived medusae without stomach or marginal tentacles

3. Hydranth completely retractable into hydrotheca. Hydrotheca usually radially symmetrical, occasionally thickened and with bilateral tendencies
   - Hydranth not completely retractable into hydrotheca. Hydrotheca always bilaterally symmetrical and grossly thickened

4. Gonophores released as free medusae
   - Gonophores not released as free medusae

5

6
5. Medusa shallow, with 16 marginal tentacles, 8 statocysts and a rudimentary velum on liberation.
   - Medusa deep, with 4 marginal tentacles, numerous statocysts and a normal velum on liberation.
   
   Obelia p. 226

6. Gonophores forming degenerate medusae (meconidia) which are discharged into
   acrocysts where they become sexually mature.
   - Gonophores in the form of fixed sporoas or degenerate medusae which do not
     leave the gonotheca.

   Gonothyraea p. 224

Eulaomedea p. 223

Genus Campanularia Lamarck, 1816

Syn. Orthopyxis L. Agassiz, 1862.
   Eucopella von Lendenfeld, 1883.
   Agastra Hartlaub, 1897.

Diagnosis. Colony stolonial; hydrothecal pedicel unbranched, with at least
one terminal spherule. Hydrotheca campanulate or funnel-shaped, usually
radially symmetrical but sometimes grossly thickened on two opposite sides,
with toothed or untoothed margin. An annular perisarcal thickening present
inside base of hydrotheca. Hydranth completely retractable into hydrotheca.
Gonotheca borne on hydorhiza, containing fixed sporosacs or degenerate
medusae (eumedusae) which may rarely have a short free-swimming life.
Eumedusa, when present, without stomach, usually without marginal tentacles,
with four radial canals and eight closed statocysts.

Type species: Sertularia volubilis Linnaeus, 1758.

KEY TO SPECIES

1. Margin of hydrotheca never toothed. Perisarc capable of great thickening.
   - Margin toothed in at least some hydrothecae.

   C. integra

   2

2. Marginal teeth double or truncated.
   - Marginal teeth single; pointed or rounded.

   C. hinekii

   3

3. Perisarc never markedly thickened.
   - Perisarc of at least some hydrothecae grossly thickened.

   4

   5

   - Hydrotheca without raised rim. Gonotheca not annulated.

   C. morgans

5. Colony epizoic on Thyroscyphus. Gonotheca laterally compressed.
   - Colony growing on weed. Gonotheca round in section.

   C. laminarcarpa

   C. africana

   - Gonotheca not scallop-shaped, with terminal opening.

   7

   8

7. Hydrotheca asymmetrically thickened on the two sides. Gonophores in the form of
   fixed sporosacs.
   - Hydrotheca symmetrically thickened on two opposite sides. Gonophores eumedusoid
     with a short free-living life.

   C. roberti

   C. pecen

8. Most hydrothecae compressed, with low, rounded marginal teeth. Pedicel deeply and
   spirally grooved. Gonotheca compressed, widest at distal end.
   - Hydrotheca not, or only slightly, compressed, with deeper, triangular marginal teeth
     Pedicel closely annulated at both ends, smooth between. Gonotheca not compressed,
     widest near centre.

   C. ?delicata
Campanularia africana Stechow, 1923

Fig. 67A

Campanularia tincta: Warren, 1908: 337, fig. 18.
Campanularia africana Stechow, 1923b: 104.

Diagnosis. Colony growing on weeds and other hydroids, reaching 3 mm in height. Hydrothecal pedicel smooth or corrugated, with one spherule of smaller diameter at distal end.

Hydrotheca deep-campanulate, with almost parallel sides, 0.5–0.8 mm in depth and 0.3–0.5 mm in marginal diameter. Margin with 10–12 rounded teeth separated by rounded bays of approximately the same size. Hydranth with about 25 tentacles.

Gonotheca borne on hydrorhiza, cylindrical to ovate, round in section, smooth or with irregular corrugations, narrowing slightly towards distal end, then widening to low, everted collar around circular terminal aperture. Female containing eggs or planulae.

Remarks. Sterile colonies of this species cannot be distinguished from C. laminacarpa.

Distribution outside South Africa. Australia, Japan.

Distribution in South Africa. Natal, littoral to 48 m. Type locality: Park Rynie. 30/30 (1), 28/32 (s)

Campanularia crenata (Hartlaub, 1901)

Fig. 68A–F

Orthoplysis crenata: Ralph, 1957: 838, fig. 6g–v.
Campanularia crenata: Millard & Bouillon, 1973: 47, fig. 6B–F.

Diagnosis. Colony growing on weed, reaching 1.4 mm in height. Hydrothecal pedicel deeply and spirally grooved, with one separate spherule of smaller diameter at distal end, with thickened perisarc.

Hydrotheca deep-bell-shaped, 0.3–0.5 mm in depth and 0.18–0.4 mm in maximum diameter, depth always greater than diameter, usually compressed, perisarc often greatly thickened, especially at the narrow ends, but thinning down at margin. Margin with 12–13 low, rounded teeth.

Gonotheca borne on hydrorhiza on short, smooth pedicel, strongly compressed, truncated distally and with widest part at distal end, smooth or with irregular outline; male containing one gonophore with four columns of spermatogenic cells; female containing two gonophores, one large and one small, with eggs in longitudinal rows.

Variation. The spiral grooving on the pedicel usually extends throughout, but occasionally there are smooth areas.

In the thicker hydrothecae marginal teeth may be absent. This appears to
Fig. 67.

*Campanularia africana.* A, colony with female gonophores, redrawn from Warren (1908, as *Campanularia tineta*).

*Campanularia kinckii.* B–D, hydrothecae; E, gonotheca.

*Campanularia laminacarpa.* F–H, hydrothecae; J, male gonophore; K, female gonophore.

Scale in mm/10.
be the result of damage and loss of the 'thinned down' edge bearing the teeth. The type material had some hydrothecae without teeth.

The gonophore is reported to have a short free-living life as a eumedusa, possessing four radial canals and eight statocysts, but with no marginal tentacles or stomach (Hirohito).

**Distribution outside South Africa.** Atlantic (Sargasso Sea to Cape Verde), Mediterranean, Seychelles, Australasia, Japan, Chile. Type locality: New Zealand.

**Distribution in South Africa.** Moçambique only, Inhaca to Inhambane, littoral to 3 m. (For *Campanularia ?crenata* in Millard 1958, see *C. delicata*) 26/32 (l), 24/35 (s)

*Campanularia ?delicata* (Trebilcock, 1928)

Fig. 68G–L

*Orthopfixis delicata* Trebilcock, 1928: 3, pl. 2 (fig. 1–1f). Ralph 1957: 837, 840, fig. 7a–d.
*Campanularia ?crenata*: Millard, 1958: 170, fig. 2A–C, E.
*Campanularia delicata*: Millard & Bouillon, 1973: 48, fig. 6G–M.

**Diagnosis.** Colony usually growing on weed, reaching 4.6 m in height. Hydrothecal pedicel annulated to a varying extent at base and distal end, but always with one flattened spherule of smaller diameter at distal end.

Hydrotheca funnel-shaped, with straight or slightly curved sides widening to margin, 0.3–0.6 mm in depth and 0.2–0.6 mm in marginal diameter, depth usually more or less equal to diameter, circular in cross-section. Margin with 9–15 triangular teeth. Perisarc capable of great thickening to a level just below the margin and excluding the marginal teeth.

Gonotheca borne on hydrothiza on short, smooth pedicel; erect, circular or very slightly compressed in section, deep-oval in side view with widest part near centre.

**Variation.** The amount of annulation on the pedicel varies. At the base there may be up to 11 annulations and at the distal end up to 15, the intervening stretch being smooth or corrugated. Short pedicels are usually annulated throughout.

The annular perisarcal thickening round the base of the hydrotheca may or may not be separated from the thecal wall by a definite line.

**Remarks.** On the basis of Ralph's work (1957) Millard's material reported as *Campanularia ?crenata* in 1958 has been transferred to *C. delicata*. The two species are not easily distinguished and it may be necessary to unite them in the future. *C. delicata* is characterized by a hydrotheca which is not compressed and has deeper marginal teeth and by a gonotheca which is broadest near the centre and is not or only very little compressed. The pedicel is also different, with distinct but shallow annulations at the two ends instead of the deep spiral grooving of *C. crenata*.
Fig. 68.

*Campanularia crenata.* A–C, hydrothecae; D, t.s. hydrotheca; E, male gonophore; F, female gonophore.

*Campanularia ?delicata.* G–J, hydrothecae (the centre one the most typical); K, t.s. hydrotheca; L, male gonophores.

Scale in mm/10.
**Distribution outside South Africa.** New Zealand, Australia, Sargasso Sea, Seychelles. Type locality: Dunedin, New Zealand.

**Distribution in South Africa.** Moçambique (Kosi Bay to Inhambane), littoral to 15 m. 27/32 (l), 26/32 (1, s), 25/32, 24/35 (s)

*Campanularia hineksii* Alder, 1856

[Fig. 67B–E]

*Campanularia hineksii* Alder, 1856: 360, pl. 13 (fig. 9). Hincks, 1868: 162, fig. 18, pl. 24 (fig. 3). Millard, 1966a: 471, fig. 12A–D.

**Diagnosis.** Colony reaching a height of 8.4 mm. Hydrothecal pedicel not annulated or corrugated, but with a single spherule at distal end.

Hydrotheca deep-campanulate, large, 0.9–1.6 mm in depth and 0.5–0.9 mm in marginal diameter, depth 1 1/2–2 1/4 times diameter, longitudinally striated in distal part, polygonal in cross-section. Margin with 8–12 broad teeth which are usually hollowed distally to form two points.

Female gonotheca borne on hydrorhiza, elongate-oval, with widest part near base and narrowing slightly to truncated distal end, with about eight rounded transverse annulations, containing fixed sporosacs.

**Variation.** The hydrothecal pedicel occasionally shows irregularities such as cross-striations, but these appear to be due to regeneration after injury. Alder shows ‘two or three slight spiral twists’ at the base of the pedicel in the type material, but these have not been observed in South Africa.

The marginal teeth are occasionally truncated distally, and this appears to be the result of wearing down of the two points. The longitudinal striations on the hydrotheca start at the angles between the marginal teeth and are continued to a varying degree down its length. In some cases they reach to the base, and in others they peter out about halfway.

Male gonothecae have not been seen in South Africa and there is some doubt as to their structure. Stechow (1919b) describes smooth male gonothecae which widen distally in *C. alta*, thought by Broch (1933) to be a synonym for *C. hineksii*.

**Distribution.** Cosmopolitan. Type locality: Northumberland, U.K.

**Distribution in South Africa.** Off East London, in 86–210 m. Rare. 32/28 (s), 32/29 (d)

*Campanularia integra* MacGillivray, 1842

[Fig. 69]


*Campanularia calciculata* Hincks, 1853: 178, pl. 5 (fig. B). Hincks, 1868: 164, pl. 31 (fig. 2).

Warren, 1908: 338, fig. 19.

*Campanularia compressa* Clarke, 1876: 214, pl. 8 (figs 5–6).

*Agasta mira* Hartlaub, 1897: 504, pl. 22 (figs 5, 8–10). Russell, 1953: 303, figs 186–188, pl. 19 (fig. 1).

*Agasta rubra* Behnner, 1914: 393, figs 8–10, pl. 7 (fig. 6). Kramp, 1959: 146, fig. 183.

*Campanularia gracilis* Stechow, 1925a: 423, fig. 6.
Diagnosis. Colony growing on weeds, other hydroids and the crab *Dehaanius dentatus*, reaching 4 mm in height. Hydrorhiza reticulate, often with a flat lateral flange of perisarc. Hydrothecal pedicel spirally annulated, roughly corrugated or quite smooth, but always with one sphere of smaller diameter at distal end.

Hydrotheca campanulate, sometimes with slightly everted margin; 0.2–0.6 mm in depth and 0.2–0.5 mm in marginal diameter; in cross-section fairly thin and circular to grossly thickened, especially on two opposite sides, and then oval in cross-section and bilaterally symmetrical. Margin untoothed. Hydranth with 25–30 tentacles.

Gonotheca borne on hydrorhiza, generally laterally compressed, but sometimes round in cross-section; generally smooth and oval to pear-shaped in broad view, but often irregularly corrugated; with truncated distal end and wide operculate aperture; containing one to three (usually two: one large and one small) eumedusoid gonophores. Gonophore with four pigmented radial canals bearing irregular branching diverticula along entire length and rarely with four marginal bulbs and eight statocysts. Male with four band-like gonads extending full length of radial canals. Female with 30–40 large eggs arranged roughly in eight longitudinal rows between the diverticula of the radial canals.

Variation and remarks. All South African material appears to belong to one very variable species, here taken to be *C. integra*. Attempts to separate two species on the trophosome have been unsuccessful. Some colonies have spirally annulated pedicels throughout, others have smooth pedicels and others have a mixture of all types ranging from strongly annulated to quite smooth.

The strength of the perisarc is equally variable; in some colonies it is thin throughout with hydrothecae which are completely radially symmetrical. In others the lateral flanges of the hydrorhiza are so extensive that they fuse with one another to form a mat and the hydrothecae are grossly thickened. The thickening of the hydrotheca usually terminates just below the margin, and is always more strongly developed on two opposite sides imparting a bilateral symmetry and oval cross-section. Thickened colonies of this sort invariably have a few thin-walled hydrothecae as well.

The gonotheca is similarly variable. Though generally compressed and irregularly oval in broad view, elongate rounded forms may occur in the same colony. Many irregularities in shape occur, but never is there a spiral annulation so marked as that illustrated by Hincks (1868) for *C. integra*.

Medusae of this genus (*Agastrea*) have not been recorded from the plankton in South Africa and living material has not been seen to release active medusae, although this may possibly occur under certain conditions. In the laboratory the gonophores release their sexual products while still within the gonothecae. In partly spent gonophores the medusoid structure can sometimes be seen and is best observed by dissecting the gonophore out of the gonotheca. Specimens with four perradial marginal bulbs bearing vestigial marginal tentacles up to
Campanularia integrata. A–C, hydrothecae with smooth stems, in narrow view, broad view and t.s. respectively; D and E, hydrotheca with annulated stem in t.s. and broad view respectively; F, hydrotheca with thin perisarc; G, female gonophore with round section; H, female gonophore with flat section; J–L, female gonophores dissected from gonothecae, J immature with radial canals containing pigment, K mature, L partly spent and showing medusoid structures; M, male gonophore.

Scale in mm/10.
0,06 mm in length and with eight adradial statocysts have been observed. When the gonophore is full and mature the marginal structures are usually not visible and possibly not always present. The radial canals are often clearly demarcated by the presence of a brown pigment within them.

I have followed Broch (1909, 1918) in synonymizing C. integra and C. compressa. Both species are known to release degenerate short-lived medusae at certain seasons. The medusa of C. integra is Agastra mira, which is said to be distinguished by radial canals with a few diverticuli restricted to the central part and many small irregularly arranged eggs. The medusa of C. compressa is Agastra rubra, distinguished by radial canals bearing diverticuli along their entire length and fewer but larger eggs in longitudinal rows. Further observation is needed to determine whether or not these differences are due to seasonal variation or sex; if valid the South African material would appear to be closer to C. compressa.

**Distribution.** Cosmopolitan. Type locality: Don Mouth, U.K.

**Distribution in South Africa.** Northern South West Africa and Table Bay to Moçambique, littoral to 27 m, with a dubious record (Stechow) from 100 m, very abundant on weed in certain areas. 20/13 (l), 33/18 (l), 34/18 (l, s), 34/22 (l, s), 34/23 (d), 33/25 (s), 33/27 (s), 30/30 (l), 29/31 (l, s), 26/32 (l, s)

*Campanularia laminacarpa* Millard, 1966

Fig. 6/F–K

_Campanularia laminacarpa_ Millard, 1966a: 472, fig. 12E–K.

**Diagnosis.** Colony epizootic on _Thyroscyphus aequalis_, reaching 2,0 mm in height. Hydrothecal pedicel smooth or corrugated, with one sphure of smaller diameter at distal end.

Hydrotheca deep-campanulate, with almost parallel sides, 0,4–0,7 mm in depth and 0,2–0,3 mm in marginal diameter, depth 1½–2½ times diameter. Margin with 10–14 rounded teeth separated by rounded bays of approximately the same size.

Gonotheca borne on hydrorhiza, large, usually smooth, flattened, with truncated distal end and wide, operculate, terminal aperture. Male and female similar, but on different colonies. Female containing a single heteromedusoid gonophore with numerous small eggs; male containing a single eumedusoid gonophore with spermatogenic cells arranged in four longitudinal bands and with indications of four radial canals.

**Variation.** The gonothecae may have certain irregularities in the contours, but are always compressed.

**Remarks.** Sterile colonies of this species cannot be distinguished from _C. africana_. Fertile specimens of _C. laminacarpa_ have been found only on _Thyroscyphus_, and the species may be specific to this host. Infertile records from other
hosts have been omitted in the distribution below, and infertile records from
_Thyrosocyphus_ are given with a query.

**Distribution.** Endemic to South Africa.

**Distribution in South Africa.** Certain records: Agulhas Bank from Cape Agulhas
to East London; possibly extending farther west to False Bay and farther north
to Moçambique; 4–110 m and possibly 2–219 m. Type locality: Agulhas Bank,
34°49′S/20°21′5″E, depth about 91 m. ?34/18 (s), 34/20 (s), ?34/21 (s), 35/21
(d), 33/25 (s), ?34/25 (s), 33/26 (s), 33/27 (s), ?32/28 (s), ?29/31 (d), ?25/32 (s),
?24/35 (s)

_Campanularia morgansi_ Millard, 1957

Fig. 71C–E


**Diagnosis.** Colony generally epizootic on other hydroids, also found on _Pyura_
and _Perna perna_, reaching 2.9 mm in height. Hydrothecal pedicel roughly
corrugated in basal region, with one somewhat flattened spherule at distal end.

Hydrotheca deep-campanulate, with a distinct raised rim just below margin,
0.4–0.7 mm in depth and 0.2–0.4 mm in maximum diameter, depth 1/3–3 times
diameter. Margin with 8–13 usually bluntly rounded teeth separated by rounded
bays. Hydranth with about 16 tentacles.

Gonotheca borne on hydrorhiza on short annulated pedicel, spindle-shaped,
deeply annulated with 5–9 annulations over 3/4 length, distal region
smooth, with terminal aperture. Male and female similar, containing a single
styloid gonophore, which in the female bears numerous eggs which develop
into planulae _in situ._

**Variation.** The length of the hydrothecal pedicel is variable, and the terminal
spherule is usually, but not always, of smaller diameter than the rest. The raised
rim of the hydrotheca is always distinct and may be strongly thickened. The
marginal teeth are usually rounded, but may also be sharply pointed.

**Distribution outside South Africa.** Madagascar.

**Distribution in South Africa.** Lambert’s Bay to Inhaca, in 0–210 m. Type locality:
False Bay, 73 m. 32/18 (s), 33/18 (s), 34/18 (s, d), 34/21 (s), 34/22 (s), 35/22 (d),
33/25 (s), 33/27 (s), 32/28 (s), 32/29 (d), 29/31 (s, d), 28/32 (s), 25/32 (s)

_Campanularia pecten_ Gow & Millard, 1975

Fig. 70A–F

_Campanularia ?mollis:_ Millard, 1966a: 476, fig. 13E–J.
_Campanularia pecten_ Gow & Millard, 1975: 1, fig. 1.

**Diagnosis.** Colony growing on weeds, reaching 2.7 mm in height. Hydrothecal
pedicel smooth, with thickened perisarc and one spherule of smaller diameter
at distal end, often with regeneration nodes.
Hydrotheca deep-campanulate, 0.5–0.8 mm in depth and 0.2–0.4 mm in marginal diameter. Margin with 7–10 (usually 9) teeth with bluntly rounded apices and usually narrower than the bays between them. Perisarc capable of great thickening, particularly at two opposite sides resulting in an oval cross-section.

Gonotheca borne on hydorhiza on short, smooth pedicel, scallop-shaped and opening like a bivalve shell; lower valve flattened, upper valve thicker and convex often with concentric ridges on outer surface, containing a single eumedusoid gonophore. Eumedusoid released for a short free-living life, only male known, with four radial canals with gonads distributed along their length, eight statocysts, but no marginal tentacles or hypostome.

*Remarks.* I have included in this species the infertile material previously ascribed to *C. mollis*. In this colony the hydrothecae are a little deeper than in the holotype and the marginal teeth are sometimes bifurcated at the tip.

*Distribution.* Endemic to South Africa.

*Distribution in South Africa.* Cape Peninsula, east and west coasts, littoral. Type locality: St. James. 33/18 (l), 34/18 (l)

*Campanularia roberti* Gow & Millard, 1975

Fig. 70G–J

*Campanularia roberti* Gow & Millard, 1975: 3, fig. 2.

*Diagnosis.* Colony growing on weeds, reaching 3.5 mm in height. Hydrothecal pedicel smooth, with thickened perisarc and one spherule of smaller diameter at distal end, often with regeneration nodes.

Hydrotheca deep-campanulate, 0.6–0.9 mm in depth and 0.3–0.6 mm in marginal diameter. Margin with 9–11 triangular teeth with bluntly rounded apices. Perisarc capable of great thickening, particularly at two opposite sides and more on one side than the other resulting in an asymmetrical shape and an oval cross-section.

Gonotheca borne on hydorhiza on short, smooth pedicel, scallop-shaped and opening like a bivalve shell, recumbent, lower valve flattened, upper valve thicker and convex with concentric ridges on outer surface, containing a single gonophore in the form of a fixed sporosac. Gonophore (only female known) with four branching radial canals and over 30 eggs between the diverticuli, with no other medusoid characters. Eggs developing into planuli in situ.

*Distribution.* Endemic to South Africa.

*Distribution in South Africa.* Cape Peninsula, east and west coasts, littoral. Type locality: Partridge Point. 33/18 (l), 34/18 (l)

Genus *Clyttia* Lamouroux, 1812


*Diagnosis.* Colony usually minute and stolonial, but sometimes branching in
Fig. 70.

*Campanularia pecten.* A and B, hydrothecae; C, spent gonotheca in side view; D, eumedusa in ventral view, showing, from the centre outwards: opening to subumbrellar cavity, exumbrellar aperture, ring of statocysts, gonads on radial canals; E and F, gonothecae, F containing a male gonophore.

*Campanularia roberti.* G and H, gonothecae, H containing a female gonophore and showing pigmented radial canals; J, hydrothecae.

Scale in mm/10.
the form of a symposium. Hydrotheca deep, campanulate or funnel-shaped, radially symmetrical, usually with toothed margin. Diaphragm present, of variable thickness but always distinctly demarcated from hydrothecal wall. Gonotheca producing free medusae. Medusa hemispherical, with normal velum, hollow marginal tentacles and numerous statelyovst.

Type species: *Medusa hemisphaerica* Linnaeus, 1867

= *Sertularia volubilis* Ellis & Solander, 1786 (*non* Linnaeus, 1758)

KEY TO SPECIES

1. Hydrotheca without marginal teeth
   - Hydrotheca with teeth
     - Marginal teeth bilobed
       - Marginal teeth single
         - Hydrotheca longitudinally striated, marginal teeth keeled on inner surface
           - Hydrotheca not striated, marginal teeth not keeled
             - Pedicel corrugated at base, and with one spherule at distal end below hydrotheca
               - Pedicel closely annulated at base and at distal end
                 - Hydrotheca with depth approximately equal to diameter; marginal teeth low and rounded
                   - Hydrotheca always deeper than wide; marginal teeth triangular, usually sharp
                     - Hydrotheca not more than 1 mm deep, depth about 1\(\frac{1}{2}\)–2\(\frac{1}{2}\) times marginal diameter, never over 3 times
                       - Hydrotheca over 1 mm deep, depth 3–4 times diameter

Clytia gravieri (Billard, 1904)

Fig. 71F–H

*Campaunlaria gravieri* Billard, 1904b: 482, fig. 1.

*Obelia striata* Clarke, 1907: 9, pls 6–7.


*Clytia serrata* Millard, 1958: 173, fig. 3C, H.

*Campaunlaria (Clytia) gravieri*: Vervoort, 1967: 50, fig. 16.

Diagnosis. Colony growing on pteropod shells, weed and other hydroids, reaching 9 mm in height. Hydrothecal pedicel unbranched and bearing one hydrotheca only, or branching sympodially to give rise to several alternate hydrothecae, closely annulated at base, on origin of branches and at distal end.

Hydrotheca very delicate, deep-campanulate, expanding to margin or with almost parallel sides, longitudinally striated in distal region for about one-third of length, 0.4–1.1 mm in depth and 0.12–0.5 mm in marginal diameter, depth two to three times diameter. Margin with 8–13 sharp, pointed teeth which correspond to the striations and project inwards as longitudinal ridges, giving to the cross-section an undulating outline. Diaphragm distinctly demarcated, separating off a deep basal chamber.

Gonothecae borne on hydrorhiza or thecal pedicel, elongated pear-shaped, reaching 0.8 mm in length and 0.3 mm in maximum diameter, smooth, truncated distally, containing a string of medusa-buds. Pedicel short, annulated.
Fig. 71.

*Clytia lattitheca*. A, branching stems; B, hydrotheca.
*Campanularia morgansi*. C and D, hydrothecae; E, female gonophore.
*Clytia gravieri*. F, stem; G, hydrotheca; H, gonothecae with medusa-buds.

Scale in mm/10.
Medusa deep and with four marginal tentacles at liberation, adult medusa unknown.

_Variation._ This is one of the few species of _Clytia_ in which the pedicel may branch repeatedly producing upright stems superficially very like those of _Obelia_. The hydrotheca is extremely variable in size.

_Distribution outside South Africa._ Tropical and subtropical regions of Atlantic, Indian and Pacific Oceans. Type locality: off Djibouti in the Gulf of Aden.

_Distribution in South Africa._ On the pteropod _Hyaloea (Diacria) trispinosa_: west coast as far south as 31°S, and south-east coast between 24°E and 30°50'S. On hydroids and other substrata: Port Elizabeth to Moçambique, 0–110 m. 34/25 (d), 29/31 (s), 26/32 (l), 25/32, 23/35 (s), 21/35 (Kramp's records on pteropods in 1921 not recorded in detail).

_Clytia hemisphaerica_ (Linnaeus, 1767)

_Fig. 72A–D_

_Medusa hemisphaerica_ Linnaeus, 1767: 1098.
_Laoidea gracilis_ M. Sars, 1851: 138.
_Clytia gracilis_ Millard, 1957: 196, Millard, 1958: 172, fig. 3B, E, G.
_Clytia johnstoni_: Ralph, 1957: 820, 823, figs 1h–u, 2, 3a–f, Millard, 1958: 172, fig. 3A, D, F.
_Phaiidiun hemisphaerical_ Rusell, 1953: 285, figs 172–179, pl. 16 (fig. 1), pl. 17 (fig. 6).
_Clytia hemisphaerica_: Rees & Thursfield, 1965: 95.
_Laoidea (Phaiidiun) pelagica_ Vervoort, 1968: 15, fig. 5.

_Diagnosis._ Colony generally growing on weeds or other hydroids. Hydrothecal pedicel closely annulated at base and distal end, usually unbranched but sometimes branching sympodially once or twice. Colony reaching a maximum height of 10 mm.

Hydrotheca deep-campanulate, expanding to margin, 0.3–1.0 mm in depth and 0.13–0.6 mm in marginal diameter, depth usually 1 ½–2 ½ times diameter. Margin with 7–15 teeth, which are usually sharply pointed. Diaphragm distinctly demarcated from thecal wall, separating off a bell-shaped basal chamber.

Gonotheca borne on hydorhiza or thecal pedicel, elongated, usually constricted just below truncated distal end, generally smooth but sometimes annulated, containing about four medusa-buds.

Medusa at liberation deep bell-shaped, with four marginal tentacles. Adult medusa (not recorded from South Africa) hemispherical, reaching 20 mm in diameter, with numerous statocysts and up to 32 marginal tentacles.

_Variation._ When branching occurs the secondary pedicels immediately bend distally so that their axes are almost parallel to the primary one. The amount of annulation on the pedicel varies; most have a smooth area in the centre, but some are annulated throughout and some have scattered patches of annulation.

The hydrotheca is fairly constant in shape though the size is variable. In general larger hydrothecae occur on the west and south coasts and smaller
ones on the east coast. The marginal teeth vary in number and shape. In this
country they are always acute, covering a smaller area than the bays between
them, but the points may be sharp or bluntly rounded and are very often
asymmetrical, leaning to one side. The diaphragm varies in thickness but cannot
be confused with the annular thecal thickening of *Campanularia*.

Gonothecae are generally smooth, of the ‘*C. gracilis*’ form, but sometimes
have a few irregular corrugations, and are sometimes completely annulated
as in the ‘*C. johnstoni*’ form. The annulated gonothecae may be deep with a
wide truncated distal end, or shorter and more nearly oval with a narrower
aperture.

**Remarks.** Ralph (1957) showed that the gonotheca of *C. johnstoni* (Alder)
varies from fully annulated to smooth. Thus *C. johnstoni* becomes a synonym of
*C. gracilis* (M. Sars) = *C. pelagica* (van Breemen) = *C. hemisphaerica*. It may
be noted, however, that in South Africa the ‘*johnstoni*’ form with fully annulated
gonothecae does not occur south of Inhaca, and that at no time have fully
annulated and smooth gonothecae been found in the same colony.

**Distribution.** Cosmopolitan. Type locality: ‘Oceano Belgico’.

**Distribution in South Africa.** Northern South West Africa to Moçambique.
Common practically all round the coast, though often overlooked because of
the small size, littoral to 150 m. [18/12 (l),] 33/18 (l, s), 34/18 (s), 35/19 (s),
35/20 (d), 34/21 (s), 35/21 (d), 34/22 (s, d), 34/23 (s, d), 34/24 (d), 33/25 (s),
34/25 (s), 33/26 (s), 33/27 (s), 32/28 (s), 31/30 (l), 31/39 (s), 29/31 (l, s, h), 28/32
(l, s, d), 26/32 (l, s), 25/32, 23/35 (l), 21/35

* Clytia hummelincki* (Leloup, 1935)

Fig. 72F–H

Laomedea hummelincki Leloup, 1935: 19, fig. 7.
Clytia hummelincki: Millard, 1966a: 480, fig. 14G–L.

**Diagnosis.** Colony growing on the stalked barnacle, *Lepas*, reaching 4,9 mm in
height. Hydrothecal pedicel unbranched, closely annulated at base and some-
times at scattered intervals above this, with a single flattened segment at distal
end.

* Hydrotheca funnel-shaped, with straight sides expanding evenly to margin, 0,3–0,4 mm in depth and 0,2–0,4 mm in marginal diameter; depth approximately
equal to diameter. Margin untoothed. Diaphragm delicate, usually oblique,
separating off a funnel-shaped basal chamber.

* Gonotheca borne on hydrorhiza, elongated, smooth, truncated distally,
containing one or two medusa-buds.

* Medusa-bud deep, with four radial canals and four marginal bulbs. Adult
medusa unknown.

**Distribution outside South Africa.** Isle Bonaire, West Indies, on coral (type
locality).
Fig. 72.

*Clytia hemisphaerica*. A, two hydrothecae and a gonotheca; B, hydrotheca; C, gonotheca of 'gracilis' form; D, gonotheca of 'johnstoni' form.

*Clytia paradoxa*. E, hydrothecae, redrawn from Stechow (1925a, as Eucalix paradoxus).

*Clytia hummelinecki*. F, hydrothecae and gonotheca; G and H, gonothecae.

Scale in mm/10.
Distribution in South Africa. One record only, from Agulhas Bank, on buoy 34/25 (h)

Clytia latitheca Millard & Bouillon, 1973

Fig. 71A–B

Clytia latitheca Millard & Bouillon, 1973: 55, fig. 7H–L.

Diagnosis. Hydrothecal pedicel either unbranched and bearing a single terminal hydrotheca, or branching sympodially to form a geniculate erect stem reaching a maximum height of 6 mm. Stem closely annulated at base, distal end, on origin of branches and occasionally at other irregular intervals.

Hydrotheca obconical, with straight walls, 0.3–0.6 mm in depth and 0.4–0.6 mm in marginal diameter, depth approximately equal to diameter. Margin with 13–14 low rounded teeth. Diaphragm thin, distinct from thecal wall. Basal chamber deep. Hydranth with about 28 tentacles.

Gonotheca (not reported from South Africa) borne on stem, smooth, elongated, widening evenly to truncated distal end, containing a string of 3–6 medusa-buds, which are deep and have at least four marginal tentacles at liberation. Adult medusa unknown.

Variation. This species is very variable in form and is one of the few which may form an erect branching stem. The branching is very obviously sympodial and often two branches arise in close succession giving a subdichotomous effect. Colonies from South Africa are small, but taller ones (reaching 15 mm) occur in the Seychelles and are occasionally lightly fascicled at the base. The hydrotheca is variable in size but very characteristic in shape.

Distribution outside South Africa. Seychelles only; type locality: Praslin.

Distribution in South Africa. Inhaca in Mozambique only. 25/32

Clytia paradoxa (Stechow, 1923)

Fig. 72E

Eucalyx paradoxa Stechow, 1923b: 104. Stechow, 1925a: 433, fig. 11.

Diagnosis. Colony growing on other hyroids. Hydrothecal pedicel unbranched, corrugated in basal region, forming one spherule of lesser diameter at distal end.

Hydrotheca deep-campanulate, with a distinct raised rim just below margin, 0.4 mm in depth and 0.18 mm in marginal diameter, depth about 2½ times diameter. Margin with 9–10 triangular teeth separated by rounded bays. Diaphragm distinctly demarcated, thin, separating off a campanulate basal chamber.

Gonotheca unknown.

Remarks. This species is included in the genus Clytia on the basis of the diaphragm. For the rest its structure is reminiscent of Campanularia, particularly C. morgansi. It has not been rediscovered since Stechow’s report.
Distribution. Endemic to South Africa.

*Distribution in South Africa.* South coast from 20 to 25°E, in 100 m. Type locality: 35°27'S/20°56'E, 100 m. 35/20 (d), 34/24 (d)

*Clytia paulensis* (Vanhöffen, 1910)

Fig. 73A–D

*Campanularia paulensis* Vanhöffen, 1910: 298, fig. 19.
*Clytia paulensis*: Stechow, 1923c: 110, fig. N. Millard, 1966a: 481, fig. 15.
*?Clytia alvae* Stechow, 1919b: 47, fig. N. Stechow, 1925a: 428.

*Diagnosis.* Colony usually growing on other hydroids, reaching 3 mm in height. Hydrothecal pedicel unbranched or sparsely branched, closely annulated at base and distal end and sometimes at scattered intervals between.

Hydrotheca deep-campanulate, with almost parallel sides, 0.3–0.7 mm in depth and 0.13–0.3 mm in marginal diameter; depth two to three times diameter. Margin with 7–11 bilobed teeth, points narrow and bluntly rounded. Diaphragm very delicate, separating off a campanulate basal chamber.

Gonotheca borne on hydorhiza. elongated, smooth, truncated distally with annulated pedicel, containing one to three medusa-buds.

Medusa-bud with four marginal tentacles. Adult medusa unknown.

*Variation.* The double marginal teeth are characteristic of the species and usually very distinct. However, the bays between members of a pair are sometimes nearly as deep as the bays between pairs and the double nature of the teeth is not so easily seen. The single teeth thus vary from \( \frac{1}{3} \) to \( \frac{3}{3} \)-the length of the double teeth. Since the margin of the hydrotheca is bowed out between the teeth the distal end of the hydrotheca often appears to have longitudinal striations, especially in mounted preparations where the side-walls tend to crumple.

*Distribution outside South Africa.* North Atlantic, Mediterranean, California, Indian Ocean, Antarctic. Type locality: St. Paul, southern Indian Ocean.

*Distribution in South Africa.* South and east coasts, from Cape Infanta to Inhaca, 0–138 m. 34/20 (s), 34/22 (s), 34/23 (s), 34/24 (d), 33/25 (s), 34/25 (s), 32/28 (s), 29/31 (s, d), 28/32 (s), 26/32 (s)

*Clytia warreni* Stechow, 1919

Fig. 73E–F

*Clytia elongata* Warren, 1908: 339, fig. 20.
*Clytia warreni* Stechow, 1919b: 48.

*Diagnosis.* Colony epizootic on *Thyroscyphus*. Hydrothecal pedicel unbranched, 1.3–3.2 mm in length, closely annulated at base and distal end, the terminal segment being smaller than the rest.

Hydrotheca obconical, expanding to margin, 1.1–1.3 mm in depth and 0.3–0.4 mm in marginal diameter, depth 3–4 times diameter. Margin with about
Fig. 73.

_Clytia paulensis._ A–C, hydrothecae; D, gonotheca.

_Clytia warreni._ E, two gonothecae and a hydrotheca, redrawn from Warren (1908, as _C. elongata_); F, hydrotheca, drawn from Warren’s holotype borrowed from the Natal Museum.

_Eulaomelea calecolifera._ G, stem; H, hydrotheca and hydranth; J, male gonophore; K, female gonophore.

Scale in mm/10.
12 sharp teeth. Diaphragm distinct, separating off a deep-campanulate basal chamber.

Gonotheca borne on hydrorhiza, elongated and narrowing slightly to truncated distal end, smooth, containing three or four medusa-buds.

Adult medusa unknown.

**Distribution.** Endemic to South Africa.

**Distribution in South Africa.** Type locality and only record: Algoa Bay in 73 m.
33/25 (s)

**Genus Eulaomedea Broch, 1909**

**Diagnosis.** An upright stem present, which may be fascicled or unfascicled, branched or unbranched. Stem divided into regular internodes bearing alternate hydrothecae. Hydrotheca campanulate, radially symmetrical. Diaphragm distinctly demarcated from thecal wall. Gonothecae containing gonophores in the form of fixed sporosacs or degenerate medusae which release their sexual products within the gonothecae.

Type species: *Laomedea flexuosa* Alder, 1856.

One species only from South Africa.

*Eulaomedea calceolifera* (Hincks, 1871)

Fig. 73G–K


**Diagnosis.** Stem unfascicled, flexuous, unbranched or weakly branched, reaching 23 mm in height, geniculate, bearing alternate hydrothecae. Internodes annulated on proximal end, slender, each with a distal apophysis alternately on the right and the left, which bears a hydrotheca and/or a branch. Branches similar to stem. Hydrothecal pedicel annulated throughout or with a smooth area in centre, generally longer than hydrotheca.

Hydrotheca campanulate, 0.4–0.6 mm in depth and 0.2–0.4 mm in marginal diameter. Margin untoothed, usually slightly everted. Diaphragm straight.

Gonothecae arising in axils of thecal pedicels or branches, with annulated pedicels, male and female on separate colonies. Female gonotheca smooth, slipper-shaped, widening gradually from pedicel to distal end, which is obliquely truncated, the abcauline edge curling over to form a tube directed distally into the cavity; containing about 10 heteromedesoid gonophores, each with one egg; eggs developing into planulae within the gonotheca. Male gonotheca smooth, elongated, spindle-shaped, with small inturned terminal aperture, containing about seven styloid gonophores in one row, one upon the other.

**Distribution outside South Africa.** North Atlantic from coast of America to Europe, Mediterranean. Type locality: Salcombe Bay, U.K.
Distribution in South Africa. In Cape Town docks on ships’ hulls. An infertile record from Simon’s Bay, 70 m (Stechow 1925a). 33/18 (h), 34/18 (s)

Genus Gonothyraea Allman, 1864

Diagnosis. An upright, branching stem present, which may be fascicled or unfascicled. Stem divided into regular internodes bearing alternate hydrothecae. Hydrotheca campanulate, radially symmetrical. Diaphragm distinctly demarcated from thecal wall. Gonophores forming degenerate medusae (meconidia) which are extruded from the gonothecae into acrocysts, but remain attached and release the sexual products in position. Meconidium with marginal tentacles, but no mouth or sense organs.

Type species: Laomedea loveni Allman, 1859.

One species only from South Africa.

Gonothyraea loveni (Allman, 1859)

Fig. 74A–F

Gonothyraea Loveni: Hincks, 1868: 180, pl. 25 (fig. 2). Allman, 1871: 55, fig. 28.

Diagnosis. Stem unfascicled, flexuous, richly branched, reaching 40 mm in height, straight or weakly geniculate, bearing alternate hydrothecae and branches. Internodes annulated on proximal end, slender, each with a distal apophysis alternately on the right and the left, which bears a hydrotheca and/or a branch. Branches similar to stem. Hydrothecal pedicel annulated throughout, shorter than hydrotheca.

Hydrotheca deep-campanulate, very delicate, 0.4–0.6 mm in depth and 0.18–0.4 mm in marginal diameter. Margin with about 10 truncated teeth separated by rounded bays. Diaphragm thin, straight. Hydranth with 19–33 tentacles held alternately elevated and depressed.

Gonothecae arising in axils of thecal pedicels or branches singly or in pairs, smooth, elongated, widening gradually to truncated distal end, containing 4–5 (rarely up to 8) eumedusoid gonophores in a single row, one upon the other. Gonophores extruded through aperture as meconidia but remaining in cytoplasmic continuity with blastostyle. Meconidium with four radial canals, a circular canal and a ring of small marginal tentacles, but no mouth or sense organs. Male with about five marginal tentacles and releasing the sexual products in situ. Female with about eight marginal tentacles and 3–5 eggs, which are fertilized and develop into planulae in situ.

Colour: coenosarc creamy white throughout, tentacles transparent.

Distribution outside South Africa. Arctic and North Atlantic, from America to Europe, Morocco, Mediterranean, New Zealand, Tasmania. Probably spread to the southern hemisphere by ships. Type locality: Great Britain.
Fig. 74.

*Gonothyraea loveni.* A, stem with female gonophores; B, hydrotheca; C and D, female and male gonophores releasing meconidia; E, female meconidium with planulae; F, empty male meconidium.

*Obelia* sp., medusae. G, newly liberated; H, in a typical swimming position; J, the largest specimen seen; K, edge of bell showing tentacle roots, circular canal and statocyst.

Scale in mm/10.
Distribution in South Africa. In Cape Town docks only, on ships’ hulls, experimental submerged plates, pylons and cables. 33/18 (s, h)

Genus *Obelia* Péron & Lesueur, 1809

*Diagnosis.* An upright stem present, which may be fascicled or unfascicled, branched or unbranched. Stem divided into regular internodes bearing alternate hydrothecae. Hydrotheca campanulate, radially symmetrical, with toothed or untoothed margin. Diaphragm distinctly demarcated from thecal wall. Gonothecae releasing free medusae. Medusa shallow and saucer-shaped, with rudimentary velum, numerous solid marginal tentacles and eight statocysts, each with one concretion.

Type species: *Sertularia generculata* Linnaeus, 1758.

*Remarks on medusae* (Fig. 74G–K). The medusae of the various species of *Obelia* cannot as yet be distinguished from one another. *Obelia* medusae occur commonly in the plankton round the South African coast, and are easily recognized by their characteristic rapid pulsation and shallow bell, which often ‘turns inside out’ during swimming. The smallest ones observed, which have presumably just escaped from the gonothecae, are 1 mm in diameter and have 16 marginal tentacles. The largest ones are 4 mm in diameter and have about 140 marginal tentacles. The gonads are round and borne on the centre of the radial canals.

Colour: gonads and tentacle-bases straw-coloured, the rest transparent.

**KEY TO SPECIES**

1. Hydrothecal margin toothed
   - Hydrothecal margin untoothed
2. Marginal teeth bilobed
   - Marginal teeth single, low and rounded
   3. Stem strongly geniculate, internodes with pronounced perisarcal thickenings on alternate sides
   - Stem seldom obviously geniculate, internodes without perisarcal thickenings

*Obelia bicuspidata* Clarke, 1875

Fig. 75C–E


*Diagnosis.* Stem fascicled or unfascicled, branched or unbranched, reaching 9 mm in height, geniculate in younger regions only, bearing alternate hydrothecae. Internodes slender, with thin perisarc, with three or more close annulations at proximal end, bearing a hydrotheca on a short apophysis at distal end. Branches when present, arising next to a hydrotheca, similar to stem. Hydrothecal pedicels of variable length, annulated throughout or with smooth area in centre.
Hydrotheca deep-campanulate, polygonal in section, 0.3–1.1 mm in depth and 0.18–0.5 mm in marginal diameter, depth 1½–3½ times diameter. Margin with 8–12 teeth, each of which is bilobed, terminating in two slender, keeled spines. Diaphragm delicate, straight or slightly oblique.

Gonothecae arising in axils of hydrothecal pedicels, smooth, elongated, widening to broad distal end, with terminal aperture but no neck. Pedicel annulated.

**Variation.** The known South African material is sparsely branched with unfascicled stems. More luxurious material might be expected to have fascicled stems and more prolific branching. Variation occurs in the origin of the branches and hydrothecae, and the latter may arise in pairs.

The size of the bays between members of a pair of marginal teeth varies, and may be almost as deep as the bays between the double teeth or quite shallow. Some hydrothecae are obviously longitudinally striated, others not at all.

**Distribution.** Cosmopolitan in tropical and temperate waters. Type locality: Long Island Sound, 5–9 m.

**Distribution in South Africa.** Table Bay, and the east coast from Durban to Inhaca; on ships’ hulls, hermit shells and weed. 33/18 (h), 29/31 (s), 28/32 (s), 26/32 (l, s), 25/32

*Obelia dichotoma* (Linnaeus, 1758)

Fig. 75F–J

*Sertularia dichotoma* Linnaeus, 1758: 812.


*Obelia dubia*: Vanhöffen, 1910: 307, fig. 27.

*Laomedea dichotoma*: Vervoort, 1946a: 292, fig. 128.

**Diagnosis.** Stem unfascicled, branched or unbranched, reaching 90 mm in height but usually much less, straight or geniculate, bearing alternate hydrothecae. Internodes annulated on proximal end, slender, bearing a hydrotheca on a short apophysis at distal end. Branches alternate or subdichotomous, usually arising from the same apophysis as the hydrotheca, similar to stem in structure. Hydrothecal pedicels annulated throughout or with a smooth area in centre.

Hydrotheca campanulate, very delicate, round or polyhedral in section, 0.3–0.6 mm in depth and 0.2–0.5 mm in marginal diameter, with depth exceeding width. Margin untoothed or with about 12 low, rounded ‘teeth’. Diaphragm thin, straight or oblique.

Gonothecae arising in axils of thecal pedicels and occasionally from hydrorhiza, smooth or roughly corrugated, elongated pear-shaped, with terminal aperture on a short tubular neck. Pedicel short, annulated.

**Variation.** The branching is typically alternate, with longer branches near the base of the colony and progressively shorter ones towards the tip, but extra long branches may arise at irregular intervals, giving a pseudodichotomous
Fig. 75.

*Obelia geniculata.* A, hydrotheca and hydranth; B, stem with gonothecae containing medusa-buds.

*Obelia bicuspidata.* C, stem; D, hydrotheca; E, gonotheca.

*Obelia dichotoma.* F, stem; G, hydrotheca with untoothed margin; H, hydrotheca with toothed margin; J, gonotheca containing medusa-buds.

Scale in mm/10.
appearance. Normally a branch and a hydrothecal pedicel arise together from the same apophysis, but branches may replace hydrothecae or may arise in pairs. Two hydrothecae may arise from the same apophysis. Hydrothecal pedicels are variable in length and may be longer or shorter than the hydrothecae. The geniculate appearance of some stems is the result of curvature within the internodes rather than at the nodes.

The margin of the hydrotheca is usually very thin and delicate with no marginal teeth. Sometimes very low undulations may be seen, and rarely distinct rounded teeth with indications of longitudinal striations between them. The latter form is characteristic of *O. dubia*, which is here considered to be a synonym.

The gonothecae are usually smooth or may have irregular transverse corrugations (typical of *O. dubia*).

Colonies are commonly epizootic on other hydroids and algae, and have also been found on *Squalus acutipinnis*, *Aulacomya magellanica*, *Lepas* sp. and *Caretta caretta*. It is very common in dock areas on pylons and ships' hulls.

**Distribution.** Cosmopolitan. Type locality: south-west coast of England.

**Distribution in South Africa.** All round the coast, littoral to 100 m. 28/16 (s), 31/18 (l), 32/18 (s), 33/18 (s, h), 34/18 (l, s), 34/20 (s), 34/21 (s), 34/22 (s), 34/23 (l, s, d), 33/25 (s), 29/31 (l, h), 26/32 (l), 25/32, 23/35 (l), 21/35

**Obelia geniculata** (Linnaeus, 1758)

Fig. 75A–B

*Sertularia geniculata* Linnaeus, 1758: 812.


**Diagnosis.** Colony usually growing on weed, particularly laminarians. Stem unfascicled, unbranched (in South African material), reaching 22 mm, geniculate, bearing alternate hydrothecae. Internodes not annulated or with one or two annulations immediately above node, bearing a hydrotheca on a projecting shoulder at distal end, with perisarc grossly thickened below the shoulder on the side bearing the hydrotheca. Hydrothecal pedicels completely annulated, usually shorter than the hydrotheca.

Hydrotheca campanulate, round in section, 0,16–0,3 mm in depth and 0,15–0,4 mm in marginal diameter, depth approximately equal to diameter. Margin untoothed. Diaphragm generally thick and triangular.

Gonothecae arising in axils of thecal pedicels and from hydorhiza, smooth, elongated pear-shaped, with terminal aperture on a short, tubular neck. Pedicel short, of one or two segments.

Colour: hydranth opaque.

**Variation.** The South African material generally has very pronounced perisarcal thickenings in the stem internodes, and the walls of the hydrothecae are generally
thickened as well, especially in the region of the diaphragm. The hydrotheca is in general more stoutly built than in *O. dichotoma*. The diaphragm may also be thick, resembling superficially that of *Campanularia*, but there is always a distinct line separating it from the wall of the hydrotheca. The diaphragm may be straight or oblique, in the latter case imposing a certain asymmetry on the hydrotheca. This may be enhanced by unequally thickened thecal walls, the adcauline side tending to be thicker than the adcauline. The length of the thecal pedicel varies and it may have 1–8 segments. The gonothecae may arise in pairs.

**Distribution.** Cosmopolitan. Type locality: U.K.

**Distribution in South Africa.** Lüderitz Bay to Cape Infanta, littoral to 80 m, Inhaca (littoral) and on ships’ hulls, especially common on laminarians, also on *Jasus lalandii*. 26/15 (l, s), 32/18 (s), 33/17 (s), 33/18 (l, s, h), 34/18 (l, s), 35/19 (s), 34/20 (s), 26/32 (l, s), 25/32

**Family Syntheciidae**

**Diagnosis.** Thecate hydroids with tubular, bilaterally symmetrical hydrothecae, into which the hydranth can be completely withdrawn. Hydrotheca sessile, without operculum, with unoothed margin, with a definite floor perforated by a hydropore. Hydranth with conical hypostome and one cirsele of filiform tentacles. Nematophores absent. Gonophores in the form of fixed sporozaes.

**Introduction.** Members of the Syntheciidae have erect stems which may be small and unbranched, or may bear pinnately arranged hydrocladia. Both stem and hydrocladia bear hydrothecae. The species are seldom large, and many are minute. The stem is usually unfascicled, though fascicled in a few larger species. Stolonization is common, particularly in the genus *Synthecium*, where the tips of the stems or hydrocladia develop stolons which reunit with other parts of the colony often resulting in a tangled, bushy network.

The arrangement of the hydrothecae is used as a basis for generic diagnosis. They may be alternate, in opposite pairs, or in verticils.

The structure of the hydrotheca is very similar to that in the Sertulariidae, and undoubtedly the two families are very closely related. The Syntheciidae can be distinguished by the circular, unoothed margin to the hydrotheca and by the absence of an operculum.

The hydrotheca is sessile and seated directly on an apophysis of the stem. Its adcauline wall is at least partly adnate to the stem, and then usually bends away from it. There is no diaphragm in the strict sense of the term, but the floor of the hydrotheca is well defined and perforated in the centre by a small hydropore. By this feature the family can be distinguished from the Lafoeidae. In the stronger species the base of the adcauline wall usually extends below the level of the floor where it forms a thickened boss of perisarc. Broch (1918) states that the hydrotheca is lined with an ectodermal lamella which is continuous with the base of the hydranth, but this has not been verified for all
species. Broch also states that the hydranth usually possesses a blind caecum or bulge on the abcauline side where the endodermal epithelium is low and without digestive elements. In the South African species this caecum has been observed only in *Synthecium hians*.

The gonothecae usually spring from within the hydrothecae but may arise from the stem just below them. Stechow (1923c) used this feature to distinguish *Synthecium* from *Hincksetta*, but Billard (1925a) has shown that this is not a good diagnostic character. When the gonothecae arise below the hydrothecae they usually emerge through special thin areas of perisarc in this position which have the appearance of fenestrae and are clearly visible in the infertile colony.

**KEY TO GENERA**

[Genera not represented in South Africa are bracketed]

1. Hydrothecae alternate on stem and branches, forming two longitudinal rows  
   *Hincksetta* p. 231
   - Hydrothecae in opposite pairs or verticils on stem and branches  
     2

2. Pairs of hydrothecae always in the same plane and forming two longitudinal rows  
   *Synthecium* p. 235
   - Hydrothecae in pairs or verticils, the members of one group alternating with those of the next and forming double the number of longitudinal rows  
     [Staurotheca]

*Genus Hincksetta* Billard, 1918

**Diagnosis.** Colony with erect stem, which may or may not bear alternate hydrocladia. Stem and hydrocladia, when present, bearing alternate hydrothecae. Gonothecae springing from within hydrothecae or from stem or hydrorhiza.

_type species_: *Hincksetta sibogae* Billard, 1918.

**KEY TO SPECIES**

1. Stem unsegmented, bearing alternate, unsegmented hydrocladia  
   - Stem segmented, without hydrocladia  
     2

2. Hydrotheca adnate for about half accauline length. Stem corrugated near nodes  
   - Hydrotheca adnate for about one quarter accauline length. Stem not corrugated  

   *Hincksetta corrugata* Millard, 1958

   _Fig. 76A_

*Hincksetta corrugata* Millard, 1958: 181, fig. 5.

**Diagnosis.** Stem reaching 10 mm, unfascicled, unbranched, slightly zigzag, divided by oblique nodes into internodes, each bearing a hydrotheca. Perisarc corrugated in basal region and in neighbourhood of nodes. Hydrothecae alternate, the two rows in one plane or displaced towards anterior surface.

_Hydrotheca adnate for about half accauline length, tubular, bent slightly_
outwards, smooth or faintly corrugated, 0.6–0.7 mm in length and 0.4–0.5 mm in marginal diameter. Margin very slightly everted.

Gonothecae unknown.

Variation. In the few colonies known there is variation in internode length and in the amount of corrugation on the stem and on the hydrothecal walls.

Remarks. This species may eventually prove to be a variety of *H. cylindrica*.

Distribution outside South Africa. Madagascar.

Distribution in South Africa. Natal to Moçambique, 10–46 m, rare. Type locality: Natal. 30/30 (s), 26/32 (s), 21/35

*Hincksella cylindrica* (Bale, 1888)

*Sertularella cylindrica* Bale, 1888: 765, pl. 16 (fig. 7).
*Syntheticium cylindricum*: Nutting, 1904: 136, pl. 41 (fig. 7). Fraser, 1944: 234, pl. 48 (fig. 216).

Diagnosis. Stem unfascicled, unbranched or irregularly branched, divided by oblique nodes into internodes, each bearing a hydrotheca. Internodes without corrugations. Hydrothecae alternate, the two rows in one plane.

Hydrotheca thin-walled, adnate for ¼ to nearly ½ adcauline height, tubular, curved slightly outwards, smooth. Margin very slightly everted.

Gonotheca arising from within hydrotheca, from stem below hydrotheca or from hydorhiza, sessile or with pedicel of variable length. Male elongated and rather irregular in outline, female spherical.

Only a subspecies of this species from South Africa.

*Hincksella cylindrica pusilla* Ritchie, 1910

Fig. 76B–E

*Sertularella cylindrica* var. *pusilla* Ritchie, 1910b: 817, pl. 77 (fig. 9).
*Hincksella cylindrica pusilla*: Millard, 1964: 22, fig. 6A–D.
*Cyclonia pusilla*: Hirohito, 1969: 16, fig. 12.

Diagnosis. A dwarf form differing from the nominate subspecies in the following characters:

Stem never branched, shorter (reaching 7 mm) and with more slender internodes (diameter under 0.1 mm).

Hydrotheca adnate for about ¼ adcauline height, more slender and more definitely bent outwards near base, 0.5–0.6 mm in depth and 0.14–0.17 mm in marginal diameter.

Variation and remarks. The most obvious variation in the single sterile colony found is in the length of the internodes, which is very variable. The hydrothecae are so delicate that they crumple easily and a perfect one is seldom seen. There appears to be a certain amount of variation in shape, some being obviously
Hinckellsia corrugata. A, stem.
Hinckellsia cylindrica pusilla. B–D, hydrothecae; E, part of stem with characteristically crumpled hydrothecae.
Hinckellsia echinocarpa. F, stem; G, origin of hydrocladium.
Scale: F in cm, the rest in mm/10.
tubular and of equal diameter throughout, and others expanding slightly towards the margin.

Hirohito (1969) has for the first time described and illustrated the gono-
ephores of subspecies *pusilla*. These show sexual dimorphism and arise either from
within a hydrotheca or direct from the hydrolhiza. They are similar to those of
the nominate subspecies and explain the apparent discrepancies in the literature;
those of Torrey 1902 (repeated in Nutting 1904) being male, and those of Fraser
(1944) and Blackburn (1937) apparently being female.

*Distribution outside South Africa* (of subspecies *pusilla*). Mergui Archipelago
(type locality), East Indies, Japan, tropical West Africa, West Indies, Caribbean.

*Distribution in South Africa*. One record only, from the Agulhas Bank in 84 m.
33/28 (s)

*Hincksella echinocarpa* (Allman, 1888)

Fig. 76F–G

*Sertularia echinocarpa* Allman, 1888: 57, pl. 28 (figs 1–la).

*Hincksella echinocarpa*: Millard, 1967: 176, fig. 3A–C.

*Diagnosis*. Stem reaching a height of 90 mm; fascicled, though flexuous and
unable to support itself out of fluid; unbranched; bearing alternate hydrothecae
and alternate, flexuous hydrolcladia which generally arise below every third
hydrotheca; unsegmented. The two rows of hydrothecae and hydrolcladia in
one plane.

Hydrolcladium separated from stem apophysis by oblique node, unfascicled,
unsegmented, reaching a maximum length of 40 mm, bearing alternate
hydrothecae.

Hydrotheca adnate for less than half adcauline height, tubular, with free
part straight or curved slightly outwards, smooth, 1.2–1.3 mm in total adcauline
length (adnate plus free part) and 0.3–0.5 mm in marginal diameter.

Gonothecae (not reported in South Africa) borne below hydrothecae,
where thin oval areas occur in the perisarc. ‘Pyriform, thickly set with hollow,
blunt, spine-like outgrowths of their chitinous perisarc’ (Allman).

*Variation*. As in many deep-water species the hydrolhiza forms a branching,
fibrous rootstock for penetration of a muddy substratum.

The stem is lax and geniculate for the most part, though it may be straight
in the distal unfascicled portion. Variations occur in the distance between
consecutive hydrolcladia, with corresponding variations in the number of inter-
mediate hydrothecae. Rarely a transverse node occurs in the hydrolcladium
immediately above a hydrotheca; this appears to be the result of regeneration
rather than a normal node. Rarely, too, the hydrolcladium may rebranch.
Allman reports a height of 160 mm in material from Kerguelen.

*Distribution outside South Africa*. Only record and type locality: Kerguelen
Island in southern Indian Ocean.
Distribution in South Africa. Off the coast of Moçambique in 1 610–2 200 m.
24/36 (a), 23/37 (a)

Genus Syntheicum Allman, 1872

Diagnosis. Colony with erect stem usually (always, in South African species)
bearing hydrocladia in opposite pairs. Stem and hydrocladia bearing hydro-
thecae in opposite pairs, the pairs always in the same plane and thus forming
two longitudinal rows. Gonothecae usually dioecious, springing from within
hydrothecae.

Type species: Syntheicum elegans Allman, 1872.

KEY TO SPECIES

1. Hydrotheca widening strongly to margin ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... S. hians
   - Hydrotheca tubular, not widening markedly to margin ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... 2
2. Hydrotheca with one adcauline internal tooth in at least some hydrothecae S. dentigerum
   - Hydrotheca never with internal tooth ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... S. elegans

Syntheicum dentigerum Jarvis, 1922

Fig. 77E–H

Syntheicum dentigerum Jarvis, 1922: 344, pl. 25 (fig. 15). Totton, 1930: 172. Millard, 1964:
24, fig. 6E–J. Watson, 1973: 169, figs 17–18.

Diagnosis. Stem reaching a height of 40 mm; unfascicled; normally unbranched,
but bearing pinnately arranged hydrocladia; divided by straight nodes into
internodes, which bear a variable number of hydrocladia and hydrothecae.
The two rows of hydrocladia in the same plane.

Hydrocladium making a wide angle with stem, with straight nodes and one
pair of hydrothecae to each internode. Hydrothecae opposite, though
subopposite in proximal region.

Hydrotheca adnate for over half adcauline length, tubular, curved out-
wards, 0.5–0.6 mm in total adcauline length (adnate plus free part) and 0.16–
0.2 mm in marginal diameter. With one large internal tooth on adcauline side
in at least some hydrothecae of colony.

Gonotheca arising from within hydrotheca, pentagonal or triangular in
section, tapering distally, annulated, with 5–6 transverse folds on each flat
side, with small circular distal opening.

Variation. Branching occasionally occurs, the branches replacing hydrocladia.
The nodes of the stem may be indistinct in certain regions. On the internodes
the following are the most common arrangements:

(i) two pairs of hydrothecae, with a pair of hydrocladia between them,
(ii) one pair of hydrocladia followed by a pair of hydrothecae,
(iii) one pair of hydrothecae only.

Stolonization is common.

The presence of an internal hydrothecal tooth is a variable character.
When present it is usually large and very obvious, but it may be present in only a few hydrothecae of a colony, and is often present in one member of a pair and absent in the other. Occasional hydrothecae also possess an internal peg-like thickening of perisarc in the centre of the acauline wall.

The typical pentagonal gonothecae sometimes have two of the angles smoothed out giving the appearance of a rather flattened triangle. The annulations tend to fade out on the angles, though occasionally continue right over them. There is never a definite zigzag line as in *S. elegans*.

**Distribution outside South Africa.** Tropical Indian Ocean: Chagos (type locality) and Seychelles. South Australia.

**Distribution in South Africa.** Sparsely distributed on the Agulhas Bank in 18–46 m. 34/19 (s), 34/21 (s), 33/25 (s), 34/25 (s), 33/26 (s), 33/27 (s)

*Synthecium ?elegans* Allman, 1872

Fig. 77A–B

*Synthecium elegans* Allman, 1872: 229, fig. Allman, 1876: 266, pl. 15 (figs 1–3). ?Millard, 1957: 203, fig. 9D.

*Synthecium ramosum* Allman, 1886: 137, pl. 12 (figs 3–4).

*Synthecium subventricosum* Bale, 1914a: 5, pl. 1 (figs 3–5).


*Synthecium elegans* forma *elegans*: Ralph, 1958: 349, fig. 17a–e.

**Diagnosis.** Stem reaching a height of 20 mm; unfascicled; bearing pinnately arranged hydrocladia; divided by straight nodes into internodes, each of which normally bears two pairs of hydrothecae and one pair of hydrocladia arising between them. The two rows of hydrocladia in the same plane.

Hydrocladium with regular nodes, each internode bearing a pair of hydrothecae. Hydrothecae opposite, though subopposite in proximal regions.

Hydrotheca adnate for over \( \frac{2}{3} \) height, tubular, curved outwards, 0,5–1,0 mm in total acauline length (adnate plus free part) and 0,2–0,4 mm in marginal diameter.

Gonotheca (not reported from South Africa) arising from within hydrotheca, ovate, with prominent transverse ridges connected on two sides by zigzag longitudinal ridges, with distal aperture on short tubular neck.

**Variation.** South African material is unbranched, but Allman (1886) reports branching specimens from New Zealand reaching a height of 150 mm. The branches replace hydrocladia. Simple stems resembling solitary hydrocladia may also occur.

The arrangement on the stem internodes is very variable, particularly in the older regions, and apart from the normal arrangement each internode may bear

(i) one pair of hydrocladia only,
(ii) one pair of hydrothecae only,
(iii) one pair of hydrocladia followed by one pair of hydrothecae.
Fig. 77.

*Synthecium elegans*. A, hydrocladium; B, stem.

*Synthecium bians*. C, stem and hydrocladia from young part of colony; D, hydrocladium.

*Synthecium dentigerum*. E, hydrocladium; F, gonotheca in side view; G, a branching stem;

H, gonotheca viewed from above, X marks adcauline side.

Scale: B and G in cm, C in mm, the rest in mm/10.
The hydrocladia may have indistinct nodes, and may occasionally be branched. Stolonization is common.

Remarks. The identification of this species must remain doubtful until the discovery of gonophores in this country, for the trophosome is similar to that of several other related species. The same applies to records of \textit{S. elegans} outside the country. These are marked with a query in the distribution. Material from the Seychelles has recently been definitely identified as \textit{S. patulum} (Busk) by Millard & Bouillon (1973).

\textit{Distribution outside South Africa.} New Zealand (type locality), Australia, East Indies, ?Madagascar, ?East Africa.

\textit{Distribution in South Africa.} Sparsely distributed from False Bay, Cape, to Moçambique in 16–100 m. 34/18 (s), 35/19 (s), 34/22 (s), 34/24 (d), 30/30 (s), 29/31 (s), 28/32 (s), 24/34 (s), 21/35

\textit{Synnecium hians} Millard, 1957

\textbf{Fig. 77C–D}

\textit{Synnecium hians} Millard, 1957: 204, fig. 9A–C.

\textit{Diagnosis.} Stem reaching a height of about 60 mm; unfascicled; normally unbranched, but bearing pinnately arranged hydrocladia; divided by straight nodes into internodes, each of which normally bears three pairs of equally spaced hydrothecae and one pair of hydrocladia arising below the second pair of hydrothecae. The two rows of hydrocladia in the same plane.

Hydrocladium with irregular nodes; bearing pairs of opposite hydrothecae which may be subopposite in proximal regions.

Hydrotheca adnate for almost entire length, narrow at base, widening strongly to margin, bent very slightly outwards, 0,3–0,4 mm in total adcauline length (adnate plus free part) and 0,2–0,3 mm in marginal diameter. Margin everted. No internal teeth. Hydranth with adcauline caecum.

Gonotheca unknown.

\textit{Variation.} In rich colonies the hydrorhizal tubes may rise up from the surface in a tangled bundle simulating a fascicled stem, the individual tubes anastomosing with one another and with the bases of the stems.

The nodes of the stem may be indistinct in the older regions. The arrangement on the stem internodes sometimes varies and the following aberrations may occur:

(i) two pairs of hydrothecae per internode, with a pair of hydrocladia arising below the second pair,
(ii) one pair of hydrothecae only per internode.

In rare cases a normal hydrocladium may be replaced by a branch.

The young hydrocladium commences with an unpaired adcauline hydrotheca, which is followed by subopposite pairs gradually changing to
opposite. In older parts of the colony (possibly due to regeneration) the hydrocladium is separated from the stem by a transverse node, after which opposite or nearly opposite pairs of hydrothecae start immediately. The angle between the hydrocladium and the stem is large in the older part of the colony (almost a right angle) but tends to become more acute in the younger region.

The hydrothecae are very constant in shape though on older stems the delicate distal parts have become eroded leaving low cup-shaped scars.

**Distribution.** Endemic to South Africa. Type locality: False Bay, Cape.

**Distribution in South Africa.** Fairly common round the coast from False Bay in the Cape to Moçambique in 18–219 m. 34/18 (s), 34/20 (s), 34/21 (s), 34/22 (s), 34/23 (d), 34/25 (s), 33/26 (s), 33/27 (s), 33/28 (s), 32/28 (s), 30/30 (s), 29/31 (s, d), 29/32 (s), 28/32 (s, d), 24/35 (d)

**Family Sertulariidae**

**Diagnosis.** Hydrothecae borne on stem and hydrocladia in two or more longitudinal rows. Hydrotheca stalked or sessile and, if sessile, adnate to a varying degree, bilaterally symmetrical, usually with a toothed margin and a hinged operculum of one or more valves, with a diaphragm in stalked species and a definite floor perforated by an asymmetrical hydropore in sessile species. Hydranth with a single circle of filiform tentacles and a conical hypostome; endoderm differentiated into an aboral and an oral region, the former sometimes forming an acauline caecum on contraction. Nematothecae absent. Gonophores in the form of fixed sporosacs.

**Introduction.** The Sertulariidae is one of the largest families of Hydroida and is easily recognized by its bilaterally symmetrical and operculate hydrothecae.

In only one genus (*Calamphora*) is the colony stolonial, in all others the hydrothecae are borne on an erect stem.

The stem may be fuscicled or unfascicled, branched or unbranched. Characteristically branches arise in one plane and are opposite or alternate, often rebranching in the same way, though species with spiral or whorled branches also occur. In some cases the branches differ from the main stem in some way (e.g. in thickness, arrangement of hydrothecae) and the term hydrocladia is appropriate. In others, and particularly in the small, irregularly branched species, the branches are similar in structure to the stem, but for the sake of uniformity the term hydrocladia is used here too for the final ramifications of a pinnate stem.

The stem is termed **stiff** when it is able to support itself out of fluid and **flexuous** when it cannot. Stiff stems give rise to bushy colonies, and flexuous stems to long, straggling colonies. Stolonization from the ends of the stem or hydrocladia may occur in any species and is particularly common in *Symplectoscyphus* and *Dictyocladium*. It gives the colony a tangled and matted appearance.
Stem and branches are typically segmented, with transverse or oblique nodes. Each internode may bear one or more hydrothecae and may contain internodal septa. In certain species of *Sertularia* Hinge-joints occur, which allow for movement and provide a point of easy rupture and subsequent regeneration. Hinge-joints usually occur in pairs near the base of an unbranched stem or at the bases of the hydrocladia of a branched stem, but may also occur at irregular intervals in addition to the normal nodes.

The arrangement of the hydrothecae on the stem and hydrocladia varies. Commonly the hydrothecae are alternate (e.g. in *Surtularella* and *Symplectoscyphus*) or in opposite pairs (e.g. in many species of *Sertularia*), but they may be subalternate or subopposite. In all of these the hydrothecae form two longitudinal rows. Members of the two rows may be well separated or may be contiguous and touch one another in the centre on one surface. Occasionally the hydrothecae form more than two longitudinal rows (e.g. in *Selaginopsis* and *Dictyocladium*). In *Hydralmannia* the hydrothecae are borne in a single row on one surface of the stem, but their distal ends are bent alternately to left and to right.

Most of the Sertulariidae have sessile and bilaterally symmetrical hydrothecae, with one side adnate to the stem to a varying degree. In some of the more specialized genera such as *Thuiaaria* and *Salacia* all, or almost all, of one surface of the hydrotheca may be adnate and deeply sunk into the stem. Associated with the adnate condition the hydrotheca is usually curved, with the mouth directed away from the stem, but there may also be a double curvature—outwards and then distally.

In the genus *Surtularella* with its numerous species the curvature of the hydrotheca is important in diagnosis and thus needs precise definition. Three categories are recognized:

1. Margin perpendicular to axis. Hydrotheca not curved, and flask-shaped in lateral view. A line dropped at right angles to the margin and through its centre will bisect the hydrotheca and pass through the base of the adcauline wall.
2. Margin tilted towards adcauline side. Hydrotheca curved away from stem. A line dropped at right angles to the margin and through its centre will pass through the adcauline wall.
3. Margin tilted towards adcauline side. Hydrotheca with double curvature. A line dropped at right angles to the margin and through its centre will pass through the adcauline wall or through the hydropore.

Because of the curvature of the hydrotheca measurements may be difficult. In this work the marginal diameter and the adcauline length of the hydrotheca are usually given, and these are taken in lateral view, the length being measured as a straight line from the floor of the hydrotheca to the adcauline margin across any curvature which may be present. Occasionally the adcauline length cannot be measured accurately because the floor does not reach the adcauline wall. In such cases the adcauline length is given instead. Measurements are always exclusive of any additional margins resulting from regeneration.
Possibly as a result of curvature the hydrotheca may have internal folds, or intrathecal septa, and these may be adcauline or abcauline or on both sides. They form a useful point of attachment for the hydranth and are characteristic of many species of *Sertularia* and of the genus *Crateritheca*.

In the sessile species the hydrotheca has a definite floor of perisarc with an excentric hydropore. The hydropore is close to the abcauline side, and the floor is attached to, and continuous with, the base of the adcauline wall. The adcauline wall is often produced below the floor as a thickened knot of perisarc.

Also included in the Sertulariidae are a few genera with stalked, yet operculate, hydrothecae. These have in the past been included variously in the Campanulinidae, Campanulariidae and Sertulariidae. Mammen (1965a) created for them a new family, the Thyroscyphidae. Of these, the genera *Thyroscyphus* and *Parascyphus* were reviewed by Splettstösser (1929), who also created a new genus, *Cnidoscyphus*, for certain species on the basis of nematocyst structure and arrangement. (*Cnidoscyphus* is not recognized in the present work,
for the author feels that nematocyst structure and arrangement are not sufficient grounds for separating genera which are otherwise very similar.) These genera are usually considered to be more primitive than the sessile genera and to differ from them in the presence of a diaphragm in the hydrotheca. It is felt, however, that the diaphragm is strictly comparable with the floor of the sessile hydrothecae where the pedicel has been eliminated. The stolonial genus *Calamphora* in fact bridges the gap. *Calamphora* has unmistakable affinities with *Sertularella* and was not included in the Thyroscyphidae by Mammen. Its solitary hydrotheca has a diaphragm of the thyroscyphid type, but Leloup (1935: 35) illustrated a colony of *C. parvula* (under the name of *Thyroscyphus intermedius f. peculiaris*) with two hydrothecae to a stem, in which the proximal one is sessile and adnate as in a typical *Sertularella*. These pedicellate genera are here retained in the Sertulariidae.

In the Sertulariidae the margin of the hydrotheca is typically toothed, and the number and shape of the teeth are useful in diagnosis. For instance, *Sertularella* has four marginal teeth, *Symplectoscyphus* three and *Amphisbetia* two. In a few forms the marginal teeth are almost obsolete (e.g. in *Idiellana*) or absent (*Abietinaria, Thuaria*).

![Diagram of Sertulariidae marginal teeth and opercular valves](image)

**Fig. 79.**

Sertulariidae: marginal teeth and opercular valves (adcauline side on right).

In addition to the marginal teeth some species have internal teeth formed by pegs of perisarc projecting into the cavity of the hydrotheca just below the margin. These are particularly prevalent in *Sertularella*, where in certain cases their presence or absence, number and position may be diagnostic for the species.

The mouth of the hydrotheca is closed by an operculum consisting of one or more valves hinged at the edge. In genera with three or four marginal teeth a similar number of valves is seated in the bays between them and meet in the centre to form a pyramid, e.g. *Sertularella, Symplectoscyphus, Thyroscyphus*. Genera with two marginal teeth, as for instance *Sertularia, Amphisbetia* and *Dynamena*, have an operculum of two valves of unequal size attached at the ad-
and abcauline edges. The larger valve is adcauline in *Amphisbетia* and abcauline in *Dynamena* and *Sertularia*. In these forms the adcauline valve may be divided into two by a partition and bent at an angle like a roof. Genera with only one large opercular valve include *Diphasia, Idiellana, Abietinaria, Thuiaria* and *Salacia*. The hinge is adcauline in the first three and abcauline in the last two; it is often seated in an embayment of the margin. Sometimes the operculum is shed fairly early in development, as in some species of *Thyroscyphus*, or reduced to a membrane, as in *Craterithea acanthostoma*, or even lost altogether, as in *Stereotheca*. These genera thus show relationship to the Syntheiidae, but are retained in the Sertulariidae because of the toothed hydrothecal margin. Naumov (1960) suggests that the number of opercular valves provides an example of the evolutionary process of oligomerization, those with many valves being primitive and those with one or none being advanced. On contraction the hydranth is completely withdrawn into the hydrotheca and the operculum closed over it. Regeneration of the margin is accompanied by regeneration of the operculum, so that there may be several opercula, one above the other.

3 TEETH 4 TEETH

Fig. 80.

*Sertularella*: internal teeth (adcauline side on right).

In certain genera (*Abietinaria, Amphisbетia, Calamphora, Craterithea, Hydrallmania, Parascyphus, Sertularella, Sertularia, Symplectoscyphus* and *Thuiaria*) contraction of the hydranth into the hydrotheca causes the proximal part of the gastric cavity wall to be folded into a blind caecum on the abcauline side. This is due in part to the attachment of the ectoderm of this region to the hydrothecal wall preventing its complete withdrawal. This blind caecum is useful in generic diagnosis, but it must be borne in mind that it can only be observed in the contracted hydranth. It imparts a bilateral symmetry to the hydranth. In other genera the hydranth is withdrawn symmetrically into the hydrotheca and there is no caecum, e.g. *Dictyoocladium, Diphasia, Dynamena, Idiellana* and *Salacia*. In *Thyroscyphus* withdrawal of the hydranth causes an annular folding all round the body, and Splettstösser (1929) considers this to be an early stage in the evolution of a blind caecum.
Sertulariidae: structure of hydranth (shown retracted) in diagrammatic l.s. A, with blind caecum, e.g. *Sertularella*; B, without caecum, e.g. *Dynema*; C, with annular fold, e.g. *Thyroscyphus*.

The ectoderm of the hydranth is produced as a lining over the inner wall of the hydrotheca to a varying degree, and in *Thyroscyphus* may form a ‘Deckenplatte’ below the operculum. To this lining of ectoderm the ectoderm of the hydranth is fastened in certain strategic positions where perisarcal thickenings of the hydrotheca may develop. Although Mammen (1965a), following Nutting (1904), speaks of ‘protractor’ and ‘retractor’ muscles, to the author’s knowledge actual muscle fibres have as yet not been identified in these attachments. Nematocysts may in certain cases be present in the lining ectoderm or in the ‘Deckenplatte’, and it was on this feature that Splettstösser (1929) based his genus *Cnidosephyus*.

A peculiar structure is present in *Sertularia ligulata* (Fig. 100D) and is possibly present in other species too (it has been seen in *S. turbinata*). This is the ligula. It consists of a slender outgrowth from the base of the adcauline side of the hydranth and it protrudes as a leaf-shaped process through the mouth of the hydrotheca. It often remains clearly visible after the hydranth has contracted. Its function is not clear, but since it is well armed with nematocysts, it may serve as a nematophore. Although nematothecae do not occur in the Sertulariidae, in *Amphisbetia minima* certain small pores occur with some regularity on the internodes of the stem and each is usually surrounded by a low collar of perisarc (Fig. 82H). They have sometimes been called nematothecae, but there is as yet no proof of the presence of nematophores.

The gonothecae are usually dioecious and sometimes also dimorphic. No special protective structures are developed around them and they are not aggregated, but the perisarc may be transversely annulated or sculptured with an elaborate arrangement of spines. The eggs are usually fertilized *in situ* and
the planulae developed within the gonotheca. In some species the developing eggs are extruded through the opening of the gonotheca into an acrocyst (Fig. 90B). In Diphasia and Sertomma the spiny processes of the gonotheca may bend over and meet in the centre to enclose a brood-chamber or Marsupium. There has been much disagreement over the limitations of genera in the Sertulariidae. Broch (1918) recognizing only a few (9), and Stechow (1923c) a large number (36). The present work adopts an intermediary course, and for the limitations of the genera Diphasia, Dynamena and Salacia the views of Billard (1925a) have been accepted.

KEY TO GENERA

[Genera not represented in South Africa are bracketed]

1. Hydrotheca stalked .................................................. 2
   - Hydrotheca sessile ........................................... 4

2. Colony stolonic .....................................................
   - Colony with upright stem .................................. 3
     .... Calamphora p. 251

3. Hydrotheca with four marginal teeth and operculum of four valves. Hydranth with annular fold, but no caecum .................................................. Thyroscyphus p. 321
   - Hydrotheca with three marginal teeth and operculum of three valves (in South African species). Hydranth with abcauline caecum ........................................... Parascyphus p. 270

4. Hydrotheca with more than four marginal teeth .................................................. 5
   - Hydrotheca with no marginal teeth, or with four or less .................................................. 6

5. Hydrotheca with internal ridges or septa .................................................. 7
   - Hydrotheca without internal ridges or septa .................................................. Stereotheca p. 313

6. Hydrothecal operculum in form of pyramid, consisting of three or four valves.
   Margin with three or four teeth of equal size .................................................. 10
   - Operculum not in form of pyramid. Margin not as above; with no teeth, two teeth, or three-four teeth not equal in size .................................................. 10

7. Hydrothecae arranged in more than two longitudinal rows in at least some parts of stem .................................................. Dictyocladium p. 254
   - Hydrothecae alternate and arranged in two longitudinal rows only ........................................ 8

8. Hydrotheca with four marginal teeth and operculum of four valves. Mouth quadrangular .................................................. Sertularella p. 276
   - Hydrotheca with three marginal teeth and operculum of three valves. Mouth triangular .................................................. 9

9. Hydrothecae alternate. Hydranth with abcauline caecum .................................................. Symplectocyphus, p. 314
   - Hydrothecae opposite. Hydranth without abcauline caecum ........................................... [Sertomma]

10. Operculum of two valves, the abcauline one sometimes divided into two.
    Hydrotheca with two marginal teeth (and sometimes a minute median, abcauline one as well) .................................................. 11
    - Operculum of one valve. Hydrothecal margin generally not toothed (but toothed in Diphasia tetracanthina) .................................................. 14

11. Bases of hydrothecae forming one longitudinal row, their distal ends bending alternately to right and left. Acauline valve of operculum the larger Hydallmania p. 269
    - Bases of hydrothecae forming two longitudinal rows, more or less on the sides of the stem .................................................. 12

    - Marginal teeth of hydrotheca more or less midway between abcauline and abcauline edge. Acauline opercular valve larger than abcauline .................................................. 13
13. Hydranth without abcauline caecum. Hydrothecal pairs typically (though not always) grouped  
   - Hydranth with abcauline caecum. Hydrothecal pairs never grouped  
   *Dynamena* p. 261  
   *Sertularia* p. 305
14. Opcrum abcauline  
   - Opcrum abcauline  
   15  
   17
15. Hydrotheca expanding distally. Hydranth without abcauline caecum  
   - Hydrotheca not expanding distally  
   16
16. Hydranth without abcauline caecum. Hydrothecae all on one surface of hydrocladium  
   - Hydranth with abcauline caecum. Hydrothecae on lateral surfaces of hydrocladium  
   *Idiellana* p. 269  
   *Abietinaría* p. 246
17. Hydrothecae in more than two longitudinal rows  
   - Hydrothecae in two longitudinal rows  
   [Selaginopsis]  
   18
18. Hydranth with abcauline caecum  
   - Hydranth without abcauline caecum  
   *Thuariá* p. 320  
   *Salcacia* p. 271

Genus *Abietinaría* Kirchenpauer, 1884

**Diagnosis.** Stem erect, bearing hydrothecae, and sometimes hydrocladia as well, in two longitudinal rows. Hydrocladia different in structure to stem, with internodes of irregular length. Hydrotheca sessile, partly adnate, flask-shaped and wider at base than at margin, without distinct marginal teeth. Opcrum of one large abcauline valve. Hydranth with abcauline blind caecum.

Type species: *Sertularia abietina* Linnaeus, 1758.
One species from South Africa and one doubtful record.

*Abietinaría laevimarginata* (Ritchie, 1907)

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*Sertularia laevimarginata* Ritchie, 1907a: 507, pl. 26 (figs 5–6).
*Sertularia linealis* Warren, 1908: 308, fig. 9. Millard, 1958: 195, fig. 8D, G.
*Abietinaría laevimarginata*: Gravier, 1972: 8, fig. 2C. Millard & Bouillon, 1974: 27, fig. 7A–C, E–H.
*non Sertularia linealis* var. *longa* Millard, 1958: 197, fig. 8E.
*non Sertularia linealis* *longa*: Millard & Bouillon, 1973: 75, fig. 9E–F.

**Diagnosis.** Hydrorhiza growing on weed and typically arranged in longitudinal lines, without strengthening pegs of perisarc, but usually with four ingrowing perisarscal lobes around origin of stem. Stem unfascicled, unbranched, reaching a maximum height of 5 mm, each internode bearing a pair of opposite hydrothecae. Two (or rarely three) hinge-joints present near base of stem below thecate part, remaining nodes slightly oblique or indistinct. Members of a pair of hydrothecae contiguous in front (except sometimes for the basal pair), separate behind, their free abcauline walls typically forming a straight line at right angles to the axis of the stem.

Hydrotheca adnate for over half abcauline length, bent outwards, narrowing to margin and usually constricted just below it, with no intrathecal ridge, with thick perisarc, 0.13–0.3 mm in abcauline height and 0.08–0.11 mm in
marginal diameter. Margin especially thick on adcauline edge, with two low, rounded lateral lobes. Internal teeth present, one large adcauline, which may be double, and two low latero-acauline. Operculum shed early.

Gonotheca borne on front of stem below first pair of hydrothecae, smooth, compressed, spherical to ovoid in broad view, with a wide distal operculate aperture on a low collar, reaching 1.0 mm in length and 0.8 mm in maximum diameter.

Variation. The shape of the hydrotheca changes along the length of the stem, the distal ones being more erect and contiguous for a greater length than the basal ones. The free adcauline walls of the distal pair may thus not form a straight line but subtend an obtuse angle between them. The marginal lobes of the hydrotheca vary in development and may be quite distinct or almost obsolete.

Distribution outside South Africa. Cape Verde Islands (type locality), tropical western Indian Ocean, including Madagascar, Wasin, Cargados and Chagos.

Distribution in South Africa. Northern Natal and Moçambique, on weed in shallow water. 25/32, 26/32 (s), 27/32

Doubtful species

*Abietinaria abietina* (Linnaeus, 1758)


Remarks. There is only one record of this species from South Africa, that of Busk in 1851. Although Busk's material was correctly identified (Millard 1961), his locality is subject to doubt since the species has not been reported again. The only recent record from the Indian Ocean is that of Redier (1963) from Madagascar.

Genus *Amphisbeta* L. Agassiz, 1862


Diagnosis. Stem erect, branched or unbranched. Stem and hydrocladia bearing hydrothecae in two longitudinal rows. Hydrothecae sessile, partly adnate, with two prominent marginal teeth seated near adcauline edge and occasionally a small, median adcauline one. Operculum of two valves, a larger adcauline one and a smaller adcauline one. Hydranth with adcauline blind caecum.

Type species: *Sertularia operculata* Linnaeus, 1758.

**KEY TO SPECIES**

1. Stem unbranched, Members of a pair of hydrothecae contiguous with one another, at least in distal region of stem
   - A. minima
   - Stem branched. Members of a pair of hydrothecae never contiguous with another ... 2
2. Stem branching dichotomously. Stem and branches similar, with one pair of hydrothecae to each internode (though nodes sometimes not clearly defined) ... A. operculata
   - Branching alternate. Stem with three hydrothecae and a branch (hydrocladium) to each internode, hydrocladia with a variable number of hydrothecae to an internode ... A. mapletonii
Fig. 82.

*Amphibetia maplestonei*. A, part of stem showing gonotheca and origins of hydrocladia; B, stem; C and D, hydrotheca with and without internal teeth; E, margin of hydrotheca with operculum.

*Abietinaria laevimarginata*. F, stem with gonotheca, drawn from Warren's holotype of *Sertularia linealis*; G, distal part of hydrotheca with near wall removed to show internal teeth and operculum.

*Amphibetia minima*. H, two pairs of hydrothecae; J, stem with gonotheca; K, margin of hydrotheca with operculum.

Scale: B in cm, the rest in mm/10.
Amphibetia maplestonei (Bale, 1884)

Fig. 82A–E

*Sertularia maplestonei* Bale, 1884: 70, pl. 6 (fig. 4), pl. 19 (fig. 2).
*Sertularia bidens* Bale, 1884: 70, pl. 6 (fig. 6), pl. 19 (fig. 1). Warren, 1908: 310, fig. 10.
*Thiria maplestonei*: Billard, 1907a: 349, fig. 5, pl. 25 (figs 2–6).

**Diagnosis.** Stem unfascicled, flexuous to stiff, unbranched or branching irregularly near base, pinnate, geniculate, reaching a maximum height of 130 mm. Basal part athecate and acladiate, with a variable number of transverse nodes. Distal part divided into regular internodes by oblique nodes sloping in alternate directions. Each internode bearing one hydrocladium and three hydrothecae, one in axil and a subopposite pair above. Hydrocladia alternate, the two rows in one plane.

Hydrocladium narrower than stem, divided by straight nodes into internodes bearing a variable number of subopposite pairs of hydrothecae. Members of a pair of hydrothecae not contiguous.

Hydrotheca adnate for half to three-quarters adcauline length, the adnate part sac-shaped and curved outwards, the free part narrowing to margin and curved upwards, 0.2–0.3 mm in adcauline height (without teeth) and 0.07–0.10 mm in marginal diameter. Margin with two long and bluntly rounded latero-abcauline teeth. An internal perisarcal peg present on abcauline wall at a quarter to a third of height. Internal teeth present or absent. Hydranth with 13–14 tentacles.

Gonothecae borne on stem and hydrocladia, smooth, flat-triangular in section, pear-shaped in broad view, with two hollow distal spines arising above two of the angles and a terminal operculate aperture on a low collar, reaching 1.7 mm in height and 0.9 mm in maximum diameter.

Colour pale brown.

**Variation.** One or two hinge-joints may separate the basal athecate part of the stem (which is of variable length) from the distal part. Stem nodes may be indistinct in parts.

The two rows of hydrothecae on the hydrocladium are usually in one plane, but may be shifted towards the anterior surface. Hydrocladia occasionally branch, when the cauline arrangement is reassumed for a short interval.

The more distal hydrothecae tend to be longer than the proximal ones and to have better developed marginal teeth. The two marginal teeth are often unequally developed. The internal teeth, when present, vary in number from one (adcauline) to four (two adcauline and two abcauline.)

The gonotheca rarely has a third distal spine.

**Distribution outside South Africa.** Australia, Madagascar and Vema Seamount (South Atlantic). Type locality: Portland, Australia.

**Distribution in South Africa.** False Bay to Richard’s Bay, littoral to 84 m.
34/18 (s), 34/22 (s), 34/23 (l, s), 33/25 (s), 34/25 (s), 33/26 (s), 33/27 (s), 31/29 (l, s), 30/30 (l, s), 29/31 (s), 28/32 (s)

*Amphisbetia minima* (Thompson, 1879)

Fig. 82H–K


**Diagnosis.** Hydrohiza creeping on weed, with internal thickenings of perisarc. Stem short, reaching a maximum height of 6 mm, unfascicled, unbranched; with a very short basal thecate part terminated by 1–3 hinge-joints and a long distal part bearing up to 15 pairs of hydrothecae, one pair to an internode. Normal nodes narrow, oblique. Members of a pair of hydrothecae contiguous in front (except sometimes for the basal few), separate behind.

Hydrotheca tubular, curved outwards, almost or completely adnate, with no intrathecal ridge, 0,12–0,2 mm in abcauline height (without teeth) and 0,07–0,12 mm in marginal diameter. Margin facing upwards, with two prominent latero-abcauline teeth.

One or two pores commonly present on at least some internodes, situated on the antero-lateral edges of the internode below the hydrothecae, usually surrounded by a low perisarcal collar.

Gonothecae borne on front of stem, one to each, near base and below first or second thecal pair, compressed antero-posteriorly, smooth, pear-shaped in broad view, with terminal operculate aperture on low collar, reaching a height of 1,5 mm and a maximum diameter of 1,0 mm, male and female on separate colonies. Collar with minute internal teeth.

**Variation.** The hydrothecae differ in shape along the length of the stem, those at the base being more divergent than the rest. The two marginal teeth may be of unequal size, the more anterior one being shorter.

**Remarks.** The pores on the internodes with their surrounding collars have sometimes being called nematothecae, but there is no proof of the presence of nematophores. The coenosarc of the stem has been seen to produce an outgrowth reaching to the level of the pore, but not protruding through it. The pore is probably more comparable to the mamenon of certain Plumulariidae.

**Distribution outside South Africa.** Circumglobal in south temperate waters: Australasia, Chile, Falklands, Vema Seamount, Antarctic, Suez. Type locality: Gulf of St. Vincent, Australia.

**Distribution in South Africa.** Round coast from Lambert’s Bay on west to Inhaca on east, never common, littoral to 27 m. 32/18 (l), 33/18 (l), 34/18 (s, l), 34/22 (s), 26/32 (l, s)
**Amphisbeta operculata** (Linnaeus, 1758)

Fig. 83A–E

*Sertularia operculata* Linnaeus, 1758: 808. Hincks, 1868: 263, pl. 54. Bale, 1884: 67, pl. 6 (fig. 1), pl. 19 (fig. 3).

*Sertularia aperta* Allman, 1886: 138, pl. 13 (figs 1–2).


**Diagnosis.** Stem unfascicled, slender and flexuous, branching and rebranching dichotomously to form bushy or straggling tufts reaching a maximum height of 148 mm. No marked distinction into main stem and branches. Hydrothecae in opposite pairs, one pair to an internode, but nodes only visible in younger regions; members of a pair not contiguous except in axils of branches. Dichotomous branching in a plane at right angles to hydrothecal pairs.

Hydrotheca tubular, sloping outwards, almost or completely adnate, with no intrathecal ridge, 0.2–0.3 mm in abcauline height (without teeth) and 0.11–0.14 mm in marginal diameter. Margin facing upwards, with two sharply pointed latero-abcauline teeth, of which one is usually longer than the other.

Gonothecae borne on stem and branches, compressed, pear-shaped in broad view, smooth, with terminal operculate aperture on a low collar, reaching 2.1 mm in height and 0.9 mm in maximum diameter.

**Variation.** Although the branching is always dichotomous, one limb of the dichotomy is often much longer than the other, giving the appearance of a long stem with subsidiary branches which divide only once or twice or not at all. The length and thickness of the internodes may be somewhat greater on the main axis than on the smaller branches, but the difference is never very marked. The two rows of hydrothecae may be in the same plane or shifted onto the anterior surface of the stem.

**Distribution.** Cosmopolitan. Type locality not specified.

**Distribution in South Africa.** Common from Lüderitz Bay in South West Africa to Richard’s Bay in Natal, littoral to 100 m. 26/15 (l), 28/16 (s), 32/18 (l, s), 33/17 (s), 33/18 (s), 34/18 (s), 34/19 (s), 35/19 (s), 34/22 (l, s), 33/23 (l), 34/23 (s, d), 33/25 (s), 34/25 (s), 33/26 (s), 33/27 (s), 32/28 (s), 30/30 (l), 29/31 (l, s, h), 28/32 (s).

**Genus Calamphora** Allman, 1888

**Diagnosis.** Colony stolocial, with hydrothecae and gonothecae arising direct from hydrorhiza. Hydrotheca barrel-shaped with four marginal teeth and an operculum of four triangular valves seated in the bays between the teeth and meeting in the centre as a pyramid. Hydranth with blind caecum.

**Type species:** *Calamphora parvula* Allman, 1888.

One species only from South Africa.
Fig. 83.

*Amphisbeta operculata.* A, stem; B, part of stem with female gonophores; C and D, hydrothecae; E, margin of hydrotheca with operculum.

*Calamphora campanulata.* F, three hydrothecae, two containing hydroids with blind caecum.

Scale: A in cm, the rest in mm/10.
**Calamphora campanulata** (Warren, 1908)

Fig. 83F


**Diagnosis.** Colony creeping on weeds. Hydrotheca solitary, pedicellate. Pedicel usually shorter than hydrotheca, spirally twisted, with 2–5 turns, arising at an angle from hydrorhiza. Hydrotheca terminal, small, barrel-shaped, with 5–8 transverse annulations, 0.4–0.5 mm in height, 0.2–0.3 mm in maximum diameter and 0.14–0.2 mm in marginal diameter. No internal teeth. Hydranth with about 20 tentacles.

Gonotheca (not reported from South Africa) borne on hydrorhiza, pedicellate, barrel-shaped, broader than hydrotheca, transversely annulated, with operculum of four valves. (Mammen.)

**Remarks.** Although this is a stolonial species there is some bilateral symmetry. The blind caecum, which is normally abcauline in the Sertulariidae, is on the side closest to the hydrorhiza, and the hydropore is excentric and displaced towards the same side. The perisarc tends to be thicker on the opposite side.

**Distribution outside South Africa.** Madagascar, India, Indo-China, Japan, Australia. Type locality: Natal, South Africa.

**Distribution in South Africa.** Northern Transkei and southern Natal, littoral. 31/30 (1), 30/30 (1)

**Genus Crateritheca** Stechow, 1921

**Diagnosis.** Stem erect, unfascicled, pinnate. Stem and hydrocladia bearing two or more longitudinal rows of hydrothecae.

Hydrotheca sessile, with more than four marginal teeth, with prominent intrathecal septa and often with external longitudinal ridges. Operculum reduced; either absent altogether, or consisting of a single membranous valve. Hydranth with abcauline blind caecum.

Type species: *Pericladium novaezelandiae* Thompson, 1879.

One species only from South Africa.

**Crateritheca acaanthostoma** (Bale, 1882)

Fig. 84

?*Dynamena pluridentata* Kirchenpauer, 1864: 14, fig. 10.  
*Sertularia acaanthostoma* Bale, 1882: 11, pl. 12 (fig. 4). Bale, 1884: 85, pl. 4 (figs 7–8). Warren 1908: 303, fig. 7, pl. 46 (figs 23–26).  
*Crateritheca acaanthostoma*: Millard, 1964: 26, fig. 7.

**Diagnosis.** Stem moderately stiff, unbranched, reaching 50 mm in height; divided by transverse nodes into regular internodes, each bearing a pair of
opposite hydrothecae, and every third one a pair of opposite hydrocladia from the proximal region. The two rows of hydrocladia in one plane. Hydrocladium divided into internodes of which the first is short and athecate, the second bears one hydrotheca on the lower surface, and the rest bear a pair of subopposite hydrothecae each. The two rows of hydrothecae in one plane.

Hydrotheca adnate for a little over half adcauline height, widening evenly to mouth, straight or bent slightly outwards, 0,2-0,3 mm in adcauline height and 0,16–0,2 mm in marginal diameter. Margin with eight pairs of teeth, of which numbers 1, 3, 5, and 7 (counting from the adcauline surface) are short and bent inwards, numbers 2, 4 and 6 are long and directed slightly outwards, and number 8 is short and straight. Three intrathecal septa present: a transverse shelf about half-way up adcauline side, a transverse perforated shelf about one-quarter of the way up adcauline side, and a very narrow transverse shelf about three-quarters of the way up adcauline side forming the base of a longitudinal trough communicating with the cavity of the hydrotheca. External surface smooth and without longitudinal ridges or furrows. Hydropore funnel-shaped. Operculum a delicate membranous plate, present only in young hydrothecae. Hydranth with 23 tentacles. Hydrotheca lined with a thin layer of ectoderm which continues into the adcauline trough where it bears a cluster of large nematocysts.

Gonotheca (not recorded from South Africa) long, obovate, smooth, with wide operculate distal aperture.

Variation. In the basal part of the stem there may be two to six athecate internodes of irregular length and one to four pairs of hydrothecae before the hydrocladia commence. The hydrocladia normally arise from every third internode, but at times any number from one to six pairs of hydrothecae may be present between two consecutive pairs of hydrocladia. The hydrocladia occasionally branch in the same manner as the stem.

Distribution outside South Africa. Australia (type locality), Madagascar.

Distribution in South Africa. Natal coast, littoral to 34 m. 31/29 (s), 31/30 (l), 30/30(l), 29/31 (l), 28/32 (s)

Genus Dictyoecodium Allman, 1888

Diagnosis. Stem erect, branched or unbranched. Hydrothecae in opposite or subopposite pairs, alternate pairs staggered in at least some regions of stem to give the appearance of four longitudinal rows. Hydrotheca sessile, with three or four marginal teeth and an operculum with a corresponding number of valves. Hydranth with no adcauline caecum.

Type species: Dictyoecodium dichotomum Allman, 1888.

One species only from South Africa.
Crateritheca acaustostoma. A, hydrotheca in side view, adecauline side on right; B, stem; C, part of stem with origins of hydrocladia; D, hydrotheca viewed from above, showing marginal teeth, the aperture closed by operculum; E, t.s. adecauline wall viewed from above, showing upper adecauline septum (c); F, t.s. hydrotheca at deeper level viewed from above, showing adecauline septum (a) and lower adecauline septum (b).

Scale: B in cm, the rest in mm/10.
Dictyoelodium coactum Stechow, 1923

Fig. 86F–H


Diagnosis. Hydrorhiza attached to substratum at intervals only. Stem flexuous, unfascicled, normally unbranched, reaching 28 mm in height, with nodes at irregular intervals and a varying number of hydrothecae to a node. Hydrothecae alternate to opposite, alternate pairs typically staggered to give four longitudinal rows. Stem narrowed and devoid of hydrothecae in region of nodes.

Hydrotheca sunk into stem for all, or almost all, acauline length, curved outwards, with distinct bulge in lower part of acauline wall, 0.2–0.4 mm in acauline height and 0.16–0.2 mm in marginal diameter. Margin with four low, but distinct, teeth. Operculum of four triangular valves seated in the bays between the marginal teeth and meeting in the centre as a pyramid.

Gonothecae borne on the stem on the proximal parts of the internodes, ovate, deeply annulated throughout or in distal part only, with terminal aperture but no collar.

Variation. Branching stems occur rarely, the branches arising from within hydrothecae and exactly resembling the stem. Stolonization is not so profuse as in the type species of the genus and only occasionally do the terminal ends of the stems form stolons which attach to the substratum.

The arrangement of the hydrothecae on the stem is very variable. The number to an internode varies and so does the number of longitudinal rows. Usually there are two longitudinal rows in the lower region formed by alternate, subopposite or opposite pairs of hydrothecae, changing to four longitudinal rows of tightly packed hydrothecae in the upper part. In one case five longitudinal rows were seen, three on one side and two on the other. Often there are two longitudinal rows at the base of an internode and four at the distal end. Occasional stems have two rows throughout. Along the length of the stem there is a change in the shape of the hydrotheca, the proximal ones being strongly bent outwards with their margins almost parallel to the axis of the stem, and the distal ones less so. The bulge on the acauline wall of the hydrotheca varies in degree, sometimes it is very marked and there is a transverse groove immediately above it. Isolated hydrothecae in a colony may have an acauline internal tooth which may be very large.

Distribution. Endemic to South Africa. Type locality: Agulhas Bank.

Distribution in South Africa. South coast, from False Bay to Natal in 0–155 m. 34/18 (s), 34/19 (s), 35/22 (d), 34/24 (d), 34/25 (s), 33/26 (d), 33/27 (s), 32/28 (s), 29/31 (s), 28/32 (s)

Genus Diphasia L. Agassiz, 1862

Syn. Nigellastrum Oken, 1815.

Diphasiella Stechow, 1921.
Diagnosis. Stem erect, branched or unbranched, fascicled or unfascicled. Stem and hydrocladia bearing a double, or rarely a triple, row of hydrothecae. Hydrotheca sessile, tubular and usually expanding distally, usually without marginal teeth, with an operculum of one large abcauline valve. Hydranth without abcauline caecum. Gonotheca unprotected, usually dioecious and provided with projecting ridges or spines, with marsupium in female.

Type species: *Sertularia rosacea* Linnaeus, 1758.

**KEY TO SPECIES**

(Doubtful species not included; for these see p. 260)

1. Hydrotheca with four small marginal teeth  
   - Hydrotheca with no marginal teeth  
     D. tetratricholina
2. Hydrotheca with abcauline intrathecal septum  
   - Hydrotheca without intrathecal septum  
     D. heurtelii  
     D. digitalis

*Diphasia digitalis* (Busk, 1852)

Fig. 85E

*Sertularia digitalis* Busk, 1852: 393.
*Nigellastrum digitale*: Marman, 1965a: 57, fig. 89.
*Diphasia digitalis*: Vervoort, 1968: 37, fig. 17. Millard & Bouillon, 1973: 67, fig. 9A. Millard & Bouillon, 1974: 31, fig. 6B.

Diagnosis. Stem stiff, unfascicled, branched or unbranched, reaching a maximum height of 44 mm; with transverse nodes visible in younger regions only, each internode bearing a pair of hydrothecae; a hinge-joint present near base below first pair of hydrothecae. Hydrocladia alternate, arising from posterolateral surface of stem usually after every two pairs of hydrothecae and forming almost a right angle with stem, the two rows in one plane. Hydrothecae in opposite pairs, consecutive pairs close, separated from one another by a distance of less than 1/6 height or overlapping. In lower region of stem members of a pair of hydrothecae placed on lateral surfaces, not contiguous with one another, and adnate to stem for about 1/6 height; in distal region and on hydrocladia members of a pair placed on anterior surface, contiguous with one another and adnate for up to entire length.

Hydrotheca tubular, widening gently to margin, smoothly curved outwards, usually polygonal in section with 3–5 angles which are visible in front view as longitudinal ridges, perisarc thickened on abcauline wall, 0.7–1.0 mm in abcauline height and 0.3 mm in marginal diameter. Margin untoothed, saddle-shaped.

Gonotheca (not reported from South Africa) borne on stem, elongate, covered with short, curved spines arranged in 10–16 longitudinal rows.

Variation. Regeneration of the hydrotheca is often indicated by the persistence of an old operculum below the new one, although the old margin seldom leaves a regeneration line.

The variation in the hydrothecae along the length of the stem is characteristic of the species and is indicated in the diagnosis.
Distribution outside South Africa. Circumglobal in tropical and subtropical waters. Type locality: Torres Straits.

Distribution in South Africa. Inhaca only. 26/32 (s)

*Diphasia heurleti* Billard, 1924

Fig. 85A–D

*Diphasia pinaster* Billard, 1907a: 357.
*Diphasia heurleti* Billard, 1924: 67, fig. 2.
*Diphasia heurleti* var. *simplex* Billard, 1933: 19, fig. 7.
*non Diphasia heurleti*: Nutting, 1927: 218, pl. 42 (figs 5–7).

**Diagnosis.** Stem fairly stiff, unfascicled, unbranched or, rarely, with one lateral branch, reaching a maximum height of 27 mm, with a basal atthecate part terminated by an oblique hinge-joint, the remainder bearing hydrothecae in strictly opposite pairs. Consecutive pairs of hydrothecae separated by slightly oblique nodes in some regions only, pairs close to one another and often overlapping. Members of a pair not in contact with one another.

Hydrotheca tubular, widening to margin, curved outwards, flattened on abcauline side in basal region and with the angles of this flat surface continued as two longitudinal ridges almost to margin, three other longitudinal ridges present but less distinct, one abcauline and two latero-adauline; adnate for \( \frac{1}{10} - \frac{2}{3} \) of adcauline side, 0.4–0.7 mm in abcauline height and 0.16–0.3 mm in marginal diameter. Acauline wall thickened and an abcauline intrathecal septum usually present, well developed and curved distally, the base forming a crescent-shaped figure when viewed externally. Margin untoothed, facing upwards and almost perpendicular to stem.

Female gonothecae borne in a single row on front of stem, arising immediately below hydrothecae on one side, saccular, with wide distal aperture, bearing irregularly arranged short, blunt spines on distal half, containing many small eggs. Male gonothecae unknown.

**Variation.** In the younger regions and sometimes in complete young stems the intrathecal septum may be absent as in var. *simplex* Billard, 1933. The abcauline wall of the hydrotheca is, however, thickened in this region.

In addition to the normal operculum many hydrothecae have one or two supplementary opercula hinged to the adcauline wall just below the level of the intrathecal septum.

**Remarks.** This is the first discovery of the gonothecae of *D. heurleti* in the type area. Gonothecae of material from the China Sea attributed to *D. heurleti* were described by Nutting (1927). These are completely different in structure, and I must therefore exclude Nutting’s material from the synonymy.

*D. heurleti* is very similar to *D. mutulata*, a species well illustrated by Billard (1933). The main differences are the shorter free part of the hydrotheca in the latter, and the structure of the gonotheca which in *D. mutulata* has a narrow distal aperture.
Fig. 85.

*Diphasia heurteli.* A, stems; B, part of stem (some hydrothecae with supplementary opercula); C, hydrotheca; D, gonotheca.

*Diphasia digitata.* E, unbranched stem.

*Diphasia tetraclocha.* F, stem; G, gonotheca; H, a pair of hydrothecae viewed from above to show asymmetry (operculum in position on right).

Scale: A in cm, the rest in mm/10.
Distribution outside South Africa. Moçambique (type locality), Gulf of Suez.

Distribution in South Africa. Natal to Moçambique, 2–100 m, rare. 29/31 (s), 28/32 (d), 24/35 (s)

*Diphasia tetravlochina* Billard, 1907

Fig. 85F–H

*Diphasia tetravlochina* Billard, 1907a: 358, fig. 7. Millard, 1964: 28, fig. 8. Millard & Bouillon, 1974: 31, fig. 6C.

*Diagnosis.* Hydrorhiza creeping on weed, with internal thickenings of perisarc. Stem short, reaching a maximum height of 7 mm, unfascedled, unbranched, divided by markedly oblique nodes into internodes each bearing a pair of opposite hydrothecae. Members of a pair separate in front, sometimes contiguous behind in distal region of stem.

Hydrotheca tubular, widening to margin, curved outwards, not bilaterally symmetrical but twisted towards anterior surface, adnate for \( \frac{1}{2} - \frac{2}{3} \) length, 0.3–0.5 mm in abcauline length and 0.15–0.3 mm in marginal diameter. Margin with four small, pointed teeth, one adcauline, two abcauline and one anterior.

Gonothecae borne on stem, one to each, below first pair of hydrothecae, elongate-oval, bearing small spines in distal half, reaching 0.8 mm in length and 0.5 mm in maximum diameter. Aperture terminal, small, circular, on a raised neck.

*Variation.* The distal region of the stem normally has longer internodes and larger hydrothecae than the proximal region. The perisarc is sometimes thickened in the centre of the abcauline thecal wall and occasionally around the margin.

*Distribution outside South Africa.* Madagascar only. Type locality: Fort Dauphin.

*Distribution in South Africa.* Two areas only: Agulhas Bank south of East London, and Inhaca district. 33/27, 25/32, 26/32 (s)

**Doubtful species**

*Diphasia attenuata* (Hincks, 1866)

*Sertularia rosacea:* Busk, 1851: 118.


*non Sertularia rosacea* Linnaeus, 1758: 807.

*Remarks.* Busk reported this species from Algoa Bay as *Sertularia rosacea* (see Millard 1961). It has not been reported since and the record must be regarded as doubtful.

*Diphasia bipinnata* Allman, 1886

*Diphasia bipinnata* Allman, 1886: 136, pl. 12 (figs 1–2).

*Remarks.* Allman was doubtful about the locality of the material on which this species was founded, giving it as ‘Cape of Good Hope?'. The species has never been recorded again, and from Allman's description and figures it might well be a synonym for the well-known *Diphasia fallax* (Johnston 1847).
Monograph on the Hydroidea of Southern Africa

Diphasia nigra (Pallas, 1766)

Sertularia nigra Pallas, 1766: 135. Busk, 1851: 118.
Sertularia pinnata Pallas, 1766: 136.

Remarks. For this species there is only Busk's record of 1851. Since it has not been reported from South Africa since, the record must be regarded as doubtful.

Genus Dynamena Lamouroux, 1812

Syn. Pasythea Lamouroux, 1812.
Pasya Stechow, 1922.

Diagnosis. Stem erect, branched or unbranched. Stem and branches bearing hydrothecae in two longitudinal rows. Hydrothecae in opposite or subopposite pairs, which are often concentrated in groups. Hydrotheca sessile, partly or completely adnate, with two marginal teeth seated more or less midway between adcauline and abcauline edge, and usually a small, median adcauline one. Operculum of two valves, a smaller adcauline one and a larger abcauline one, the former often divided into two by a median partition. Hydranth with no abcauline caecum.

Type species: Sertularia pumila Linnaeus, 1758.

Key to Species

(Doubtful species not included; for these see p. 268)

1. Hydrothecae on simple stems and on hydrocladia of branching stems in subopposite pairs. Members of a pair never contiguous
   - Hydrothecae on simple stems and on hydrocladia of branching stems always in strictly opposite pairs. Members of at least some pairs contiguous
     1. Hydrothecae on simple stems and on hydrocladia of branching stems never grouped, with only one pair to an internode
        D. cornicina
     2. Hydrothecae tubular and not narrowing to mouth. Hydrothecae on simple stems and on hydrocladia of branching stems never grouped, with only one pair to an internode
        D. obliqua
     3. Hydrotheca tubular but bulging at base of abcauline side, with greatest width half or less than half abcauline height
        D. quadridentata

Dynamena cornicina McCrady, 1858

Fig. 86A–E

Dynamena cornicina McCrady, 1858: 102. Billard, 1925a: 188, fig. 40, pl. 7 (fig. 23). Vervoort, 1941: 206, fig. 3. Millard, 1964: 29, fig. 9.

Diagnosis. Stem unfascicled, either simple or pinnately branched.

Branching stem reaching 60 mm, divided by straight nodes into regular internodes, each bearing one hydrocladium and three hydrothecae (one in axil and a subopposite or alternate pair above). Hydrocladia alternate, the two rows in one plane. Hydrocladium arising from short apophysis, with one basal thecate internode terminated by a hinge-joint, and a series of thecate internodes each bearing a pair of opposite hydrothecae. Members of a pair of
Fig. 86.

*Dynamena cornicina.* A, colony with simple and branched stems; B, margin of hydrotheca with operculum (abcauline valve in broken line); C and D, the upper two and the lower two pairs of hydrothecae of a simple stem bearing 12 pairs in all; E, gonotheca.

*Dictyocladium coactum.* F and G; hydrothecae, G with an internal tooth; H, part of colony with two stems and gonothecae.

Scale: A in cm, the rest in mm/10.
hydrocladial hydrothecae always contiguous in front, separate behind, placed on upper surface of hydrocladium.

Simple stem reaching a height of 9 mm. Basal athecate part terminated by oblique hinge-joint. Remainder with transverse or slightly oblique nodes. Each internode bearing one pair of opposite hydrothecae. Hydrothecae not grouped. Members of a pair of hydrothecae contiguous in front (except sometimes in proximal region of stem), separate behind.

Hydrotheca tubular and of more or less equal diameter throughout; adnate for over half acauline length, then curved outwards, 0.2-0.5 mm in acauline height and 0.13-0.20 mm in marginal diameter, acauline wall thickened below margin. Lateral marginal teeth large, delicate, triangular. Acauline marginal tooth small.

Gonotheca arising from hydorhiza or occasionally from base of stem, ovate, deeply annulated, with broad aperture and flat operculum, reaching 1.4 mm in length and 0.9 mm in maximum diameter.

Variation. In South African material the stem internodes (in simple stems) or hydrocladial internodes (in pinnate stems) are regular and short, with the interval between consecutive pairs of hydrothecae less than the hydrothecal length, but in other localities the internode length is reported as variable, and the interval between consecutive pairs of hydrothecae may exceed the hydrothecal length.

A change in shape of the hydrotheca takes place along the length of the simple stem and hydrocladium of pinnate stems, those at the base being shorter, less adnate and more markedly bent out than the distal ones. The axillary hydrothecae are less adnate and more sharply curved out than the rest.

Distribution. Cosmopolitan. Type locality: Charleston harbour.

Distribution in South Africa. Port Elizabeth to Inhaca, littoral to 14 m. 33/25 (s), 34/25 (s), 31/29 (l), 26/32 (l, s), 25/32, 21/35

Dynamena crisioides Lamouroux, 1824

Fig. 87A-F

Dynamena crisioides Lamouroux, 1824: 613, pl. 90 (figs 11-12). Billiard, 1925a (including all varieties): 181, figs 36-39, pl. 7 (figs 21-23), pl. 8 (fig. 24). Millard, 1968 (including var. gigantea): 183, fig. 6C. Mammen, 1965a: 51, figs 84-85. Vervoort, 1968: 38, fig. 18. Millard & Bouillon, 1974: 32, fig. 6D.

Thuitaria tubuliformis: Warren, 1908: 314, fig. 12.

Thuitaria interrupia: Gravely, 1927: 13, pl. 2 (figs 7, 12).

Diagnosis. Stem unfascicled, straight or zigzag, reaching a maximum height of 160 mm, bearing alternate hydrocladia; with a short basal athecate part terminated by a transverse node, then thecate internodes separated by transverse or slightly oblique nodes, each internode normally bearing one hydrocladium near base, one hydrotheca in the axil and a variable number of subopposite pairs of hydrothecae above. Hydrocladium borne on long apophysis, which may be
separated from the stem by a partial or complete node, divided by straight
nodes into internodes which bear a variable number of subopposite pairs of
hydrothecae. The two rows of hydrothecae in one plane; members of a pair not
contiguous with each other, though consecutive pairs on an internode may
overlap to form groups.

Hydrotheca tubular, adnate for half to over nine-tenths of adcauline length,
then bent outwards, 0.3–0.7 mm in adcauline height and 0.09–0.2 mm in mar-
ginal diameter. Margin facing outwards, parallel to axis or nearly so, with two
broad and triangular lateral marginal teeth and one smaller adcauline one.
Hydranth with about 19 tentacles.

Gonotheca arising from stem or branch below hydrotheca, occasionally
from within hydrotheca, smooth or irregularly folded, ovate, with curved distal
neck and operculum.

Variation. This is a very variable species, and a number of varieties and forms
are on record. It does not seem practicable to use subspecific rank for these,
since in many cases intermediate forms are known (Billard 1925a; Gravely
1927; Mammen 1965a). Several occur in South Africa.

The normal form typically has a short (about 20 mm), zigzag stem which
is narrow at the base (0.4 mm or less), so that members of a pair of hydro-
thecae are separated by a distance less than the diameter of one of them.

Forma gigantea Billard, 1925 has a taller (100–160 mm) stem, which
is straight except for the extremity and is much wider at the base (0.5–0.9 mm)
so that members of a pair of hydrothecae are separated by a distance at least
equal to, and usually considerably greater than, the diameter of one of
them.

Forma alternata Billard, 1925 shows no grouping of the hydrothecae on
the hydrocladium, but has only one subopposite pair to each internode. The
hydrotheca is smaller and less adnate than in the typical form (half to two-
thirds as against two-thirds or more) and the hydrocladial apophysis arises
below the third hydrotheca on each normal stem internode.

Billard (1925a) also distinguishes a var. peculiaris with internal teeth in some
hydrothecae, either one adcauline or one adcauline or both. In South Africa
internal teeth may occur in certain hydrothecae of any of the above forms,
thought never in the whole colony.

All the forms show variation in the number of hydrothecae to an inter-
node; the usual number on the stem is three, but there may be more or less;
on the hydrocladia the number varies from two to ten. The number of
hydrocladia to a stem internode may vary from nought to two.

Distribution outside South Africa. Cosmopolitan, mainly in tropical and
subtropical waters. Type locality: Moluccas.

Distribution in South Africa. East coast, from the Haven northwards, littoral.
32/28 (L), 31/29 (L), 31/30 (L), 30/30 (L), 29/31 (L), 26/32 (L), 25/32, 23/35 (L), 21/35
Fig. 87.

_Dynamena crisioides_. A, gonothecae; B, part of stem of normal form with origins of hydrocladia; C, hydrocladium of normal form; D, hydrocladium of forma _alternata_; E, hydrocladium of forma _gigantea_; F, stems of normal form (left) and forma _alternata_ (right).

_Dynamena quadridentata_. G, gonotheca; H, unusual stem with most of the hydrothecal pairs ungrouped; J, typical stem.

Scale: F in cm, the rest in mm/10.
Dynamena obliqua Lamouroux, 1816

Fig. 88F–G

Pasythea quadritentata var. Belet Billard, 1907a: 355, fig. 6.

Diagnosis. Hydrorhiza with or without internal perisarcal thickenings. Stem unfascicled, unbranched, reaching a maximum height of 17 mm. Normal nodes indistinct. Oblique hinge-joints present (a) terminating basal athecate part of stem, and (b) at irregular intervals in distal region, each forming the termination of a separate, narrow, athecate internode. Each thecate internode usually bearing only one pair of opposite hydrothecae, rarely a group of two pairs contiguous with each other. Members of a pair of hydrothecae contiguous in front (except in basal region of stem), separate behind.

Hydrothecae swollen but narrowing to mouth, bent outwards, adnate for over half adcauline length, 0.2–0.3 mm in adcauline height and 0.12–0.14 mm in marginal diameter, aperture directed obliquely forwards. Lateral marginal teeth broad, triangular, sharp or bluntly rounded. Adcauline marginal tooth distinct.

Gonotheca (not reported from South Africa) borne on front of stem near base, barrel-shaped, with four or more transverse annulations, with a broad distal aperture on a low neck and a flat operculum.

Variation. In this species there is less tendency towards grouping of thecal pairs than, for instance, in D. quadritentata, and many stems bear only one pair per internode throughout. In South Africa no more than two pairs have been observed on an internode, although as many as four have been observed elsewhere.

Internal teeth occasionally occur in some hydrothecae of a stem, and there may be one adcauline and one adcauline, or one adcauline and two latero-adcauline, or one adcauline and two latero-adcauline teeth.

Distribution outside South Africa. Australasia (type locality), Japan, Moçambique.

Distribution in South Africa. Natal and Inhaca, 10–66 mm. 30/30 (s), 29/31 (s), 26/32 (s)

Dynamena quadritentata (Ellis & Solander, 1786)

Fig. 87G–J

Sertularia quadritentata Ellis & Solander, 1786: 57, pl. 5 (fig. g, G).
Pasythea quadritentata: Warren, 1908: 312, fig. 11.
Dynamena gibbosa: Billard, 1925a: 199, fig. 45.

Diagnosis. Hydrorhiza creeping on weed, commonly with internal perisarcal thickenings. Stem unfascicled, unbranched, reaching a maximum height of
Fig. 88.

*Idiellana pristis*. A, stem; B, part of stem in anterior view with origins of hydrocladia; C and D, lateral and abcauline views of operculum; E, hydrothecae.

*Dynamera obliqua*. F, upper part of stem; G, complete stem.

Scale: A in cm, the rest in mm/10.
7 mm. Normal nodes transverse and often indistinct. Oblique hinge-joints present (a) terminating basal athecate part of stem, and (b) at irregular intervals in distal region, each forming the termination of a separate, narrow, athecate internode. Each thecate internode bearing one or a group of pairs of opposite hydrothecae; the pairs in a group up to four in number, contiguous with one another and showing a difference in shape, the proximal pair being more divergent and less adnate than the distal one. Members of a pair of hydrothecae contiguous in front, separate behind.

Hydrotheca tubular but narrowing to margin, bent outwards, adnate for over half adcauline length, 0.17–0.4 mm in adcauline height and 0.07–0.13 mm in marginal diameter, with or without internal teeth; members of solitary pairs and the basal pair of a group with a distinct outward bulge in base of adcauline wall. Lateral marginal teeth broad and triangular. Adcauline marginal tooth small but distinct.

Gonotheca borne on front of stem at base of first thecate internode, barrel-shaped, with 3–6 distinct transverse annulations, with broad distal aperture and flat operculum.

Variation. In this species there is a greater tendency towards grouping of hydrothecal pairs than in D. obliqua, and single pairs are rare and usually occur only in the proximal region of the stem. Hinge-joints are more common than in D. obliqua.

The presence of internal thecal teeth is a variable character and there may be one adcauline and one or two adcauline ones.

In the literature a number of varieties of this species has been described which tend to grade into one another. The South African material appears to be intermediate between var. nodosa Hargitt, 1908, and Dynamena gibbosa Billard, 1924, which is considered to merit varietal rank only. Both are distinguished by an outward bulge in the adcauline wall of the basal hydrotheca of a group, more distinct in v. gibbosa than in v. nodosa.

Distribution outside South Africa. Circumglobal in tropical and warm temperate waters. Type locality: west coast of Africa near Ascension Island.

Distribution in South Africa. Port St. Johns to Moçambique, littoral to 49 m. 31/29 (s), 30/30 (l), 29/31 (l, s), 27/32 (l), 26/32 (l, s), 25/32, 24/35 (s), 23/35 (l), 21/35.

Doubtful species

Dynamena pumila (Linnaeus, 1758)


Remarks. This species has been reported once only, by Krauss, from Mossel Bay. No diagrams are given and the identification is dubious.
Genus *Hydrallmania* Hincks, 1868

*Diagnosis*. Stem erect, giving off spirally arranged branches. Branches pinnate, bearing alternate hydrocladia. Hydrocladium in mature colony bearing hydrothecae in one longitudinal row, their distal ends directed alternately to left and right. Hydrotheca sessile, usually partly adnate, with two lateral and often ill-defined marginal teeth. Operculum of two delicate valves, a larger adcauline one and a smaller adcauline one which is not easily recognizable. Hydranth with adcauline blind caecum.

Type species: *Sertularia falcata* Linnaeus, 1758.

A doubtful record of one species only in South Africa.

**Doubtful species**

*Hydrallmania falcata* (Linnaeus 1758)

*Sertularia falcata* Linnaeus, 1758: 810
*Plumularia falcata*: Busk, 1851: 118

*Remarks*. This species occurs exclusively in the North Atlantic. Busk’s record from South Africa must be regarded as doubtful although his material was correctly identified (Millard 1961). It has never again been reported from this country.

Genus *Idiellana* Cotton & Godfrey, 1942

Syn. *Idiella* Stechow, 1919.

*Idia* Lamouroux, 1816.

*Diagnosis*. Upright colonies with pinnate stems bearing alternate hydrocladia. Stem and hydrocladia bearing a double series of alternate or subalternate hydrothecae on anterior surface. Hydrotheca sessile, with two poorly developed lateral lobes. Operculum of one adcauline valve. Hydranth with no adcauline caecum.

Type species: *Idia pristis* Lamouroux, 1816.

One species only from South Africa.

*Idiellana pristis* (Lamouroux, 1816)

Fig. 88A–E


*Idiellana pristis*: Ralph, 1961a: 766, fig. 5c–e.

*Diagnosis*. Stem unfascicled, reaching 60 mm in height, divided into regular internodes by oblique nodes which slope in alternate directions; each internode bearing one hydrocladal apophysis and three hydrothecae (one in axil and an alternate pair above); the two rows of hydrothecae not contiguous. Hydrocladium unsegmented or with a few sparse nodes at long intervals, bearing a double row of alternate, overlapping hydrothecae on the anterior face, the two rows contiguous with one another.
Hydrothecae tubular, adnate for over half length, then free and bent out at a wide angle, 0.4–0.6 mm in adcauline height, and 0.13–0.20 mm in marginal diameter. Margin with two broadly triangular lateral lobes; rotated to face distally and posteriorly. No internal teeth. Operculum not sharply demarcated from hydrotheca at adcauline edge, with a median ridge dividing it into two for part of its length.

Gonotheca (not reported from South Africa) borne on front of stem below hydrotheca, urn-shaped, longitudinally ridged, with short pedicel and circular distal aperture on a raised tubular collar.

Remarks and variation. The broad hydrocladia with their double row of projecting hydrothecae resemble the rostrum of the saw-fish, Pristis, after which the species was named. The overlapping of the hydrothecae gives the impression of a division of the hydrocladium into a double series of chambers. Rejuvenation of the margin of the hydrotheca is common, resulting in variation in length of the free part. Axillary hydrothecae on the stem are less bent outwards than the others. A longitudinal ridge is sometimes visible on the anterior surface of the hydrotheca.

The hydrotheca is commonly described as having a median adcauline marginal tooth, but there is no sign of this in the South African material. The operculum in fact is continuous with the adcauline edge as described by Ritchie (1910b) and there is no hinge. It opens by bending and in old hydrothecae tends to collapse into the cavity.

Distribution outside South Africa. Circumglobal in tropical seas, extending into temperate waters in certain areas. Type locality: New Holland (Australasia).

Distribution in South Africa. East coast: Natal and Moçambique, 0–44 m. 30/30 (s), 26/32 (l), 25/32 (s), 21/35

Genus Parascyphus Ritchie, 1911

Diagnosis. Stem erect, unbranched or little branched, bearing two rows of alternate hydrothecae. Hydrotheca pedicellate and free from stem, elongated, bilaterally symmetrical. Margin with three or four teeth. Operculum pyramid-shaped, of three or four valves. Diaphragm small or incomplete. Hydranth with adcauline caecum.

Type species: Laomedea simplex Lamouroux, 1816.

One species only from South Africa.

Parascyphus simplex (Lamouroux, 1816)

Fig. 89A–B

Laomedea simplex Lamouroux, 1816: 206.
Parascyphus simplex: Splettstösser, 1929: 100, 126, figs 92–94. Millard, 1968: 268, fig. 4D.

Diagnosis. Stem stiff, unfascicled. unbranched or sparsely branched, reaching
12 mm in height. The two rows of hydrothecae more or less in one plane. Stem and hydrocladia divided into internodes by slightly oblique nodes, each internode bearing a hydrotheca on an apophysis near the distal end.

Hydrothecal pedicel short, a little narrower than apophysis, not annulated, separated from apophysis by a partial or complete node. Hydrotheca small to medium, elongate, markedly convex on adcauline side, straight or with a double curvature on abcauline side, 0.5–0.6 mm in height from diaphragm and 0.19–0.2 mm in marginal diameter. Margin with three tall pointed teeth, one adcauline and two latero-abcauline, separated by deep bays. Operculum of three valves. Diaphragm present on adcauline side only.

Gonothecae (not recorded from South Africa) borne on lower part of stem, elongate-oval, smooth, with rounded distal end and small circular aperture (Bale 1915).

Variation. The rim of the hydrotheca may be thickened to a varying degree. Stolonization may occur.

Distribution outside South Africa. Australasia (type locality), Scotland, Gough Island, Vema Seamount (South Atlantic).

Distribution in South Africa. One record only, from the Natal coast in 91 m, 30/31 (s)

Genus Salacia Lamouroux, 1816

Syn. Dymelia Stechow, 1922.

Diagnosis. Stem erect, bearing hydrothecae in two longitudinal rows, with or without hydrocladia which may be opposite or alternate. When present, hydrocladia different in structure to stem, with internodes of irregular length. Hydrotheca sessile, partly or completely adnate, without distinct marginal teeth. Aperture triangular. Operculum of one large, abcauline valve. Hydranth without abcauline caecum.

Type species: Salacia tetracythara Lamouroux, 1816.

Remarks. The conclusions of Billard (1925a: 137) on the validity and nature of this genus have been adopted.

KEY TO SPECIES

1. Stem without hydrocladia, bearing opposite pairs of hydrothecae, one pair to an internode
   - Stem bearing opposite hydrocladia. Hydrothecae in groups, more than one pair to an internode on stem and hydrocladia
     2
   - Hydrotheca in groups, one pair to an internode on stem
     S. desmoides

2. Hydrocladia arising at right angles to stem. Groups of hydrothecae separated by a distance greater than the height of one hydrotheca
   - Hydrocladia arising at an angle of 50–60° to stem. Groups of hydrocladial hydrothecae separated by a distance less than the height of one hydrotheca
     S. articulata

S. disjuncta
Fig. 89.

*Parascyphus simplex*. A, part of stem; B, hydrotheca and hydranth.
*Salacia articulata*. C, fertile stem; D, part of stem with origins of hydrocladia; E, gonotheca; F, hydrothecae.

Scale: C in cm, the rest in mm/10.
Salacia articulata (Pallas, 1766)

Fig. 89C–F

Sertularia articulata Pallas, 1766: 137.
Thuiaria elliisii Busk, 1851: 119.
Thuiaria persocula Allman, 1876: 271, pl. 17 (figs 4–6).
Thuiaria pectinata Allman, 1888: 69, pl. 33 (figs 1–1a).
Thuiaria articulata: Ritchie, 1909: 84, fig. 6. Broch, 1914: 36, pl. 1 (fig. 3).
non Thuiaria articulata: Hincks, 1868: 277, pl. 60.
non Dymella articulata: Vervoort, 1946a: 264, fig. 116.

Diagnosis. Stem moderately stiff, unfascicled, unbranched, bearing opposite hydrocladia, reaching a maximum height of 220 mm but more commonly 40–80 mm, divided by straight nodes into fairly regular internodes which normally bear three pairs of opposite hydrothecae and one pair of hydrocladia arising between the first and second pairs of hydrothecae. Hydrocladia forming a wide angle with the stem (50–60°), the two rows in one plane. The two rows of hydrothecae seated on the sides of the stem, and well separated from one another.

Hydrocladium narrower than stem, with distinct nodes at irregular intervals, each internode bearing a variable number of subopposite to opposite pairs of hydrothecae. The two rows of hydrothecae seated on the sides of the hydrocladium and not contiguous with one another.

Hydrotheca tubular, curved outwards, adnate for all or almost all adcauline length, narrowing slightly to margin, 0.2–0.4 mm in adcauline height and 0.11–0.18 mm in marginal diameter. Margin untoothed, thickened on adcauline edge. No internal teeth.

Gonotheca borne on stem or hydrocladia, ovoid, smooth or transversely annulated, truncated distally, with a broad terminal aperture on a low collar, reaching 3 mm in height and 1.5 mm in maximum diameter.

Variation. Irregularities occasionally occur in the arrangement of the stem internodes, which may bear but one pair of hydrothecae and no hydrocladia, or two pairs of hydrothecae and one pair of hydrocladia. In the basal region of the stem below the first hydrocladium there is a variable number of hydrothecae to an internode. The interval between successive pairs of hydrothecae also varies and the pairs tend to be more closely placed on the hydrocladia, where they may overlap one another, than on the stem, where there is usually a short interval separating two pairs. Members of a pair of hydrothecae are opposite on the stem, but subopposite in the proximal regions of the hydrocladia, gradually changing to opposite more distally. Stolonization from the ends of hydrocladia is common. Rarely branching hydrocladia occur.

Remarks. There has been much confusion in the literature between this species and S. lonchitis (Ellis & Solander, 1786). The latter has a northern habitat and can be distinguished by its alternate hydrocladia.
Distribution outside South Africa. Vema Seamount (South Atlantic), tropical South West Africa. Type locality: Atlantic Ocean.

Distribution in South Africa. All round the coast, particularly common in the south-west area; littoral to 135 m. [19/12(l)], 26/15 (s), 27/15 (s), 32/18 (s), 33/17 (s), 33/18 (l), 34/18 (l, s), 34/21 (s), 35/21 (d), 34/22 (s), 34/23 (s), 34/24 (d), 33/25, 34/25 (s), 33/26 (s), 33/27 (l, s), 32/28 (s), 33/28 (s), 30/30 (s), 30/31 (s), 29/31 (s), 28/32 (s), 26/33 (d), 24/35 (d)

Salacia desmoides (Torrey, 1902)

Fig. 90A–C

Sertularia desmoidis Torrey, 1902: 65, pl. 8 (figs 70–72).
Sertularia desmoides: Nutting, 1904: 56, pl. 3 (figs 1–3).

Diagnosis. Stem unfascicled, usually unbranched, slender, reaching a maximum height of 4 mm and bearing up to seven pairs of well-spaced opposite hydrothecae. Nodes very oblique and resembling hinge-joints; usually one below each pair of hydrothecae. Members of a pair of hydrothecae contiguous in front, separate behind.

Hydrotheca adnate for over half length, then curved outwards, 0,14–0,3 mm in abcauline height and 0,11–0,15 mm in marginal diameter. Margin unoothed, thickened on abcauline edge. No internal teeth.

Gonothecae borne on front of stem below hydrothecal pairs, barrel-shaped, with shallow transverse annulations and broad distal aperture containing a ring of internal spiny processes, male and female on separate stems. Male reaching 1,2 mm in length and 0,8 mm in maximum diameter. Female reaching 1,5 mm in length and 1,1 mm in maximum diameter, with external marsupium.

Variation. Although the type material of this species was said to branch ‘sparely and irregularly’, the South African material only rarely produces a single short lateral branch. The spacing of the hydrothecal pairs is always regular, though occasionally one of the oblique nodes may be missing.

Distribution outside South Africa. California (type locality) and neighbouring areas of the eastern Pacific, Walter’s Shoal in southern Indian Ocean.

Distribution in South Africa. Transkei coast, littoral, on coralline algae. 31/29 (l), 31/30 (l)

Salacia disjuncta Millard, 1964

Fig. 90D–F

Salacia disjuncta Millard, 1964: 31, fig. 10A–F.

Diagnosis. Stem moderately stiff, unfascicled, bearing opposite hydrocladia, reaching a maximum height of 36 mm, divided by straight nodes into fairly
Fig. 90.

*Salacia desmoides*. A, stem with male gonophores; B, stem with female gonophore; C, hydrothecae with hydranths and opercula.

*Salacia disjuncta*. D, stem; E, part of stem with origins of hydrocladia; F, hydrothecae.

Scale: D in mm, the rest in mm/10.
regular internodes, each of which bears three pairs of opposite or subopposite hydrothecae and one pair of hydrocladia arising between the first and second pairs of hydrothecae. Hydrocladia forming a right angle with stem, the two rows in one plane. The two rows of hydrothecae seated on the sides of the stem and well separated from one another.

Hydrocladium much narrower than stem, with very distinct, constricted nodes at irregular intervals, each internode with a long slender proximal part without hydrothecae and a wider distal part bearing a closely compressed group of 2–3 pairs of opposite or subopposite hydrothecae. The two rows of hydrothecae seated on the sides of the hydrocladia and not contiguous with one another in the centre.

Hydrotheca tubular, curved outwards, adnate for \( \frac{1}{4} \text{ to } \frac{3}{4} \) length, narrowing slightly to margin, 0.3–0.4 mm in abcauline height and 0.10–0.14 mm in marginal diameter. Margin untoothed, transversely widened, thickened on abcauline edge. No internal teeth.

Gonothecae unknown.

Variation. Stem internodes occasionally bear only one pair of hydrothecae; those at the base of the stem are irregular in length and bear no hydrocladia.

Distribution. Endemic to South Africa. Type locality: Agulhas Bank, 32°15.2'S/28°57.7'E, 50 m.

Distribution in South Africa. False Bay and Agulhas Bank, 29–84 m. 34/18 (s), 32/28 (s), 33/28 (s)

Genus Sertularia Gray, 1847

Syn. Thecocladia Allman, 1886.

Diagnosis. Stem erect, branched or unbranched. Stem and hydrocladia bearing alternate hydrothecae which form two longitudinal rows. Hydrotheca sessile, with four marginal teeth and an operculum of four triangular valves seated in the bays between the teeth and meeting in the centre as a pyramid. Hydranth with abcauline caecum.

Type species: Sertularia polyzonias Linnaeus, 1758.

KEY TO SPECIES

(Doubtful species not included: for these see p. 305; for types of hydrothecal shape see p. 241)

1. More than one hydrotheca to an internode
   - Only one hydrotheca to an internode (though nodes may be indistinct in older stems) 3

2. Cauline hydrothecae regularly spaced, three to an internode. Hydrocladal hydrothecae grouped, with a variable number to an internode. Hydrocladia arising below cauline hydrothecae
   - Stem and hydrocladia similar, with grouped hydrothecae, a variable number to an internode. Hydrocladia arising from within cauline hydrothecae S. diaphana
   - Stem and hydrocladia similar, with grouped hydrothecae, a variable number to an internode. Hydrocladia arising from within cauline hydrothecae S. flabellum 4

3. Internal teeth present within hydrothecal margin
   - No internal teeth 13
4. Three internal teeth, one of them median acauline or acauline (sometimes two small additional ones too)... 5
   - Four internal teeth, which always alternate with marginal teeth (one or more occasionally missing)... 11
5. Hydrotheca very large (over 0.7 mm in acauline height)... 6
   - Hydrotheca small to medium (under 0.8 mm in acauline height). Internal teeth always one acauline, two latero-adauline... 7
6. Hydrotheca adnate for over half height. Internal teeth one acauline, two latero-adauline...  S. goliathus
   - Hydrotheca adnate for under half height. Internal teeth one acauline, two latero-adauline...  S. leiocarpa
7. Mature stem fascicled and usually strongly branched. Branching typically pinnate and in one plane... 8
   - Mature stem unfasicled, short, unbranched or at most with 1–5 irregular branches... 10
8. Hydrotheca not annulated, axis distinctly bent outwards and margin tilted away from stem... 9
   - Hydrotheca with distinct transverse annulations...  S. orbicula
9. Hydrotheca small (under 0.5 mm in acauline height), markedly narrowing to mouth (which is under 0.2 mm in diameter); margin perpendicular to axis or tilted away from stem...  S. gilchristi
   - Hydrotheca of medium size (0.5–0.7 mm in acauline height), not markedly narrowing to mouth (which is over 0.2 mm in diameter); margin perpendicular to axis or tilted towards stem...  S. aguillensis
10. Hydrotheca annulated on acauline wall. Acauline margin not produced and margin tilted away from stem...  S. natalensis
    - Hydrotheca not annulated. Acauline margin generally produced and margin either tilted towards stem or perpendicular to axis...  S. mediterranea
11. Mature stem fascicled, branching pinnately and in one plane. Hydrotheca distinctly annulated on acauline surface...  S. pulchra
    - Mature stem unfaicled, unbranched or branching irregularly. Hydrotheca not, or only faintly, annulated...  S. pulchra
12. Stem short, unbranched, or at most with one or two branches. Hydrotheca with margin perpendicular to axis and with convex or straight acauline wall...  S. fasiformis
    - Stem long, flexuous and straggling, with irregular branches. Hydrotheca with margin tilted away from stem and with concave acauline wall...  S. polyzonias
13. Hydrotheca with distinct ridged annulations continued all the way round wall... 14
    - Hydrothecal wall smooth, or with weak annulations on acauline surface only... 16
14. Hydrotheca usually with six or seven annulations spread evenly over entire length, never less than four; acauline marginal tooth produced and longer than others...  S. striata
    - Hydrotheca with not more than three annulations restricted to free part; marginal teeth of equal size... 15
15. Stem long and tangle, branching irregularly. Hydrotheca adnate to stem for half or more of height...  S. capensis
    - Stem short and unbranched, bearing at most eight hydrothecae and often only one Hydrotheca adnate to stem for less than half height...  S. annulaventricosa
16. Hydrocladial hydrothecae overlapping, the tip of one reaching about half-way up the next. Free part of acauline wall of hydrotheca almost touching internode, with an open angle of less than 20°...  S. congregata
    - Hydrothecae not overlapping, the tip of one seldom reaching above base of next. Free part of acauline wall of hydrotheca standing well away from internode, with an open angle of over 40°... 17
17. Stem flexuous and straggling (unable to support itself out of fluid)...  S. polyzonias
    - Stem stiff (able to support itself out of fluid)... 18
18. Stem strongly fascicled and branching in one plane; final branches pinnate, giving off regularly alternate hydrocladia...  S. dubia
Sertularella africana Stechow, 1919

Fig. 91A–C

Sertularella fusiformis: Warren, 1908: 295, fig. 5C–D.

Diagnosis. Stem stiff, short, unfasciolated, unbranched or at most with a few short branches, reaching 18 mm in height; divided into internodes by oblique nodes sloping in alternate directions, each internode bearing one hydrotheca; usually with an annulation above each node.

Hydrotheca small, adnate for about half adcauline length, with weak transverse annulations on free part of adcauline wall, with adcauline margin and tooth produced so that margin is tilted towards adcauline side, adcauline wall more or less straight, adcauline wall convex, 0.4–0.6 mm in adcauline height and 0.18–0.3 mm in diameter. No internal teeth.

Gonothecae borne on front of stem immediately below the hydrothecae, ovate, annulated, male with three distinct marginal spines and narrow aperture, female with less distinct spines, wider aperture and external marsupium.

Variation. Although most hydrothecae conform to the characteristic shape, those near the base of the stem are often nearly symmetrical in side view, with the margin perpendicular to the axis, thus approaching the shape of S. fusiformis. Sometimes a few hydrothecae of a colony have the adcauline wall of the hydrotheca slightly bent out, which also causes the margin to be perpendicular to the axis. The adcauline annulations are variable and may extend all round the wall, or be absent altogether in certain (generally older) hydrothecae.

The gonothecae vary in the extent and number of the annulations, and may rarely have only two, or as many as four, marginal spines.

Distribution. Endemic to South Africa. Type locality: Park Rynie, Natal.

Distribution in South Africa. Lambert's Bay to Natal, littoral to 27 m. One of the few hydroids which is fairly common in the littoral region. 32/18 (s), 33/17 (l), 33/18 (l), 34/18 (l, s), 34/21 (l), 33/25 (l, s, on turtle), 33/27 (l), 32/28 (l), 30/30 (l)
*Sertularella agulhensis* Millard, 1964

**Fig. 91D–E**

*Sertularella agulhensis* Millard, 1964: 35, fig. 12A.

**Diagnosis.** Stem stiff, fascicled, branched or unbranched, giving off alternate or subalternate hydrocladia in one plane, reaching 82 mm in height. Hydrocladia arising from immediately below hydrothecae. Stem and hydrocladia divided into internodes by oblique nodes sloping in alternate directions, but nodes often indistinct in older parts; each internode bearing one hydrotheca.

Hydrotheca of medium size, adnate for about half adcauline length, annulated, with about six transverse annulations continued all round wall, adcauline wall more or less straight, with margin more or less perpendicular to axis and not particularly narrowed, 0.5–0.7 mm in adcauline height and 0.2–0.3 mm in marginal diameter. Three small internal teeth, one adcauline and two latero-adcauline.

Gonotheca unknown.

**Variation.** The hydrocladia are usually alternate, arising below every third hydrotheca, but sometimes subalternate, arising below every first and third hydrotheca. Other variations may also occur.

The adcauline side of the thecal margin is sometimes more produced than the rest, with the result that the margin may be tilted slightly towards the adcauline side. There may or may not be a slight concavity in the adcauline wall. The internal teeth are constant in number and position, but may vary in size, e.g. the latero-adcauline teeth may be smaller than the adcauline and vice versa.

**Distribution.** Endemic to South Africa. Type locality: Agulhas Bank, 34°51'S/19°55'E, 22 m.

**Distribution in South Africa.** False Bay and Agulhas Bank south of Cape Agulhas, 22–42 m, rare. 34/18 (s), 34/19 (s)

*Sertularella annulaventricosa* Mulder & Trebilcock, 1915

**Fig. 91F–H**

*Sertularella tenella*: Hartlaub, 1901a: 64 (pp., material from Algoa Bay), pl. 5 (fig. 24).
*Sertularella annulaventricosa* Mulder & Trebilcock, 1915: 54, pl. 7 (fig. 1), pl. 8 (figs 4–4a).
Watson, 1973: 172, fig. 23.
*Sertularella undulata* Bale, 1915: 285, pl. 46 (fig. 1).
*Sertularella capensis delicata* Millard, 1964: 38, fig. 12B–D.

**Diagnosis.** Stem unfascicled, unbranched, short and slender, geniculate, reaching 5 mm in maximum height; divided into internodes by oblique nodes sloping in alternate directions, each internode bearing one hydrotheca; with not more than eight hydrothecae and often only one; generally annulated at base and in region of nodes.

Hydrotheca small, adnate for under half adcauline height, with one, or
Sertularella africana. A, hydrothecae; B, stem; C, male gonotheca.
Sertularella agulhensis. D, hydrothecae; E, stem.
Sertularella annulaventricosa; F, solitary hydrotheca and upright stem; G and H, solitary hydrothecae.
Sertularella arbuscula. J, stem; K, hydrothecae; L, gonotheca.

Scale: B, E and J in cm, the rest in mm/10.
occasionally two, sharply ridged annulations continued all the way round free part, barrel-shaped with margin perpendicular to axis, 0.3–0.5 mm in abcauline height and 0.3 mm in marginal diameter. No internal teeth. Mouth wide, its diameter only slightly less than the widest part of the hydrotheca, round in section.

Gonotheca unknown.

Variation and remarks. The stem is always delicate, but varies in the length of internode and amount of annulation. Stems with only one hydrotheca are common; these can be distinguished from the genus Calamphora by the extension of the growing point of the internode behind the hydrotheca.

This material was originally described as a subspecies of S. capensis, to which the hydrotheca shows a similarity. However, the growth-form is different and Mrs J. Watson was kind enough to draw my attention to the resemblance to S. annulaventricosa, with which it has now been synonymized.

Distribution outside South Africa. South Australia and Tasmania. Type locality: Queenscliff, Australia.

Distribution in South Africa. Port Elizabeth to Durban in 47–53 m. 33/25, 32/28 (s), 31/29 (s), 29/31 (s)

Sertularella arbuscula (Lamouroux, 1816)

Fig. 91J–L

Sertularia arbuscula Lamouroux, 1816: 191, pl. 5 (fig. 4).
Sertularella crassipes Allman, 1886: 133, pl. 8 (figs 4–5).

Diagnosis. Stem stiff, fascicled, branching irregularly near base but pinnately and in one plane near extremities, reaching 300 mm in height. Hydrocladia arising from immediately below hydrothecae, the two rows in one plane. Stem and hydrocladia divided into short internodes by oblique nodes sloping in alternate directions, each internode bearing one hydrotheca.

Hydrotheca small to medium, adnate for about half abcauline length, smooth, with axis distinctly bent outwards and margin tilted towards abcauline side, 0.4–0.6 mm in abcauline height and 0.15–0.3 mm in marginal diameter. Three internal teeth, one abcauline and two latero-abcauline.

Gonothecae borne on stem and hydrocladia immediately below the hydrothecae, spindle-shaped, quite smooth or (occasionally) annulated in distal half; margin with a variable number of short spines.

Variation. Once known this common species is easily recognized in spite of much variability. Occasionally the ‘outward bend’ in the hydrotheca is not so marked as usual and occasionally the abcauline side of the margin is slightly produced. Neither variation is sufficiently marked to prevent the perpendicular passing through the abcauline wall, and both are usually limited to a few hydrothecae of a colony. The width of the thecal mouth is variable and a form with
an extra narrow mouth often occurs, a variation usually common to all hydrothecae of a colony. The internode length and amount of adcauline thecal wall which is *adnate* to the internode are likewise variable. The internal thecal teeth are constant in position, though occasionally they may be missing in a few hydrothecae of a colony with thin perisarc or in very old hydrothecae. Two small accessory internal teeth, one on each side of the adcauline one, commonly occur, and the adcauline wall may be thickened below the level of the adcauline tooth.

The smooth gonotheca is most characteristic, but occasional examples occur with corrugated or annulated walls, both in the male and in the female. The width of the mouth and the number of marginal spines are variable. Some gonothecae bear an external marsupium.

*Distribution outside South Africa.* Australasia, southern and western Indian Ocean, Vema Seamount. Type locality: Australasia.

*Distribution in South Africa.* Very common round most of the coast from Saldanha Bay to Moçambique, littoral to 219 m. 33/17 (s), 33/18 (l, s), 34/18 (s), 34/20 (s), 35/20 (d), 34/21 (s), 35/21 (d), 34/22 (s), 35/22 (d), 34/23 (s, d), 34/24 (d), 33/25 (s), 34/25 (s), 33/26 (s), 34/26 (d), 33/27 (s), 33/28 (s), 32/28 (s), 32/29 (d), 31/29 (s), 31/30 (s), 30/30 (s), 30/31 (s, d), 29/31 (s, d), 29/32 (s), 28/32 (s, d), 26/32 (s), 24/35 (s, d)

*Fig. 92H–K*

*Sertularella capensis* Millard, 1957

*Sertularella capensis* Millard, 1957: 210, fig. 10H.

*Sertularella capensis capensis*: Millard, 1964: 38, fig. 12F.

*Diagnosis.* Hydrorhiza profuse and tangled, not firmly attached to substratum. Stem unfasciied, flexuous and straggling, branching irregularly, with a tendency towards stolonization resulting in a tangled mass reaching 40 mm in height; divided into internodes by oblique nodes sloping in opposite directions, each internode bearing one hydrotheca. Branches arising from below hydrothecae, similar to stem.

Hydrotheca small, *adnate* for half adcauline height or a little more, with 1–3 (usually 2) sharply ridged annulations continued all the way round free part, fusiform, with margin generally perpendicular to axis, but sometimes tilted slightly towards adcauline side, 0.4–0.5 mm in adcauline height and 0.2–0.3 mm in marginal diameter. No internal teeth. Mouth wide, its diameter only slightly less than the widest part of the hydrotheca.

Gonothecae borne on front of stem immediately below hydrothecae, elongate-oval, annulated throughout, with up to 16 narrow, ridged annulations. Margin with four or more spines. No external marsupium.

*Variation and remarks.* The appearance of the stem is variable and subject to abnormalities resulting from stolonization. It may be straight or geniculate, and there may be a suggestion of an annulation immediately above and below
each node. The gonotheca may have as many as seven marginal spines.

The hydrotheca is similar to that of *Sertularia annulata* Allman, 1888 (=*Sertularella gayi* var. *annulata*), but the growth-form is different, the latter species having a stiff and fascieled stem. It also shows resemblances to *S. tenella* (Alder, 1856), but differs in the wider mouth, smaller number of annulations and larger proportion of wall adnate. It might possibly be included as a variety of *S. polyzonias*, but lacks the concave abcauline wall of the latter.

*Distribution.* Endemic to South Africa. Type locality: False Bay, 27–28 m.

*Distribution in South Africa.* False Bay, and Agulhas Bank in the East London area, 27–58 m. 34/18 (s), 33/27, 33/28 (s), 32/28 (s)

*Sertularella congregata* Millard, 1964

Fig. 92D–G

*Sertularella congregata* Millard, 1964: 39, fig. 13A–D.

*Diagnosis.* Stem stiff, fascieled, branched or unbranched, giving off alternate hydrocladia in one plane, reaching 70 mm in height. Hydrocladia arising from immediately below every third hydrotheca of stem, alternately on right and left. Stem and hydrocladia typically divided into short internodes by oblique nodes sloping in alternate directions, each internode bearing one hydrotheca, but hydrothecae crowded and overlapping in distal parts of hydrocladia where also nodes are not visible.

Hydrotheca small, adnate for half or more abcauline length, smooth, axis straight in basal half and curved outwards in distal half, margin tilted towards abcauline side, walls practically parallel, 0.4–0.5 mm in abcauline height and 0.19–0.2 mm in marginal diameter. No internal teeth. A perisarcal thickening present on abcauline wall and continued half-way round wall as a ridge below margin.

Gonotheca borne on anterior surface of hydrocladium next to the base of a hydrotheca, spindle-shaped, with about eight low annulations in distal region; margin with five short spines.

*Variation.* The stem may be simple and pinnate, or spreading and fan-shaped in which case one or more hydrocladia are replaced by long, fascieled and pinnate branches.

The interval between successive hydrothecae is variable. The latter are moderately well spaced on the stem, with the margin of one just overreaching the base of the next on the opposite side, but very close-set towards the distal parts of the hydrocladia, with the margin of one sometimes reaching the base of the next on the same side. Nodes may be completely invisible (in fascieled parts of stem and crowded regions of hydrocladia) or quite distinct. The shape and structure of the hydrotheca is very constant in the specimens known, though it is possible that the thickening on the abcauline thecal wall may, as in many other species, be a variable feature.
Fig. 92.

*Sertularella flabellum.* A, hydrothecae; B, gonotheca; C, colony.

*Sertularella congregata.* D, part of stem and hydrocladium; E, gonotheca; F, stem; G, hydrothecae.

*Sertularella capensis.* H, hydrothecae; J, gonotheca; K, colony.

Scale: C, F and K in cm, the rest in mm/10.
Distribution. Endemic to South Africa. Type locality: Agulhas Bank, 33°7.3'S/28°1'E, 88 m.

Distribution in South Africa. Two records only from the same area on the Agulhas Bank, 86–88 m. 33/28 (s)

Sertularella diaphana (Allman, 1886)

Fig. 93A–D

Thuiaria diaphana Allman, 1886: 145, pl. 18 (figs 1–3).
Sertularella diaphana: Billard, 1925a: 157, fig. 22, pl. 7 (figs 12–13). Millard, 1958: 188, fig. 7C–D.

Diagnosis. Stem thick and fascicled, branching profusely and irregularly, reaching 150 mm in height. Final branches pinnate, giving rise to alternate hydrocladia which are more or less in one plane. Stem and branches divided into internodes by oblique nodes sloping alternately to left and right; each internode bearing three hydrothecae and one hydrocladium, the latter arising just below the third hydrotheca. Hydrocladium with distant oblique nodes and a variable number of hydrothecae at an internode. The two rows of hydrothecae on stem, branches and hydrocladia not in one plane but shifted onto the anterior surface.

Hydrotheca completely adnate or very nearly so, smooth, curved outwards, with margin tilted towards abcauline side, 0.4–0.6 mm in abcauline height and 0.2 mm in marginal diameter. Marginal teeth low. No internal teeth.

Gonothecae borne on the anterior surface of the hydrocladia, elongated, tapering proximally, truncated distally, with faint longitudinal striations. No external marsupium. No marginal spines.

Variation. Billard (1925a) distinguished several varieties of this species from the Dutch East Indies, but all South African material belongs to the normal variety.

The perisarc is thin in the younger parts of the colony but heavier in older parts, where the abcauline thecal wall is thickened just below the margin.

Distribution outside South Africa. Circumglobal in tropical and subtropical waters. Type locality: Moreton Bay, Queensland, Australia.

Distribution in South Africa. Coasts of Natal and Moçambique from Durban northwards, 12–64 m. 30/30 (s), 29/31 (s), 26/32 (s), 25/33 (s)

Sertularella dubia Billard, 1907

Sertularella dubia Billard, 1907a: 344, fig. 3, pl. 25 (fig. 1).

Diagnosis. Stem stiff, fascicled, branched, giving off alternate hydrocladia in one plane. Hydrocladia arising from immediately below every third hydrotheca, alternately on right and left. Stem and hydrocladia divided into internodes by poorly marked oblique nodes sloping in alternate directions, each internode bearing one hydrotheca.
**Sertularella diaphana.** A, stem; B, gonotheca; C, part of stem with origins of hydrocladia; D, hydrothecae.

**Sertularella fusiformis.** E, fertile colony; F, male gonotheca; G, hydrothecae (form with crowded hydrothecae).

Scale: A and E in cm, the rest in mm/10.

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Fig. 93.
Hydrotheca small to medium, adnate for about half adcauline height, usually smooth, adcauline wall curved or bent outwards, adcauline wall straight or slightly concave; margin usually tilted towards adcauline side, narrowed. No internal teeth. A perisarcal thickening present on adcauline wall at about two thirds height.

*Distribution.* Macalonga, Moçambique, 22 m (type locality).

Only the following subspecies present in South Africa.

*Sertularella dubia magna* Millard, 1958

*Fig. 94A–F*

*Sertularella dubia var. magna* Millard, 1958: 189, fig. 7A.
*Sertularella dubia magna:* Millard, 1964: 41, fig. 14A–F.

*Diagnosis.* Similar to nominal subspecies but of larger dimensions, hydrotheca over 0.45 mm in adcauline height (0.5–0.7 mm) and over 0.20 mm in marginal diameter (0.2–0.3 mm). Stem reaching 135 mm in height.

Gonotheca (not known in the nominal subspecies) borne on hydrocladium immediately below hydrotheca, spindle-shaped, annulated in distal region; margin with a variable number of short spines.

*Variation.* The internode length varies, so that the hydrotheca may be well spaced or set fairly close together. Nodes are visible only in the young parts of the colony.

The hydrotheca are very variable in shape and appearance. They may have light corrugations on the free part of the adcauline wall and thus resemble those of *S. gayi*, or the adcauline marginal tooth may be elongated, with the result that the margin may be tilted towards the adcauline side. All intermediate forms may occur. More heavily chitinized hydrotheca have a very distinct adcauline perisarcal thickening, but this is scarcely noticeable in lightly built colonies and young hydrotheca.

*Remarks.* The general appearance and growth-form are similar to those of *S. arbuscula* and *S. gayi*. From the former it is distinguished by the absence of internal teeth, and from the latter by the nature of the gonotheca (bilabiate in *S. gayi*).

Some specimens show resemblances to *S. crassicaulis*, but can be distinguished from it by the method of growth (dichotomous in *S. crassicaulis*).

*Distribution.* Endemic to South Africa. Type locality: off Cone Point, Natal, 62 m.

*Distribution in South Africa.* False Bay to northern Natal on the east, 27–232 m. 34/18 (s), 34/21 (s), 33/25 (s), 34/25 (d), 33/27 (s), 33/28 (s), 32/28 (s), 30/30 (s), 30/31 (s), 29/31 (s, d), 29/32 (s), 28/32 (s, d)
Sertularella dubia magna. A–D, hydrothecae; E, gonotheca; F, stem.
Sertularella gilchristi. G, stem; H, gonotheca; J, hydrothecae.
Scale: F and G in cm, the rest in mm/10.

Fig. 94.
**Sertularella flabellum** (Allman, 1886)

Fig. 92A–C


**Diagnosis.** Hydrorhiza attached at intervals only. Stem unfascicled, unbranched or branching irregularly, with branches always arising from within hydrothecae, reaching 99 mm in height. Stem and branches similar, in one plane, with distant nodes and a variable number of hydrothecae to each internode. The two rows of hydrothecae in one plane.

Hydrotheca adnate for two-thirds of abcauline height or more, smooth, curved outwards, with margin tilted towards abcauline side, 0.4–0.5 mm in abcauline height and 0.2–0.4 mm in marginal diameter. Marginal teeth low. No internal teeth.

Gonothecae borne on stem immediately below hydrothecae, pear-shaped, strongly annulated. No external marsupium. No marginal spines.

**Variation.** This species is easily recognized by its characteristic growth-form. Both stems and branches have a strong tendency towards stolon formation. The hydrothecae may be closely set, so that the margin of one almost overlaps the base of the next on the same side, or may be much more distant, when two hydrothecae on the same side are separated by a distance equal to their own length.

The hydrotheca normally has a thin perisarc, but may be thickened at the margin and at the point where the abcauline caecum attaches. There is a marked tendency towards regenerated margins.

The gonotheca is annulated to a varying degree. The annulations normally extend from the distal end downwards for about two-thirds of the length, but may reach almost to the base.

**Distribution.** Endemic to South Africa and the Vema Seamount. Type locality unknown.

**Distribution in South Africa.** Common from Saldanha Bay on the west round the south coast to Richard’s Bay on the east, 10–232 m. 33/17 (s), 33/18 (s), 34/18 (s), 34/19 (s), 34/20 (s), 34/21 (s), 35/21 (d), 34/22 (s), 35/22 (d), 34/23 (d), 33/25 (s), 34/25 (s, d), 33/26 (s, d), 33/27 (s), 32/28 (s), 30/30 (s), 30/31 (s), 29/31 (d)

*Sertularella fusiformis* (Hincks, 1861)

Fig. 93E–G

*Sertularia fusiformis* Hincks, 1861: 253, pl. 6 (figs 7–8).
*Sertularella lineata*: Stechow, 1925a: 469, fig. 29.
*Sertularella fusiformis* forma *glabra* Broch, 1933: 69, fig. 27.
*Sertularella fusiformis*: Millard, 1957: 213, fig. 10C–E.

**Diagnosis.** Stem short and stiff, unfascicled, unbranched or with at most one or two short branches, reaching 22 mm in height. Branches, when present, arising
from below hydrothecae. Stem and branches divided into internodes by oblique nodes sloping in alternate directions, each internode bearing one hydrotheca.

Hydrotheca small to medium, adnate for $\frac{1}{3}-\frac{1}{2}$ abcauline length, smooth or faintly annulated, generally symmetrical and flask-shaped in side view, with margin perpendicular to axis, 0.4–0.6 mm in abcauline height and 0.17–0.3 mm in marginal diameter. Four small and delicate internal teeth of which one or more may be missing, alternating with marginal teeth.

Gonotheca borne on front of stem immediately below hydrotheca, spindle-shaped, annulated at least in distal half; margin narrow, with three or four spines.

Variation. This small species is common as an epizoote on other hydroids. The stem may be geniculate or quite straight, and often has one or more distinct annulations at the base of each internode. The two rows of hydrothecae may be in one plane, or displaced onto one surface of the stem. The hydrothecae may be well separated or overlapping.

In the hydrotheca the most common variations are an elongation of the abcauline margin and tooth, and a bending out of the abcauline wall. Since both variations usually occur together, the line drawn perpendicular to the margin may be displaced so that it passes through the abcauline wall or, rarely in the other direction, so that it passes through the hydropore. The abcauline wall may be convex, straight, or slightly concave. The wall is normally quite smooth, but occasionally shows faint indications of transverse annulations, but never as pronounced as in f. ornata Broch. The internal teeth are constant in size and position, but the full complement of four is not always present. There may be a low thickening on the abcauline wall below the level of the internal teeth.

Remarks. This is one of the more difficult ‘intergrading’ species and shows variations in thecal shape approaching the polyzonias type (with concave abcauline wall), and the africana type (with straight, elongated abcauline wall). The form with overlapping hydrothecae is reminiscent of S. congregata. The criterion for identification is taken to be the presence of small internal teeth, which always alternate with the marginal teeth. Thus, even though some teeth are missing, the species can be distinguished from the three-toothed ones by the position.

Distribution outside South Africa. North Atlantic and Mediterranean, with one record from the west coast of North America. Type locality: South Devon, U.K.

Distribution in South Africa. Lambert’s Bay to East London, littoral to 70 m. 32/18 (l), 33/17 (l), 33/18 (l, s), 34/18 (l, s), 34/22 (s), 33/27, 32/28 (s)

Sertularella gilchristi Millard, 1964

Fig. 94G–J

Sertularella gilchristi Millard, 1964: 44, figs. 12E, G–H.

Diagnosis. Stem stiff, fascicled, branching and rebranching profusely in an
irregular pinnate fashion and usually in one plane, reaching 69 mm in height. Final branches (hydrocladia) arising from immediately below hydrothecae with irregular spacing. Stem and hydrocladia divided into internodes by oblique nodes sloping in alternate directions, but nodes indistinct in older parts; each internode bearing one hydrotheca.

Hydrotheca small, adnate for just under half adequualine length, annulated, with three or more transverse annulations usually continued all round wall, fusiform and usually slightly curved outwards, markedly narrowing to margin, with margin tilted towards adequualine side, 0.3–0.4 mm in adequaline height and 0.11–0.14 mm in marginal diameter. Three internal teeth, one large adequaline and two smaller latero-adequaline.

Gonothecae borne on hydrocladia immediately below hydrothecae, spindle-shaped, annulated, with very narrow opening and three or (rarely) four sharp marginal spines.

*Variation.* The general effect of the colony is bushy, for branching is not always strictly in one plane. The two rows of hydrothecae are usually in one plane, but may be slightly offset to one surface. A spiral annulation may or may not be present above each node. The internode length is variable.

The amount of annulation on the hydrotheca is variable, and may be indistinct or confined to the adequaline side. The hydrotheca is sometimes quite symmetrical, but is more typically bent outwards and the margin tilted towards the adequaline side. Rare hydrothecae may occur in which the mouth is less narrow. The internal teeth are constant in position, and always well developed, and in many hydrothecae two minute extra ones occur, one on each side of the median adequaline one.

*Distribution.* Endemic to South Africa. Type locality: Agulhas Bank, 33°3′S/27°55′E, 27 m.

*Distribution in South Africa.* Agulhas Bank, in the Port Elizabeth–East London area, 27–90 m. Rare. 34/25 (s), 33/27 (s)

*Sertularella goliathus* Stechow, 1923

Fig. 95A–C


*Diagnosis.* Stem stiff and fascicled, giving off hydrocladia in an irregularly pinnate fashion, reaching 79 mm in height. Hydrocladia arising from immediately below hydrothecae, the two rows in one plane. Stem and hydrocladia divided into short internodes by oblique nodes sloping in alternate directions, but nodes indistinct in older parts; each internode bearing one hydrotheca.

Hydrotheca large, adnate for about two-thirds adequaline length, smooth, adequaline wall bent sharply outwards at top of adnate part, margin perpendicular
to axis, abcauline and free part of abcauline wall slightly concave, margin narrow; 0.9–1.1 mm in abcauline height and 0.3–0.4 mm in marginal diameter. Three large internal teeth, one abcauline and two latero-abcauline.

Gonothecae borne on hydrocladial internodes on the same level as, and on the opposite side to, the base of the hydrotheca, spindle-shaped, with about five rounded annulations; margin with three spines.

Variation. Although the mature colony is fascicled, young stems are unfascicled and often without hydrocladia.

Although the thecal margin is normally perpendicular to the axis, slight deviations to either side may occur, so that the perpendicular may pass through the lower part of the abcauline wall or through the hydropore. Usually the free part of the abcauline wall is at right angles to the internode, but the angle may be smaller than this, particularly at the distal ends of hydrocladia. Internal teeth are always present, and constant in number and position.

The gonotheca may have as few as three annulations restricted to the distal end, but this is rare.

Distribution. Endemic to South Africa. Type locality: Agulhas Bank.

Distribution in South Africa. West coast of Cape Peninsula to Mossel Bay in 8–155 m. 34/18 (s), 34/20 (s), 35/20 (d), 34/21 (s), 35/22 (d)

Sertularella leiocarpa (Allman, 1888)

Fig. 95D–F

Sertularia leiocarpa Allman, 1888: 52, pl. 25 (fig. 1–1a).

Diagnosis. Stem moderately stiff (just able to support itself out of fluid), unfascicled or lightly fascicled at base, giving off roughly alternate hydrocladia in one plane, reaching 42 mm in height. Hydrocladia arising from immediately below hydrothecae. Stem and hydrocladia divided into fairly long and slender internodes by oblique nodes sloping in alternate directions, but nodes indistinct in older parts; each internode bearing one hydrotheca.

Hydrotheca tubular, adnate for 1/4–1/3 abcauline length, smooth, curving gently outwards, with straight or concave abcauline wall and smoothly convex abcauline wall, narrowing markedly to mouth, margin tilted towards abcauline side, 0.7–1.2 mm in abcauline height and 0.2–0.4 mm in marginal diameter. Usually without internal teeth.

Gonothecae borne on stem on the same level as, and on the opposite side to, the base of the hydrotheca, spindle-shaped, completely smooth; margin with three or four short spines.

Variation. A few hydrothecae show very faint traces of annulation on the free part of the abcauline wall. Although normally there are no internal teeth, one of the larger colonies has minute internal teeth in some hydrothecae only, either
Fig. 95.

Sertularella goliathus. A, gonotheca; B, hydrothecae; C, stem (somewhat damaged).
Sertularella leiocarpa. D, hydrotheca; E, part of colony; F, part of stem with hydrothecae and gonotheca.

Scale: C and E in cm, A and F in mm, the rest in mm/10.
two latero-adcauline, or two latero-adcauline plus one adcauline. Vervoort reports traces of four internal teeth in some hydrothecae of his material. This is a species in which the presence or absence of internal teeth is variable.

**Distribution outside South Africa.** South Atlantic and southern Indian Ocean. Type locality: Nightingale Island, 183–274 m.

**Distribution in South Africa.** A deep-water species. Scattered records from the west coast of the Cape Peninsula, Agulhas Bank, Natal and Moçambique, 200–595 m. 34/18 (d), 35/22 (d, vd), 29/31 (d), 25/35 (vd)

*Sertularella mediterranea* Hartlaub, 1901


*Sertularella ellisi f. mediterranea* Patriti, 1970: 38, fig. 49.

**Diagnosis.** Stem stiff, unfascicled, unbranched or with a few irregular branches, divided into internodes by oblique nodes sloping in alternate directions, each internode bearing one hydrotheca. Branches similar to stem.

Hydrotheca smooth, narrowing to mouth; with more or less straight adcauline wall and double curvature in adcauline wall, first convex, then concave; with adcauline margin and tooth typically produced and margin thus tilted towards stem. Three strong internal teeth, one adcauline and two latero-adcauline.

Gonothecae borne on the stem opposite the bases of the hydrothecae, spindle-shaped, annulated in distal half to a varying degree, with three or four marginal spines and distinctly narrowed just below them.

**KEY TO SUBSPECIES**

1. Hydrotheca bilaterally symmetrical, with lateral teeth equally developed; adnate for not less than $\frac{2}{3}$ adcauline length ... *S. m. mediterranea*
   - Most of the hydrothecae with right and left margins not symmetrical, one lateral tooth being larger than the other. Hydrotheca adnate for not more than $\frac{2}{3}$ adcauline length ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... 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abcauline marginal tooth and a margin tilted towards the stem, but this is not
a constant character and in some colonies the teeth are of equal size and the
margin perpendicular to the axis, so that the perpendicular passes through the
hydropore or through the abcauline basal thickening, but never through the
abcauline wall as in the closely related S. natalensis. The width of the hydro-
thecal margin varies and occasional hydrothecae have particularly narrow
mouths. The three internal teeth of South African specimens are very constant
in size and position; sometimes two minute extra ones occur, one on each side
of the abcauline one. In only one hydrotheca of one colony were four internal
teeth seen, the abcauline tooth being replaced by two small ones. Variation in
the number of internal teeth has been reported for specimens from the
Mediterranean and other areas.

**Distribution outside South Africa.** Mediterranean and Red Sea, east coast of
Atlantic as far south as the Vema Seamount and Angola with scattered reports
from the Indian Ocean and Australasia. Type locality: Rovigno.

**Distribution in South Africa.** West coast of Cape Peninsula to Natal, littoral to
73 m. 33/18 (l), 34/18 (s), 34/23 (s), 33/25 (s), 30/30 (l), 29/31 (l, s), 28/32 (s)

*Sertularella mediterranea asymetrica* Millard, 1958

Fig. 96A

*Sertularella mediterranea, var. asymetrica* Millard, 1958: 191, fig. 7B.

**Diagnosis.** Stem unbranched, reaching a maximum height of 14 mm, the two
rows of hydrothecae not in one plane but shifted on to anterior surface.

Hydrotheca not bilaterally symmetrical but with one of the lateral marginal
teeth distinctly longer than the other, smaller and less adnate than the nominate
subspecies, adnate for $\frac{1}{4} - \frac{2}{3}$ abcauline height, 0.3–0.6 mm in abcauline height
and 0.14–0.2 mm in marginal diameter.

Female gonotheca with external marsupium.

**Distribution.** Endemic to South Africa. Type locality: Inhaca Island, Delagoa
Bay, littoral.

**Distribution in South Africa.** South coast from Mossel Bay to East London and
Inhaca Island, littoral to 46 m. 34/22 (l), 33/27 (s), 26/32 (l, s)

*Sertularella megista* Stechow, 1923

Fig. 97A–D

*Sertularella megista* Stechow, 1923b: 111. Stechow, 1925a: 480, fig. 36. Millard, 1957: 217,
figs 10L, 11J. Millard, 1964: 45. Millard, 1967: 180, fig. 4D.

**Diagnosis.** Stem moderately stiff (just able to support itself out of fluid), unfasci-
cled or lightly fascicled at base, unbranched or giving off a few long branches
at irregular intervals, reaching 140 mm in height. Branches arising from
immediately below hydrothecae, the two rows in one plane. Stem and branches
Fig. 96.

*Sertularella mediterranea.* A, subsp. *asymmetrica,* hydrothecae; B, nominal subsp., hydrothecae; C, nominal subsp., male gonotheca.

*Sertularella natalensis.* D, gonotheca; E, hydrotheca; F, part of stem.

*Sertularella pulchra.* G, hydrothecae; H, gonotheca; J, stem.

Scale: J in cm, the rest in mm/10.
divided into short internodes by oblique nodes sloping in alternate directions, but nodes indistinct in older parts; each internode bearing one hydrotheca.

Hydrotheca large, with thick perisarc, adnate for \( \frac{1}{4} \) \( \frac{3}{4} \) adcauline length, smooth, adcauline wall bent sharply outwards at top of adnate part, margin more or less perpendicular to axis, free part of adcauline wall straight or concave, never convex; 0.8–1.9 mm in adcauline height and 0.3–0.6 mm in marginal diameter. No internal teeth.

Gonothecae borne on stem or branches on the same level as, and on the opposite side to, the base of the hydrotheca, spindle-shaped, with about five rounded annulations; margin with three or four pointed spines.

**Variation.** Individual stems and branches of this species are easily recognized, though the form of the colony as a whole varies. There is a tendency to produce long unfascicled and unbranched stems or sections thereof. This is possibly characteristic of sheltered waters, whereas shorter, fascicled, and more branched colonies may be characteristic of exposed waters.

The shape of the hydrotheca varies between two extremes; one which is adnate for over half the length and with a comparatively short free portion, and one where the free part is much produced and may be twice as long as the adnate part (forma *elongata*). In the latter the free part has practically parallel walls but the mouth is no narrower than in the normal form.

Variation also occurs in the degree of bending in the adcauline wall, and in the angle of the margin. A line drawn at right angles to the latter may pass through the hypodote or through the adcauline wall. Rarely the free part of the adcauline wall may be faintly corrugated.

The annulation of the gonotheca varies and may be more pronounced or very indistinct.

**Distribution outside South Africa.** Vema Seamount. Type locality: Francis Bay, South Africa, in 100 m.

**Distribution in South Africa.** All round coast from St. Helena Bay to Mozam- bique, 0–347 m. 32/18 (s), 33/18 (s), 34/18 (s), 34/21 (s), 36/21 (d), 34/22 (s), 34/23 (s, d), 34/24 (d), 33/25 (s), 34/25 (s, d), 33/26 (d), 34/26 (d), 33/27 (s), 32/28 (s), 33/28 (s), 30/30 (s), 30/31 (s, d), 29/31 (s, d), 29/32 (s), 28/32 (d), 24/35 (d)

*Sertularella natalensis* Millard, 1968

Fig. 96D–F

*Sertularella natalensis* Millard, 1968: 271, fig. 4E–G.

**Diagnosis.** Stem stiff, unfascicled, unbranched or with at most one branch, reaching 34 mm in height, divided into internodes by oblique nodes sloping in alternate directions, each internode bearing one hydrotheca. Branches similar to stem.

Hydrotheca of medium size, adnate for \( \frac{1}{4} \) \( \frac{3}{4} \) adcauline length, free part
Sertularella megista. A, colony; B, hydrothecae; C, hydrotheca of forma elongata; D, male gonotheca.
Sertularella striata. E, stem and hydrothecae; F, gonotheca.
Scale: A in cm, the rest in mm/10.
directed outwards and narrowing to just below the margin, generally with one to four vertical striations which start on free part of adcauline wall and run for a varying distance parallel to adnate wall, 0.5–0.7 mm in adcauline height and 0.2–0.3 mm in marginal diameter. Margin tilted towards adcauline side. Five or three internal teeth, one very large adcauline, two large latero-adcauline and sometimes two minute latero-adcauline.

Gonothecae borne on stem opposite the bases of the hydrothecae, spindle-shaped, annulated in distal half, with three or four marginal spines.

**Variation.** The striations on the hydrothecal wall are characteristic of the species and always occur in some hydrothecae of a colony. They may be faint or absent in other hydrothecae, particularly the older ones.

**Distribution.** Endemic to South Africa. Type locality: off Natal, 29°47.5'S/ 31°12' E, 64 m.

**Distribution in South Africa.** Natal and Moçambique, 1–64 m. 29/31 (s), 26/32 (s), 25/33 (s), 24/34 (s)

*Sertularella polyzonias* (Linnaeus, 1758)

*Sertularia polyzonias* Linnaeus, 1758: 813.

**Diagnosis.** Stem unfascicled or weakly fascicled, flexuous and straggling (unable to support itself out of fluid), irregularly branched. No obvious distinction between main stem and branches. Branches arising from below hydrothecae, often rebranched. Stem and branches divided into internodes by oblique nodes sloping in alternate directions, each internode bearing one hydrotheca.

Hydrotheca adnate for about half adcauline length, smooth, with distal half curved outwards and margin tilted towards adcauline side, adcauline wall concave in distal half. Internal teeth generally absent, occasionally four minute ones alternating with marginal teeth.

Gonothecae borne on stems and branches from immediately below hydrothecae, elongate-spindle-shaped, annulated at least in distal half; margin with about four spines; female with external marsupium, larger than male.

**Remarks.** The discovery that *S. xantha* may sometimes possess four internal teeth means that the distinction between this species and *S. falsa*, which always possesses internal teeth, falls away. Both are regarded as subspecies of *S. polyzonias*. The distinction between subspp. *xantha* and subspp. *polyzonias* (both normally without internal teeth) is mainly one of size, the former having long, weakly fascicled stems and larger hydrothecae, the latter having short, unfascicled stems and smaller hydrothecae. *S. polyzonias* from other parts of the world is known to vary greatly in size, though fascicled stems have as yet not been reported.
There is some doubt as to the exact nature of *S. polyzonias*, since the type material has never been re-examined and described. The authorities quoted above give a fair indication of the present-day concept of the species.

**KEY TO SUBSPECIES**

1. Four minute internal teeth present, alternating with the marginal teeth ... *S. p. falsa*  
   - No internal teeth ......... 2
2. Hydrotheca very large, over 1 mm in abcauline height .... *S. p. gigantea*  
   - Hydrotheca small to medium, under 1 mm in abcauline height ... 3
3. Stem often weakly fascicled, reaching great lengths (generally over 30 mm and up to 270 mm) ... *S. p. xantha*  
   - Stem never fascicled, short (generally under 30 mm, never exceeding 50 mm) ... *S. p. polyzonias*

**Sertularella polyzonias polyzonias** (Linnaeus, 1758)

*Fig. 98F–H*

**Diagnosis.** Stem slender, unfascicled, short (usually under 30 mm, maximum height 48 mm), unbranched or branching sparsely, with a tendency towards stolon formation.

Hydrotheca small to medium, 0.3–0.6 mm in abcauline height and 0.18–0.3 mm in marginal diameter. No internal teeth.

Gonotheca under 2.3 mm in length, with 3–6 marginal spines.

**Variation.** This is the most delicate of the four subspecies and is a common epizoote of other hydroids. The stem varies considerably in length of internode; it is sometimes geniculate and sometimes not, and often has a distinct annulation immediately above each node. The two rows of hydrothecae are usually in one plane, but sometimes shifted on to one surface.

The hydrotheca sometimes has the abcauline margin and marginal tooth slightly produced so that a line drawn perpendicular to the margin passes through the abcauline basal thickening instead of through the abcauline wall, thus approaching *S. africana*. Occasionally vague transverse corruagations occur, as are also characteristic of the latter species. These variations, however, are seen only in isolated hydrothecae of a colony. The width of the mouth is variable within a colony.

**Distribution.** Cosmopolitan, mainly North Atlantic. Type locality: U.K.

**Distribution in South Africa.** Table Bay to Moçambique, littoral to 111 m. 33/18 (s), 34/18 (l, s), 34/20 (s), 34/22 (s), 34/23 (s, d), 33/25 (s), 34/25 (s), 33/26 (s), 33/27 (s), 32/28 (s), 30/30 (s), 29/31 (s), 28/32 (s, d), 24/34 (s)

**Sertularella polyzonias falsa** Millard, 1957

*Fig. 98D–E*

**Sertularella falsa** Millard, 1957: 211, figs 10F, 11D.

**Diagnosis.** Stem unfascicled, short (under 30 mm), branching irregularly.

Hydrotheca small to medium, 0.4–0.6 mm in abcauline height and 0.19–
0.3 mm in marginal diameter. Four small internal teeth present, alternating with marginal teeth.

Gonotheca of medium size (reaching 2.6 mm in length), with 3–4 marginal spines.

**Variation.** This subspecies is very similar to the nominal one in appearance and dimensions, its main diagnostic character being the presence of internal teeth. These may not be visible in older hydrothecae. *S. polyzonias f. glabra* Broch, 1933 is also described as having internal teeth in most of the hydrothecae, but the shape of the hydrotheca is rather different, being more constricted at the margin. As in the nominal subspecies the abcauline margin and marginal tooth may be slightly produced so that the perpendicular passes through the abcauline basal thickening. The abcauline wall may have a low thickening below the margin.

**Distribution.** Endemic to South Africa. Type locality: False Bay, about a kilometre east of Seal Island, 27 m.

**Distribution in South Africa.** False Bay and Knysna Estuary, littoral to 40 m. 34/18 (1, s), 34/23 (s)

*Sertularella polyzonias gigantea* Hincks, 1874

Fig. 98J

*Sertularella polyzonias* var. *gigantea* Hincks, 1874: 151, pl. 7 (figs 11–12). Stechow, 1925a: 478, fig. 6.

**Diagnosis.** Stem ?unfascicled, ?unbranched, reaching 17 mm in height, with one or two weak annulations at the base of each internode. Perisarc very thick in stem, thin in hydrothecae.

Hydrotheca very large, 1.2 mm in abcauline height and 0.5 mm in marginal diameter, adnate for about one-third height. No internal teeth.

**Distribution outside South Africa.** Uncertain. Type locality: Iceland.

**Distribution in South Africa.** One record only (Stechow 1925a), from Plettenberg Bay, 100 m. 34/23 (d)

**Remarks.** No further material resembling that ascribed by Stechow to var. *gigantea* has been found. Since Stechow’s description was based on one infertile stem only, the nature of the colony cannot be diagnosed with certainty. It is also not certain whether var. *gigantea* of Hincks is synonymous with *S. gigantea* Mereschkowsky, 1878.

*Sertularella polyzonias xantha* Stechow, 1923

Fig. 98A–C


**Diagnosis.** Stem often weakly fascicled at base, reaching great lengths (up to
Fig. 98.
Sertularella polyzonias. A–C, stem, hydrothecae and gonotheca of subsp. xantha; D and E, hydrothecae and gonotheca of subsp. falsa; F–H, colony, hydrothecae and gonotheca of subsp. polyzonias; J, hydrothecae of subsp. gigantea, redrawn from Stechow (1925a).
Scale: A in cm, the rest in mm/10.
270 mm), branching and rebranching repeatedly. Internodes often very long and nodes not visible in older regions.

Hydrotheca of medium size, adnate for over half height, 0,5-0,7 mm in abcauline height and 0,2-0,3 mm in marginal diameter. Usually without internal teeth.

Gonotheca long, over 2,5 mm, with 3-4 marginal spines.

Variation. In this subspecies it is only the older colonies which have fascicled stems, and even these always retain the slender and flexuous appearance typical of the species. In some colonies the branching may show a tendency towards a regular pinnate arrangement, but it is more often quite irregular. Both internode length and thickness of perisarc vary tremendously, young parts of the colony having short internodes, thin perisarc and distinct nodes, and older parts having longer internodes, thicker perisarc and no nodes. With thicker perisarc, a thickening on the abcauline wall of the hydrotheca is apparent, which, however, is never so marked as, for instance, in S. arbuscula.

The hydrorhiza, which is typically creeping, may become branching and filamentous in deep-water specimens for penetration of mud.

In the hydrotheca the perpendicular always passes through the abcauline wall, though the concavity in the abcauline wall may at times be very slight. Usually there is no sign of internal teeth, but certain stems in a colony may have four minute internal teeth alternating with the marginal teeth.

Distribution. Endemic to South Africa. Type locality: off Cape Town, 33°41,2'S/18°0,3'E, 178 m.

Distribution in South Africa. Common on the south coast from Table Bay to East London, also off Durban, 7-350 m. 33/18 (s, d), 34/18 (s, d), 35/19 (s), 34/20 (s), 34/21 (s), 35/21 (d), 34/22 (s, d), 35/22 (d), 34/23 (s, d), 34/24 (d), 33/25 (s), 34/25 (d), 34/26 (d), 33/27 (s), 29/31 (s, d)

Sertularella pulchra Stechow, 1923

Fig. 96G-J


Diagnosis. Stem stiff, fascicled, giving off alternate hydrocladia in one plane, reaching 74 mm in height. Hydrocladia arising from immediately below every third hydrotheca at a wide angle, alternately on the right and left. Stem and hydrocladia divided into internodes by oblique nodes sloping in alternate directions, each internode bearing one hydrotheca.

Hydrotheca of medium size, long and slender, adnate for about half abcauline length, with three or four distinct transverse striations on free part of abcauline wall, abcauline wall straight or slightly concave, margin perpendicular to axis or tilted slightly towards abcauline side, 0,6-0,8 mm in abcauline height
and 0.2–0.3 mm in marginal diameter. Four internal teeth of equal size alternating with marginal teeth.

Gonothecae borne on stem and hydrocladia immediately below the hydrothecae on the same or the opposite side, spindle-shaped, annulated; margin with 4–6 spines.

Variation. The long, slender hydrotheca with adcauline striations is characteristic and easily recognized. Usually the axis is straight, but sometimes it is slightly curved. In general the tendency is to bend away from the stem, but occasional examples occur in which the adcauline marginal tooth is slightly elongated so that the perpendicular passes through the hydropore. The adcauline striations are occasionally faint or invisible, though only in a few hydrothecae of a colony. The internal teeth are constant in number and position, though occasionally absent in the youngest hydrothecae of a colony or in very young stems with extra thin perisare.

Distribution. Endemic to South Africa. Type locality: Simon’s Bay, 70 m.

Distribution in South Africa. South coast, from False Bay to East London, 40–120 m. 34/18 (s), 34/21, 34/23 (s), 34/25 (s), 33/26 (d), 33/27 (s), 33/28 (s), 32/28 (s)

Sertularella striata Stechow, 1923

Fig. 97E–F


Diagnosis. Stem short and stiff, unfascicled, unbranched or with at most one or two short branches, reaching 11 mm in height. Branches, when present, arising from immediately below the hydrothecae. Stem and branches divided into internodes by oblique nodes sloping in alternate directions, each internode bearing one hydrotheca and usually with an annulation at the base.

Hydrotheca small, adnate for about half adcauline length, with about six or seven distinct, ridged annulations evenly spaced over entire length and continued right round wall, adcauline wall more or less straight, adcauline marginal tooth generally produced and margin perpendicular to axis or tilted slightly towards adcauline side, 0.4–0.5 mm in height and 0.15–0.2 mm in marginal diameter. No internal teeth.

Gonothecae borne on front of stem immediately below the hydrothecae, spindle-shaped, annulated; margin generally with three or four minute spines. An external marsupium present in female.

Variation. The hydrotheca is characteristically asymmetrical in side view with the adcauline tooth produced, but a slight outward bend usually results in a margin perpendicular to the axis. Occasionally, however, completely symmetrical hydrothecae are found. The strength and number of the striations is variable, and in the same colony examples may be found with about nine distinct striations and others with only four or five rather indistinct ones, the former predominating.
The gonothecae tend to be completely annulated, though the striations may fade out in the lower region. Marginal spines vary in number, and may be as many as five or six.

**Distribution.** Endemic to South Africa. Type locality: Cape Agulhas, 35°2,5'S/19°58,5'E, 80 m.

**Distribution in South Africa.** Agulhas Bank, from Cape Agulhas to East London, 9–100 m. Not common. 35/19 (s), 34/22 (s), 34/23 (d), 33/25 (s), 33/27 (s)

**Doubtful species**

*Sertularella gayi* (Lamouroux, 1821)

*Sertularia gayi* Lamouroux, 1821: 12, pl. 66 (figs 8–9).

**Remarks.** Previous records of this species from South Africa are as follows:
Johnston (1838) as *Sertularia polyzonias* var. β. This material was ascribed to *S. gayi* by Hincks (1868) and Nutting (1904). Diagram and description inadequate.
Bush (1851) as *Sertularia polyzonias*. An infertile stem of Bush’s material was ascribed to *S. gayi* by Millard (1961) but the hydrotheca was without adcauline annulations and might equally well be *S. dubia*.

None of these records is conclusive evidence that the species occurs in South Africa. Picard (1956) maintains that *S. gayi* can be distinguished from closely related species by the bilabiate aperture of the gonotheca. Infertile material could be confused with *S. capensis* or *S. dubia*, in which the margin of the gonotheca bears several minute spines.

*S. gayi* is common in the Atlantic and has been reported from tropical west Africa by Vervoort (1959, 1966b). It might be noted that some of Vervoort’s material is without the characteristic annulations on the adcauline wall of the hydrotheca, thus approaching the condition in *S. dubia*.

**Genus Sertularia** Linnaeus, 1758

**Diagnosis.** Stem erect, branched or unbranched. Stem and branches bearing hydrothecae in two longitudinal rows. Hydrotheca sessile, partly adnate, with two marginal teeth seated more or less midway between adcauline and adcauline edge and usually a small, median adcauline one. Aperture triangular. Operculum of two valves, a smaller adcauline one and a larger adcauline one, the former often divided into two sections by a median partition. Hydranth with an adcauline caecum.

Type species: *Sertularia cupressina* Linnaeus, 1758.

**KEY TO SPECIES**

[Doubtful species not included, for these see p. 313]

1. Stem normally branching, branches alternate. Hydrotheca with adcauline intrathecal septum
   - Stem normally unbranched; if branched, branches not alternate
   - Stem normally branching, branches alternate

2. *S. marginata*
2. Hydrotheca with abcauline intrathecal septum ... ... ... ... ... ... ... ... ... ... 3
   - Hydrotheca without intrathecal septum ... ... ... ... ... ... ... ... ... ... 4
3. Hydrotheca erect and only slightly bent out in distal region. Marginal teeth low and poorly developed ... ... ... ... ... ... ... ... ... ... ... ... S. ligulata
   - Hydrotheca strongly bent out at about half height. Marginal teeth usually triangular and well developed ... ... ... ... ... ... ... ... ... ... S. turbinata
4. Hydrotheca bulging near base and narrowing markedly to margin. Perisarc thickened around thecal margin ... ... ... ... ... ... ... ... ... ... S. longa
   - Hydrotheca slender, with more or less parallel sides, narrowing only slightly to margin. Perisarc of hydrotheca not thickened ... ... ... ... ... ... S. distans

Sertularia distans (Lamouroux, 1816)

Fig. 99E–H

Dynamena distans Lamouroux, 1816: 180, pl. 5 (fig. 1).
Sertularia gracilis Hassall, 1848: 2223. Hincks, 1868: 262, pl. 53 (fig. 2).
Sertularia heterodonta Ritchie, 1909: 79, fig. 4.
Sertularia distans: Billard, 1925b: 197, fig. 1.

Diagnosis. Stem unfascicled, unbranched, 3–12 mm in height, each normal internode bearing a pair of opposite hydrothecae. Normal nodes straight. Hinge-joints present (a) terminating basal athecate part of stem, and (b) sporadically in distal region, each terminating a separate, narrow, athecate internode. Members of a pair of hydrothecae contiguous in front (except occasionally in basal part of stem), separate behind.

Hydrotheca tubular, not swollen and with more or less parallel sides in basal part, narrowing slightly to margin, distal part bent outwards at an angle of about 70° with stem, with evenly concave abcauline wall; adnate 1/3–3/4 abcauline length; with no intrathecal septum, 0.19–0.3 mm in abcauline height and 0.07–0.09 mm in marginal diameter. Margin with two moderately well-developed lateral teeth and a small abcauline one.

Gonotheca oval, smooth, circular in cross-section, with wide distal aperture on a short collar, with external marsupium in female.

Variation. There seems to be little ground for specific, or even varietal, differentiation between S. distans and S. gracilis, the differences noted by various authors (Billard 1925b; Picard 1951) being minor ones of size only. Thin etiolated stems (said to be characteristic of S. distans) may occur in the same colony as thicker stems (said to be characteristic of S. gracilis).

Regular branching does not occur, but occasional instances of branches arising from within hydrothecae have been seen. Considerable variation in growth-form can occur, including such characters as the presence or absence of internal perisarcal thickenings in the hydrotheca, the length of the basal athecate part of the stem, the number of hinge-joints terminating this region (1–3), the length of the thecate internodes, and the presence of nodes (which may be indistinct or invisible). Variation may also occur along the length of a stem,
the distal pair of hydrothecae being more erect, longer, and contiguous with one another for a greater length than the basal one.

Internal pegs of perisarc in the basal region of the hydrotheca are very characteristic, although not invariably present. These include one on the abcauline wall near the base, and one on the base medial to the hydropore. Internal teeth may also occur in the hydrotheca just below the margin—a single abcauline tooth is common and usually well developed when present, and occasionally two extra teeth may occur in a latero-abcauline position.

**Distribution outside South Africa.** Common in the tropical and temperate regions of the Atlantic and Indian Oceans; also Japan. Type locality: Atlantic Ocean.

**Distribution in South Africa.** Present at numerous localities from False Bay to Santa Carolina in Moçambique, though not common in any one place, littoral to 100 m. 34/18 (s), 34/20 (l), 34/22 (s), 33/25 (s), 33/27 (s), 32/28 (l, s), 31/29 (l, s), 31/30 (l), 30/30 (s), 29/31 (s), 28/32 (s, d), 26/32 (l) 25/23 (s), 24/34 (s), 24/35 (s), 23/35 (s), 21/35

*Sertularia ligulata* Thornely, 1904

Fig. 100A, D


**Diagnosis.** Stem unfascicled, usually unbranched but rarely with 1–3 branches, reaching a height of 27 mm, with a short basal athecate part terminated by a hinge-joint and a long distal part bearing hydrothecae in opposite pairs. Members of a pair of hydrothecae contiguous in front, separate behind. Branches, when present, similar to stem.

Hydrotheca with an abcauline intrathecal septum; swollen below septum, narrowing to mouth above it; erect and parallel to stem for half or more of height, then bent out; adnate for two-thirds or more of abcauline length, 0.2–0.3 mm in abcauline height, 0.11–0.16 mm in marginal diameter. Margin very delicate, more or less parallel to axis of stem, with two low and poorly developed lateral teeth and a small abcauline one. No internal teeth. Adcauline opercular flap very small. A leaf-shaped process, the ligula, present on adcauline side of hydanth body, arising from base of hydanth and projecting through mouth of hydrotheca when extended, well-armed with nematocysts and probably functioning as a nematophore.

Gonotheca (not reported from South Africa) borne on stem below hydrotheca, barrel-shaped, with about three transverse annulations (Thornely).

**Variation.** Branching, when it occurs, is not regularly alternate; the branches arise from the front of the stem below the thecal pairs and slightly to one side, they project diagonally forwards and the hydrothecae face towards the mid-line. There is no disturbance of the arrangement of the cauline hydrothecae as, for
Fig. 99.

*Sertularia marginata*. A, pinnate stem showing origins of hydrocladia and one rebranching hydrocladium; B, pinnate stem; C, hydrothecae; D, simple stem.

*Sertularia distans*. E and F, hydrothecae from middle and lower parts of stem respectively, F with hinge-joint; G, gonotheca; H, stem.

Scale: B in cm, the rest in mm/10.
instance, in *S. marginata*. Stems and branches often form stolons which reattach and result in a tangled colony. Branches may also arise from within the hydrothecae.

The stem nodes are variable. They may be absent, suggested only by a shallow groove, or present and then straight or slightly oblique.

The hydrothecae change in shape along the length of the stem, the distal ones being more erect, and contiguous and adnate for a greater amount than the basal ones. The margin tends to be directed slightly upwards in the distal hydrothecae and slightly downwards in the basal ones.

**Distribution outside South Africa.** Tropical Indo-Pacific, tropical West Africa and Japan. Type locality: Gulf of Manaar, Ceylon.

**Distribution in South Africa.** Moçambique: Inhaca to Santa Carolina, 0–15m. 26/32 (l, s), 23/35 (s), 21/35

*Sertularia longa* Millard, 1958

Fig. 100F–H

*Sertularia linealis* var. *longa* Millard, 1958: 197, fig. 8E.


*Sertularia linealis longa*: Millard & Bouillon, 1973: 75, fig. 9E–F.

*Sertularia longa*: Millard & Bouillon, 1974: 33, fig. 7D, J.

**Diagnosis.** Hydrocoriza usually growing on weed and with internal strengthening pegs of perisarc. Stem unfascicled, unbranched, reaching a maximum height of 9 mm, each normal internode bearing a pair of opposite hydrothecae. Normal nodes oblique or indistinct. A hinge-joint (or rarely, two) present near base of stem below thecate part, and at irregular intervals within thecate part where it terminates a short intermediate athecate internode. Members of a pair of hydrothecae contiguous in front (except sometimes in basal part of stem), separate behind.

Hydrotheca adnate for over half height, bent outwards, swollen below and narrowing to mouth, with concave abcauline wall but not evenly so and with a definite kink in lower or middle part, with no intrathecal septum, 0,16–0,2 mm in abcauline height and 0,07–0,11 mm in marginal diameter. Margin usually thickened, with two well-developed, roundly triangular lateral marginal teeth and a very small abcauline one. Internal teeth absent.

Gonotheca borne on front of stem below first pair of hydrothecae, smooth, compressed, curved pear-shape in broad view, with a wide distal operculate aperture on a short collar, reaching 1,1 mm in length and 0,6 mm in maximum diameter.

**Variation.** The shape of the hydrotheca changes along the length of the stem, the distal ones being more erect and contiguous for a greater length than the proximal ones.

**Distribution outside South Africa.** Seychelles.
Fig. 100.

*Sertularia ligulata.* A, stem; D, hydrotheca with hydranth, showing caccum, ligula and operculum (broken line).

*Sertularia turbinata.* B, forma *acuta*, stem; C, forma *turbinata*, stem; E, forma *acuta*, gonotheca.

*Sertularia longa.* F, hydrotheca; G, stem; H, stem with gonotheca.

Scale in mm/10.
Distribution in South Africa. Coast of Moçambique, littoral to 42 m. Type locality: Inhaca Island. 26/32 (l, s), 25/32, 25/33 (s), 23/35 (l)

*Sertularia marginata* (Kirchenpauer, 1864)

Fig. 99A–D

*Dynamena marginata* Kirchenpauer, 1864: 13, fig. 8.
*Desmoscyphus inflatus* Versluys, 1899: 42, figs 11–13.

**Diagnosis.** Stem unfascicled, reaching a height of 30 mm, either pinnate, or simple and unbranched. Pinnate stem with a short basal athecate part terminated by a hinge-joint, and a long distal thecate part bearing alternate hydrocladia. Thecate part divided by oblique nodes into internodes which bear either one hydrocladium and three hydrothecae (one in axil and an alternate pair above), or one pair of opposite or subopposite hydrothecae. Stem geniculate at least in distal part. The two rows of hydrocladia in one plane. Members of a pair of hydrothecae not contiguous except in distal region of stem.

Hydrocladium borne on long apophysis of stem and separated from it by a hinge-joint. Apophysis containing a transverse node which may be indistinct. Hydrocladium divided by nodes, which vary from very distinct and oblique to indistinct and transverse, into internodes, each of which bears a pair of opposite hydrothecae on anterior surface. Members of a pair of hydrothecae contiguous in front (except sometimes in basal region of hydrocladium), separate behind.

Simple stem similar to hydrocladium.

Hydrotheca with an abcauline intrathecal septum, swollen below septum, narrowing to mouth above it, bent outwards and slightly forwards, adnate for over half abcauline length, 0,15–0,3 mm in abcauline height, 0,09–0,19 mm in marginal diameter. Margin with two well-developed, triangular and sharp lateral teeth and a small abcauline one. No internal teeth.

Gonotheca (not reported from South Africa) borne on front of stem, ovate, compressed, with 5–9 transverse ridges, terminal opening and two distal spines.

**Variation.** The hydrorhiza may contain internal perisarcal thickenings in certain regions.

The basal athecate part of the stem is of variable length and may contain one or more transverse nodes. The arrangement on the rest of the stem depends on the presence or absence of hydrocladia. An internode bearing a hydrocladium typically has three hydrothecae arranged as described above, and an internode without a hydrocladium typically has a pair of opposite hydrothecae. When the first condition changes to the second the hydrothecae on successive internodes are gradually displaced from the alternate to the opposite position, and vice versa. A varying number of thecate internodes (up to four) without
branches may occur at the proximal and the distal end of a branching stem and occasionally at intervals along its length. Hydrocladia are normally unbranched, but may branch in a similar way to the stem, with the same modifications.

Hinge-joints may occasionally occur in the thecate part of the stem, but are not so common as in certain other species (e.g. S. distans). Such a hinge-joint always forms the termination of a short, intermediate, athecate internode.

In unbranched regions of the stem or hydrocladia the amount of contiguity between members of a pair of hydrothecae is variable and tends to increase towards the distal end. This is particularly well shown in simple stems, where the proximal pairs usually do not touch one another at all. The structure of the hydrotheca shows a similar gradation, those at the distal end being more erect than the proximal ones and without the intrathecal septum.

Distribution outside South Africa. Common in all tropical oceans, and extending into temperate areas in the Atlantic and southern Pacific (New Zealand). Type locality: Pacific Ocean.

Distribution in South Africa. False Bay to Inhaca, 0–46 m. Not common. 34/18 (s), 34/25 (s), 26/32 (s)

*Sertularia turbinata* (Lamouroux, 1816)

Fig. 100B–C, E

*Dynamena turbinata* Lamouroux, 1816: 180.
*Sertularia localosa* Warren, 1908: 306, fig. 8, pl. 48 (fig. 37).
*Tridentata acuta* Stechow, 1921b: 231.
*Sertularia acuta*: Millard, 1958: 192, fig. 8A, F.

Diagnosis. Stem unfascicled, unbranched, reaching a height of 25 mm, with a short basal athecate part terminated by a hinge-joint and a long distal part bearing hydrothecae in opposite pairs. Hinge-joints also occurring sporadically in distal region, each forming the termination of an extra, narrow, athecate internode. Members of a pair of hydrothecae contiguous in front (except sometimes in basal region of stem), separate behind.

Hydrotheca with an abcauline intrathecal septum, swollen below septum, narrowing to mouth above it, curved outwards and members of a pair with their axes diverging progressively from base to margin, adnate for $\frac{1}{3}$–$\frac{2}{3}$ abcauline length, 0.16–0.3 mm in abcauline height, 0.09–0.17 mm in marginal diameter. Margin usually facing upwards and outwards, with two well-developed, triangular lateral teeth and a small abcauline one. No internal teeth.

Gonotheeca borne on stem below hydrothecae, barrel-shaped, annulated, with wide distal aperture.

Variation. This species occurs in two forms, which were originally considered to be separate species but which have been shown (Millard 1964) to grade into one another.
Forma turbinata (Lamx.) has long internodes (approx. 0.8 mm) and long hydrothecae (abcauline length approx. 0.3 mm) and the nodes are generally oblique. Forma acuta (Stechow) has short internodes (approx. 0.5 mm) and short, squat hydrothecae (abcauline length approx. 0.2 mm) and the nodes are generally straight. In both forms the nodes may be indistinct in the lower part of the stem.

The shape and position of the hydrotheca changes along the length of the stem—the members of the distal pair being more erect and more contiguous to one another than those of the proximal pair.

The perisarc is thin in young colonies, though with a tendency for thickening of the abcauline thecal wall distal to the intrathecal septum. In old colonies all the perisarc is thickened.

Vervoort has observed two minute distal spines on the gonotheca of f. turbinata; these have not been seen in f. acuta.

*Distribution outside South Africa*. Circumglobal in tropical and subtropical waters. Type locality: Australasia.

*Distribution in South Africa*. Mossel Bay on the south coast to Inhambane on the east, littoral to 48 m. 34/22 (s), 33/27 (s), 31/29 (l), 30/30 (l), 29/31 (s), 28/32 (s), 26/32 (l), 24/35 (s), 23/35 (l, s)

Doubtful species

*Sertularia argentea* Linnaeus, 1758


*Remarks*. This common North Atlantic species has only been recorded from South Africa by Busk (1851). The identification of Busk’s material was confirmed by Millard (1961), but the species has never been found again. Its presence in South African waters needs confirmation.

Genus *Stereotheca* Stechow, 1919


*Diagnosis*. Stem erect, unfascicled, pinnate. Stem and hydrocladia bearing two longitudinal rows of hydrothecae. Hydrotheca sessile, with more than four well-developed marginal teeth, with no intrathecal septa and no external ridges or furrows. No operculum.

Type species: *Sertularia elongata* Lamouroux, 1816.

One species only from South Africa.

*Stereotheca elongata* (Lamouroux, 1816)

Fig. 101D, E

*Sertularia elongata* Lamouroux, 1816: 189, pl. 5 (fig. 3). Allman, 1886: 140, pl. 15.

*Stereotheca elongata*: Ralph, 1961a: 762, fig. 4e–k.

*Diagnosis*. Stem moderately stiff (able to support itself out of fluid), unfascicled,
unbranched, reaching 58 mm; bearing alternate hydrocladia; divided into regular internodes by oblique nodes sloping in alternate directions. Each internode bearing one hydrocladium and three hydrothecae (one axillary and a subopposite pair above). The two rows of hydrocladia in one plane. Hydrocladium borne on a short apophysis; divided into internodes of irregular length by slightly oblique nodes; each internode bearing one to three pairs of subopposite hydrothecae. The two rows of hydrothecae in one plane.

Hydrotheca tubular, with axis straight or bent outwards, adnate for over three-quarters of abcauline height, smooth, 0.2–0.3 mm in abcauline height and 0.14–0.20 mm in marginal diameter. Margin with six teeth which are very irregular in size, shape and position.

Gonotheca borne on stem immediately below third hydrotheca of internode, smooth, compressed, widening from base to truncated distal end, which bears a terminal aperture on a short collar and two hollow spines.

Variation. Much variation occurs in the shape of the hydrotheca and its marginal teeth. The hydrotheca is usually asymmetrical, bending slightly to one side, and there may also be an asymmetry of the teeth, with those of one side better developed than those of the other. One marginal tooth may be very much broader and longer than the others.

The distal horns of the gonotheca are also reported to vary in length, though not noticed in South Africa; they are usually long, though one or both may be reduced to short knobs.

Distribution outside South Africa: Australasia (type locality), North Sea.

Distribution in South Africa. Algoa Bay. 33/25

Genus Symplectosephyphus Marktanner-Turneretscher, 1890

Diagnosis. Stem erect, branched or unbranched. Stem and hydrocladia bearing alternate hydrothecae which form two longitudinal rows. Hydrotheca sessile, generally more cylindrical than in Sertularella, with three marginal teeth, one median abcauline and two latero-abcauline, and an operculum of three triangular valves seated in the bays between the teeth and meeting in the centre as a pyramid. Hydranth with abcauline caecum.

Type species: Symplectosephyphus australis Marktanner-Turneretscher, 1890 (= Sertularia johnstonti Gray, 1843).

KEY TO SPECIES

(Doubtful species not included. For these see p. 319)

1. Hydrotheca large (over 0.7 mm in abcauline height), tubular, curved smoothly outwards.
   Distal part of stem slender and geniculate
   Hydrotheca small to medium (under 0.7 mm in abcauline height). Stem not geniculate  2

2. Stem fascicled and freely branching. Hydrotheca with wide mouth (= half or more abcauline length). Gonotheca annulated
   S. arboriformis
Fig. 101.
Symplectocephalus arboriformis. A, hydrotheca; B, stem; C, hydrocladium and gonotheca.
Stereotheca elongata. D, part of stem showing origins of hydrocladia and gonotheca;
E, hydrotheca.

Scale: B in cm, the rest in mm/10.
- Stem unfascicled, usually unbranched. Hydrotheca with narrow mouth (= half or less abcauline length) ... ... ... ... ... ... ... 3

3. Gonotheca smooth, aperture on slender neck ... ... ... \textit{S. macrogonus}
- Gonotheca transversely annulated, no neck ... ... ... ... \textit{S. secundus}

\textit{Symplectoscyphus arboriformis} (Marktanner-Turneretscher, 1890)

\textit{Sertularella arboriformis} Marktanner-Turneretscher, 1890: 228, pl. 4 (fig. 5). Stechow, 1912: 358, fig. C.

\textit{Diagnosis}. Stem stiff, fascicled, branching and rebranching in a roughly alternate fashion and in one plane, reaching 110 mm in height. Hydrocladia arising from below hydrothecae, the two rows in one plane. Stem and hydrocladia divided into internodes by oblique nodes sloping in alternate directions, each internode bearing one hydrotheca. The two rows of hydrothecae in one plane.

Hydrotheca small to medium, adnate for \(\frac{1}{3}-\frac{1}{2}\) abcauline length, smooth, curved outwards and margin tilted towards abcauline side, 0,3–0,6 mm in abcauline height and 0,3–0,4 mm in marginal diameter. Margin not constricted. No internal teeth.

Gonothecae borne on stem and hydrocladia immediately below the hydrothecae, obovoid, transversely annulated in distal part, reaching 1,9 mm in height and 1,0 mm in maximum diameter. Aperture small and circular, on a raised collar.

\textit{Distribution}. Endemic to South Africa. Type locality: ‘Indian Ocean’.

\textit{Distribution in South Africa}. From the Orange River mouth in the west to Natal in the east, 10–219 m. 28/16 (s), 33/18 (s), 34/18 (s), 34/21 (s), 35/21 (d), 34/22, 35/22 (d), 33/25 (s), 34/25 (s, d), 33/26 (d), 34/26 (d), 33/27 (s), 33/28 (s), 32/28 (s), 29/31 (d)

\textit{Symplectoscyphus macrogonus} (Trebilcock, 1928)

\textit{Sertularella macrogonus} Trebilcock, 1928: 11, pl. I (figs 4–4d).

\textit{Diagnosis}. Stem stiff, unfascicled, generally unbranched, reaching 32 mm in height, but usually under 10 mm. Stem divided into internodes by oblique nodes sloping in alternate directions, each internode bearing one hydrotheca. The two rows of hydrothecae usually shifted onto anterior surface.

Hydrotheca small, adnate for less than half abcauline length, smooth, tubular, curved outwards and then upwards, 0,2–0,3 mm in abcauline height and 0,09–0,15 mm in marginal diameter; margin perpendicular to axis or tilted towards abcauline side; abcauline wall straight or concave. Three internal teeth usually present alternating with marginal teeth.

Gonotheca borne near base of stem, smooth, compressed, obovoid in
broad view, with a broad, concave distal end from the centre of which arises a slender collar bearing a terminal aperture, reaching 1.4 mm in length and 1.1 mm in maximum diameter.

Colour: stem horn-coloured, hydranths creamy white.

Variation. This species commonly grows on weeds, and its appearance varies from a sparse carpet of unbranched stems to a bushy growth of irregularly branched and anastomosing stems. The two rows of hydrothecae sometimes lie in the same plane, but more often they form an angle between them which may be as small as 45°. At the base of the stem are two or more close annulations. Internal teeth may be absent in complete stems of a colony or in just some hydrothecae of a stem.

Distribution outside South Africa. New Zealand, tropical South West Africa. Type locality: Dunedin, New Zealand.

Distribution in South Africa. From the northern border of South West Africa to East London, common on the west coast, littoral to 37 m. 20/13 (l), 26/15 (l), 28/16 (s), 32/17 (l), 32/18 (l, s), 33/17 (s), 33/18 (l, s), 34/18 (l, s), 34/19, 33/25 (s), 33/26 (l), 33/27 (l), 32/28 (s)

Symplectoscyphus paulensis Stechow, 1923

Fig. 102A–C


Diagnosis. Stem moderately stiff, generally unfascicled, unbranched or with one or two alternate branches, reaching a maximum height of 47 mm. Stem divided into internodes by oblique nodes sloping in alternate directions (but nodes often indistinct), each internode bearing one hydrotheca, geniculate and very slender in distal regions. The two rows of hydrothecae and branches in one plane.

Hydrotheca large, adnate for one-third or less adcauline length, smooth, tubular, curved outwards, not narrowing to margin, 0.7–0.9 mm in adcauline height and 0.4 mm in marginal diameter. No internal teeth. A pair of oval fenestrae closed by thin perisarc present below the base of each hydrotheca.

Gonothecae borne on stem or branches, obovoid, with several transverse undulations and a terminal aperture on a slender collar, reaching 1.5 mm in length and 1.1 mm in maximum diameter.

Variation. Stechow described this species as having a strongly fascicled stem, but South African material is at most lightly fascicled in the larger stems only. Possibly more mature colonies are more strongly fascicled.

Many of the hydrothecae have a thickened rim around the margin.

Distribution outside South Africa. South-west Indian Ocean and South Atlantic. Type locality: east of St. Paul, Indian Ocean.
Fig. 102.

*Symplectocyphus paulensis.* A, hydrotheca; B, fertile stem; C, part of stem with gonotheca.

*Symplectocyphus macrogonus.* D, female gonotheca; E, stem and male gonotheca; F and G, hydrothecae.

*Symplectocyphus secundus.* H, hydrothecae and gonotheca, redrawn from Kirchenpauer (1884, as *Sertularella secunda*).

Scale: B in cm, the rest in mm/10.
Distribution in South Africa. Off Natal and Moçambique in 347–440 m. A deep-water species. 29/31 (d), 24/35 (d)

*Symplectoscyphus secundus* (Kirchenpauer, 1884)

Fig. 102H

*Sertularella secunda* Kirchenpauer, 1884: 50, pl. 15 (figs 7–7a). Hartlaub, 1901a: 75, pl. 2 (figs 31, 38).
*Sertularella limbata* Allman, 1886: 134, pl. 9 (figs 3–4).

**Diagnosis.** Stem unfascicled, unbranched or weakly branched, reaching 7 mm in height, divided into short internodes by oblique nodes sloping in alternate directions, each internode bearing one hydrotheca. The two rows of hydrothecae not in one plane but shifted onto the anterior surface of the stem.

Hydrotheca small, adnate for less than one-third length, smooth, flask-shaped, 0.3–0.4 mm in abcauline height and 0.17–0.2 mm in marginal diameter; margin tilted towards abcauline side due to elongation of abcauline marginal tooth; abcauline wall more or less straight. Three internal teeth sometimes present, alternating with marginal teeth.

Gonothecae borne on stem, ovoid to spherical, with a few transverse annulations in distal half; aperture terminal, without neck; with external marsupium.

**Remarks.** This species has not been recorded since the time of Kirchenpauer and Allman. The type material was redescribed by Hartlaub.

The measurements given in the diagnosis were taken from Allman's material in the British Museum. The internal teeth were observed in this material, although not mentioned in the literature. The species is very similar to *S. macrogonus*, but has a different gonotheca.

**Distribution.** Endemic to South Africa.

**Distribution in South Africa.** Both Kirchenpauer and Allman give the locality simply as Cape of Good Hope.

Doubtful species

*Symplectoscyphus filiformis* (Allman, 1888)

*Sertularia gracilis* Allman, 1888: 51, pl. 24 (figs 1–1a).
*Sertularia filiformis* Allman, 1888: pl. 24 (figs 1–1a).
*Sertularella filiformis* var. *reticulata* Ritchie, 1907b: 535.
*Symplectoscyphus filiformis*: Totton, 1930: 194, fig. 42, pl. 3 (fig. 9). Rees & Thursfield, 1965: 129.

**Remarks.** This species is known from Patagonia, Burdwood Bank and the Falklands. Ritchie also recorded it from 'eight miles north of Dassen Island, Cape Colony'. However, the South African material was not mentioned by Rees & Thursfield in their revision of Ritchie's collection and one must assume that it no longer exists. Since the identification cannot be checked and since there are so many closely related species of *Symplectoscyphus*, the record is best regarded as doubtful until such time as it can be confirmed.
**S. filiformis** is rather similar in appearance to **S. arboriformis** but has smaller hydrothecae with a greater proportion adnate, and the gonotheca has very prominent transverse ridges.

**Symplectoscyphus indivisus** (Bale, 1882)

*Sertularella indivisa* Bale, 1882: 24, pl. 12 (fig. 7).


**Remarks.** The only record of this species is two slides from Busk’s collection reputed to come from Algoa Bay and identified by Millard (1961). It has not been discovered since and as with several of Busk’s records needs confirmation before acceptance.

*S. indivisus* differs from other South African species of the genus in its annulated hydrothecae.

**Symplectoscyphus johnstoni** (Gray, 1843)

*?Sertularia gaudichaudi*: Busk, 1851: 118.

**Remarks.** Busk recorded the presence of *‘Sertularia gaudichaudi’* in South Africa. Since that time Billard (1922 and other papers) has shown that *Sertularia gaudichaudi* Lamouroux, 1824 is a *Sertularella*. Millard (1961) showed that Busk’s material, reputedly from Algoa Bay, is neither a *Sertularia* nor a *Sertularella*, but a species of *Symplectoscyphus*, possibly *S. divaricatus* (Busk, 1852) or *S. johnstoni* (Gray, 1843). Ralph (1961a), in a revision of the New Zealand species of *Symplectoscyphus*, described and figured the type material of both *S. divaricatus* and *S. johnstoni*. From this account it is clear that Busk’s South African material is closer to the latter species. However, since the material is badly preserved and the species has not been reported again, the record is better dropped until such time as it can be confirmed.

**Symplectoscyphus unilateralis** (Lamouroux, 1824)

*Sertularella unilateralis* Lamouroux, 1824: 615, pl. 90 (figs 1–3). ?Busk, 1851: 118.

*Sertularella unilateralis*: Hartlaub, 1901a: 42, fig. 20.

**Remarks.** Busk attributed material from Algoa Bay to this species with a query. Busk’s material could not be found in the British Museum and probably no longer exists. The record should be dropped.

**Genus Thuiaria** Fleming, 1828

**Diagnosis.** Stem erect, bearing hydrothecae in two longitudinal rows and hydrocladia in whorls or in two longitudinal rows. Hydrocladia different in structure to stem, with internodes of irregular length, often branched. Hydrotheca sessile, partly or completely adnate, without distinct marginal teeth. Operculum of one large, abcauline valve. Hydranth with abcauline caecum.

**Type species:** *Sertularia thuja* Linnaeus, 1758.

**Remarks.** The opinion of Billard (1925a: 137) is adopted that *Thuiaria* and *Salacia* are separate species distinguished by the presence or absence respectively of an abcauline caecum.

There are no species in South Africa which can be attributed to this genus with any certainty.

**Doubtful species**

*Thuiaria doliolum* Kirchenpauer, 1884

*Thuiaria doliolum* Kirchenpauer, 1884: 27, pl. 13 (fig. 4).
Remarks. This species is insufficiently described and has not been reported again. Kirchenpauer gives the locality as 'Cape of Good Hope'. His figures suggest Salacia articulata, in which species the gonothecae are occasionally annulated (Ritchie 1909: fig. 6).

Leloup (1974) refers T. doliolum to a new genus Parathuiaria created for Sertulariidae with hydrothecae in opposite pairs and without operculum, but there is no real information as to the presence or absence of an operculum or abcauline caecum.

Genus Thyroscyphus Allman, 1877

Diagnosis. Stem erect, branched, bearing two rows of alternate hydrothecae. Hydrotheca pedicellate and free from stem, large, campanulate to tubular. Margin with four teeth which may be indistinct. Operculum pyramid-shaped, of four valves, sometimes shed early. Diaphragm present. Hydranth without caecum but with an annular fold. Nematocysts of at least two kinds, large and small.

Type species: Thyroscyphus ramosus Allman, 1877.

KEY TO SPECIES

1. Hydrotheca funnel-shaped, radially symmetrical or nearly so, never concave on abcauline side. Smaller branches zigzag . . . . . . . . . . . . . . . . . T. aequalis
   - Hydrotheca tubular and bilaterally symmetrical, usually concave on abcauline side. Smaller branches not zigzag . . . . . . . . . . . . . . . . . T. fruticosus

Thyroscyphus aequalis Warren, 1908

Fig. 103

Thyroscyphus aequalis Warren, 1908: 344, fig. 23, pl. 48 (figs 38–40). Millard, 1964: 52, fig. 16.
Thyroscyphus regularis: Jäderholm, 1923a: 5. Stechow, 1925a: 463.
Cnidoscyphus aequalis: Splettstösser, 1929: 82, 124, figs 78–82.

Diagnosis. Stem stiff and woody, fascicled near base in larger colonies, giving off irregularly alternate branches, reaching 400 mm in height but usually much less. Smaller branches (hydrocladia) distinctly zigzag. The two rows of branches and hydrothecae in one plane. Stem and branches divided into internodes by oblique nodes sloping in alternate directions, each internode bearing a hydrotheca on an apophysis at distal end.

Hydrothecal pedicel short, about half width of apophysis, spirally grooved. Hydrotheca large, more or less funnel-shaped and expanding to margin, but occasionally with slight bilateral tendencies; abcauline wall never concave; 0,8–1,3 mm in height from diaphragm and 0,4–1,2 mm in marginal diameter. Margin with four distinct equidistant teeth and thickened ridge just below edge. Operculum fairly persistent. Diaphragm in form of thickened perisarcral ring, more powerfully developed on abcauline side. Hydranth with about 32 tentacles.

Large nematocysts rod-shaped, present in two batteries (abcauline and abcauline) in distal part of ectodermal lining of hydrotheca (Fig. 81C).
Fig. 103.

*Thyroscyphus aequalis*. A, stems; B, hydrocladium; C-F, hydrothecae; G, male gonothece.

Scale: A in cm, B in mm, the rest in mm/10.
Gonotheceae borne on stem apophyses, male elongated, widening towards distal end which is obliquely truncated, smooth or roughly corrugated, with external marsupium, reaching 2,5 mm in length and 1,5 mm in maximum diameter. Female unknown.

Colour: opaque yellowish-white when preserved.

Variation. The nodes of the stem are usually distinct, but sometimes only faintly indicated. Sometimes two hydrotheceae arise from the same apophysis.

The spiral grooving of the hydrothecal pedicel is variable, it may reach a maximum development of $2\frac{1}{2}$ turns, usually with half a turn more on the abcauline side, or it may be barely visible. Regeneration nodes commonly occur in the pedicel and obscure the grooving. The shape and size of the hydrotheca vary, from a large form with a wide mouth and practically symmetrical sides, to a smaller form with narrower mouth and protruberant abcauline wall. The hydrotheca often possesses an extra internal ridge of perisarc at about one-third of its height for the attachment of the annular fold of the hydranth, but this is only present in the older hydrothecae.

Distribution outside South Africa. Tropical East Africa, Madagascar, India. Type locality: Algoa Bay, South Africa.

Distribution in South Africa. False Bay to Moçambique, common on the Agulhas Bank and in Natal, littoral to 219 m. 34/18 (s), 34/20 (s), 34/21 (s), 35/21 (d), 34/24 (d), 33/25 (s), 34/25 (s), 33/26 (s), 33/27 (s), 32/28 (s), 33/28 (s), 31/29 (l), 30/30 (s), 30/31 (s, d), 29/31 (s, d), 28/32 (s, d), 25/32, 25/33 (s), 24/34 (s), 24/35 (s)

**Thyroscyphus fruticosus** (Esper, 1793)

Fig. 104

*Spongia fruticosa* Esper, 1793: 188.


Diagnosis. Stem stiff and woody, unfascicled, giving off irregularly alternate hydrocladia in one plane, reaching 130 mm, with segmentation visible on smaller branches only, branches not zigzag. The two rows of hydrocladia and hydrothecae in one plane.

Hydrothecal pedicel short, borne on a wide apophysis of stem from which it is separated by a partial or complete node, unsegmented, but normally demarcated from hydrotheca by a shallow groove on abcauline side. Hydrotheca tubular, not expanding to margin, curved outwards, with abcauline wall convex and abcauline wall straight or slightly concave, 0,7–1,1 mm in abcauline height and 0,4–0,5 mm in marginal diameter. Margin with four low, rounded teeth and thickened ridge just below edge. Operculum shed early. Diaphragm in form of thickened perisarcal ring, more powerfully developed on abcauline side.
Large nematocysts bean-shaped, present in body of hydranth only (Splettstösser).

Gonotheca arising from stem apophysis below hydrotheca, elongate-oval, smooth, a little larger than hydrotheca, female obliquely truncated distally, containing one egg which develops into a planula in situ. No external marsupium.

Colour: pale rose when living, yellow when preserved.
Remarks. The female gonotheca is reported to be wider and shorter than the male.

Distribution outside South Africa. Indo-Pacific and mainly tropical, from the Mediterranean and east coast of Africa through India and the East Indies to Fiji and New Zealand.

Distribution in South Africa. Inhaca, Moçambique. 26/32 (I)

Family Plumulariidae

Diagnosis. Hydrothecae borne on hydrocladia and sometimes on stem also, always on one surface and forming a single row. Hydrotheca sessile, and at least partly adnate, without a true diaphragm but with a definite floor, without operculum, bilaterally symmetrical. Hydranth with a single circle of filiform tentacles and a conical hypostome. Nematophores always present and usually contained in nematothecae. Gonophores in the form of fixed sporosacs.

Introduction. The Plumulariidae form a fairly well-defined family, the members being easy to recognize. But subdivision within it is not easy, as many characters are variable both between and within species. There are four subfamilies, which, though easily recognized by an expert, are not easily separated in a key. These are the Halopterinae, Kirchenpaueriinae, Plumulariinae and Aglaopheniinae. Members of a subfamily are related by a set of characters, all of which do not necessarily occur in every genus. Thus the key on p. 329 is for convenience only; it does not attempt to include all possible characters. The reader should turn to the diagnoses of the subfamilies for confirmation.

Branching is very variable and complicated by the fact that some species can exist in more than one form. The stem may be simple and unbranched, arising directly from the hydrorhiza and bearing hydrothecae directly (in this case the terms ‘stem’ and HYDROCLADIUM are synonymous); or the stem may bear one order of branches (the branches are hydrocladia); or it may bear two or more orders (the final ones are hydrocladia) (Fig. 7).

The most characteristic type of branching is the pinnate type, with alternate or opposite hydrocladia arising from the stem or a branch thereof. Dichotomous branching occurs in Aglaophenia pluma and whorled branching in Nemertesia. A few genera exhibit sympodial branching. Thus, in Monostaechas the primary simple stem (hydrocladium) branches from the posterior surface as a helicoid symposium, but in M. quadridentes branching starts as a dichotomous symposium and changes more distally to a helicoid symposium. In Thecocarpus flexuosus the main stem gives rise to a number of scorpoid sympodia, each of which is twisted into a spiral and bears hydrocladia.

Hydrocladia are usually simple, but may also branch. If this branching occurs regularly it may be used as a diagnostic character, as in Monostaechas and Schizotricha (sympodial branching) and in Oswaldella (dichotomous branching)
The stem may be fascicled or unfascicled. Two types of fasciculation occur. In the first and most common, the stem has a single axial tube, which alone bears the hydrocladia and is surrounded to a greater or lesser extent by peripheral tubes. Branches may arise from the axial tube (e.g. *Cladocarpus lignosus*) or from the peripheral tubes (e.g. *Nemertesia ciliata*).

![Diagram](image)

**Fig. 105.**

Plumulariidae: fascicled stems and branching. A, branching from the axial tube as in *Cladocarpus*; B, branching from a peripheral tube as in *Nemertesia*; C, branching by separation of similar tubes as in *Corhiza*.

The second type of fasciculation occurs in *Corhiza*, where the stem has no special axial tube, but consists of a bundle of similar tubes, any one of which may diverge to form a hydrocladium. Branching here is simply a separation of groups of tubes.

Some species may exist in two growth-forms, though usually one or the other is dominant. Thus, in *Antennella secundaria* the simple stem is normal, but opposite pinnate branching of the first order may occur. In *Halopteris pseudoconstricta*, *Plumularia filicaulis* and *Gattyia humilis* alternate pinnate branching of the first order is normal, though simple stems may also occur.

A number of branching species are known to have epizooitic forms in which the growth is stunted and seldom develops further than the simple stage (e.g. *Gymnangium arcuatum*, *G. exsertum* and *G. africanum*). These forms when first described were placed in separate varieties or subspecies. It is now recognized that they are growth-forms only. Sometimes such stunted forms occur on the normal form of the same species (auto-epizooitic). *Oswaldella nova*, so far
known only as an epizooite, is possibly such a stunted form, of which the normal form remains to be discovered.

In most branching genera the hydrothecae are confined to the hydrocladia, so that the stem internodes are atecate and differ from those of the hydrocladia. But in \textit{Halopteris}, \textit{Gattya} and \textit{Schizotricha} both the stem and the hydrocladia bear hydrothecae. Cauline hydrothecae occur only in the \textit{Halopterineae} and form a useful diagnostic character.

A hydrocladium may bear hydrothecae on every internode (\textit{homoemerous}), or on every alternate one (\textit{heteromerous}). The condition may vary in a single colony, when the hydrocladia tend to be homomorous proximally and heteromorous distally due to the cutting off of short atecate internodes from the longer thecate ones.

\textbf{Hinge-joints}, in the form of very pronounced oblique nodes, may occur in various parts of the colony, usually near the base of the stem, its branches or the hydrocladia.

The hydrothecae are always bilaterally symmetrical and sessile, with the adcauline wall partly or completely adnate to the hydrocladium. No true diaphragm is present, but there is a definite floor to the hydrotheca perforated by a hydropore of varying size. An intrathecal septum may be present, either adcauline or abcauline in position, e.g. \textit{Lytocarpus} and \textit{Pycnotheca}.

The hydrothecal margin may be toothed (as in \textit{Gattya}, \textit{Dentitheca} and most \textit{Aglaopheniinae}) or untoothed. Sometimes the median abcauline tooth is produced into a long hollow or solid spine (e.g. \textit{Thecocarpus}), and sometimes the perisarc along the abcauline wall of the hydrotheca is thickened and forms a keel-like ridge, which may also be produced as a spine.

Nematophores are always present, and usually they are contained in \textbf{Nematothecae}. The latter are best developed in the Plumulariinae, where they are typically movable and two-chambered, with a slender basal chamber and a funnel-shaped distal chamber. However, the structure varies and they may be fixed and one-chambered (some species of \textit{Halopteris}) or reduced to small saucer-shaped or scoop-shaped structures (\textit{Kirchenpaueria}). The final stage in reduction occurs in some species of \textit{Kirchenpaueria}, where the nematotheca is completely absent and the nematophore (usually termed a naked \textit{sarcostyle}) emerges through a hole in the perisarc (Fig. 8).

The basic arrangement of nematothecae includes one median inferior below each hydrotheca and one lateral on each side. In addition to, or instead of, the latter, one or more superior nematothecae may be seated above the level of the hydrotheca. Many variations of this pattern occur, and extra lateral or superior nematothecae may be present.

In the \textit{Aglaopheniinae} the basic three nematothecae are rigidly present; they are always one-chambered and immovable, but often develop other complexities. The laterals are fused to the side-wall of the hydrotheca and sometimes have more than one opening. The median inferior may be fused to the abcauline face of the hydrotheca and may have an opening into it. Its distal
opening may be duplicated and its distal end may be drawn out into a long tube reaching well beyond the hydrothecal margin.

In most of the Halopterinae the laterals (or the first pair of laterals if two are present) are seated on long pedicels fused to the side-walls of the hydrotheca.

In addition to those associated with the hydrothecae, nematothecae may occur on atecate stems or internodes, on the peripheral tubes of fascicled stems, on the hydrorhiza and on the gonothecae or other reproductive bodies.

Nematothecae may provide useful characters for specific diagnosis, but it must be borne in mind that they are easily lost in dredged and preserved material.

A structure of doubtful function, the mamelon, is characteristic of many Plumulariinae. It is a small nipple-like protuberance bearing a terminal opening and is seated on the upper surface of the hydrocladia-bearing apophysis of the stem. Its aperture communicates with the cavity between the perisarc and coenosarc. It possibly contains a nematophore in life, or it may be concerned with the hydrostatic pressures of the colony. In the few cases of hydroids parasitic on Plumulariidae (e.g. Hebella furax) the parasitic hydrorhiza appears to
gain entry through the mamelon. In the Aglaopheniinae the mamelon is well developed and more like a reduced nematotheca in appearance.

Gonophores are always in the form of fixed sporosacs contained in gonothecae. Many species are dioecious and in most the gonothecae are sexually dimorphic. In the Plumulariinae, Kirchenpaueriinae, Halopterinae and the genus Gymnangium among the Aglaopheniinae the gonothecae are borne singly on the stem, hydrocladia or hydorrhiza, but in other Aglaopheniinae protective branchlets or phylactocarps are present (Fig. 9). These may be formed as appendages to a hydrocladium, as in Cladocarpus, or may represent modified hydrocladia as in Lytocarpus. In the latter, hydrocladia are transformed into phylactocarps at maturity. In L. phoeniceus, for example, every third hydrocladium ruptures above the level of the first hydrotheca and regenerates as a phylactocarp. In Thecocarpus and Aglaophenia the phylactocarp, a modified hydrocladium, forms a pod-shaped structure, the corbula. This consists of a central axis and a number of lateral ribs provided with nematothecae and arching over to enclose the gonothecae. The corbula may be open, when the ribs remain separate, or closed, when the ribs fuse with one another. Among the Aglaopheniinae genera are separated largely on the reproductive structures.

**KEY TO SUBFAMILIES**

1. Paired lateral nematothecae present and fused to hydrotheca  
   AGLAOPHENINAE p. 407
   - Paired lateral nematothecae present or absent, when present not fused to hydrotheca  
   2

2. Paired lateral nematothecae absent. Median nematothecae usually reduced and  
   seldom two-chambered  
   KIRCHENPAUERINAE p. 370
   - Paired lateral nematothecae present. Nematothecae usually two-chambered, seldom reduced  
   3

3. Hydrocladia arising from erect stem. No cauline hydrothecae. Stem, when fascicled,  
   giving rise to hydrocladia from a single axial tube  
   PLUMULARINAE p. 379
   - Hydrocladia arising independently from the hydorrhiza or from erect stem. Stem or  
   branches either with cauline hydrothecae or fascicled and giving rise to hydrocladia  
   or pinnae from any of its component tubules  
   HALOPTERINAE p. 329

**Subfamily Halopterinae**

*Diagnosis.* Erect stem present or absent. Hydrocladia originating (a) independently from hydorrhiza, or (b) from a pinnate stem possessing cauline hydrothecae, or (c) irregularly from the superficial tubes of a fascicled stem or its branches. Branches when present bearing cauline hydrothecae. Hydrocladia branched or unbranched. Hydrothecae generally large (over 0.2 mm in depth), with toothed or untoothed margin. Nematothecae of variable structure, one- or two-chambered, movable or immovable, but never fused to hydrothecae, at least three associated with every hydrotheca, or else median inferior, and one pair laterals; the laterals generally borne on pedicels which are adherent to the hydrotheca. Gonothecae unprotected, not aggregated, usually dimorphic and with the female bearing nematothecae.
KEY TO GENERA

1. No erect stem; hydrocladia arising separately from hydrorhiza  
   - Erect stem present, giving rise to hydrocladia either directly or from branches; but  
     sometimes with a simple growth-form when hydrocladia arise separately from hydro-  
     rhiza (for these see key to Antennella below)  
     Antennella p. 330  
     Monostaechas p. 362  
     Gattya p. 341  
     3
2. Hydrocladia unbranched  
   Hydrocladia branching sympodially  
   Hydrotheca with toothed margin  
   Hydrotheca with untoothed margin  
   4
3. Hydrocladia branched  
   Hydrocladia unbranched  
   Hydrotheca branching sympodially from posterior surface (opposite side to hydro-  
     theca)  
   Hydrocladia branching from anterior or lateral surface immediately below hydro-  
     thecae  
   Schizotricha p. 368  
   5
4. Stem fascicled and composed of tubes of equal importance, any of which may give  
   rise to hydrocladia or branches which are irregularly arranged. Cauline hydrothecae  
   present on branches, not on stem  
   Corhiza p. 334  
   Stem fascicled or unfasicled; if fascicled with an axil tube which alone bears hydro-  
     cladia. Hydrocladia pinnately arranged. Cauline hydrothecae present  
   Halopteris p. 349

Genus Antennella Allman, 1877


Diagnosis. No true stem present. Hydrocladia arising independently from hydrorhiza, normally unbranched, unfassicled. Hydrotheca cup-shaped, with untoothed margin.

Type species: Antennella gracilis Allman, 1877

KEY TO SPECIES OF ANTENNELLA AND SIMPLE FORMS OF BRANCHING GENERA

[Species not represented in South Africa are bracketed]

1. Hydrotheca with toothed margin  
   Hydrotheca with untoothed margin  
   Gattya humilis  
   2
2. Two pairs of lateral nematothecae  
   One pair of lateral nematothecae  
   3
3. Larger pair of lateral nematothecae with wineglass-shaped distal chamber, which  
   has a deep emargination on adecauline wall  
   Corhiza pannosa  
   Larger pair of lateral nematothecae with funnel-shaped distal chamber  
   4
4. Athecate internodes. Hydrotheca adnate for about \( \frac{1}{2} \) height. At least one superior  
   nematotheca present above hydrotheca  
   Intermediate athecate internodes present. Hydrotheca adnate for about \( \frac{1}{2} \) height. No  
   superior nematothecae  
   Monostaechas natalensis  
   5
5. Athecate intermediate internodes normally bearing one nematotheca  
   Athecate intermediate internodes normally bearing two or three nematothecae  
   Antennella africana  
   Antennella quadriaurita  
   6
6. Hydrocladia branching sympodially from posterior surface, the main axis formed  
   by the bases of successive hydrocladia  
   Hydrocladia normally unbranched; if branched the main axis formed by the primary  
   hydrocladium  
   Monostaechas quadridens  
   7
7. Hydrotheca with free part of adcauline wall more or less straight. A one-chambered superior nematotheca present in angle behind adcauline wall of hydrotheca

*Antennella secundaria*

- Hydrotheca with free part of adcauline wall distinctly hollow. No superior nematotheca.

*Halopteris pseudoconstricta*

*Antennella africana* Broch, 1914

Fig. 107A–E


*Antennella africana*: Stechow, 1925a: 492, fig. 41.

*Antennella serrata*: Totton, 1930: 212, fig. 53.


**Diagnosis.** Hydrocladia arising separately or in clusters from entwined hydrorhiza, often epizootic on other hydroids and found on the spider-crab, *Macropodia falcifera* (Stimpson). Hydrocladia reaching 31 mm in height, consisting of a short basal athecate part with a variable number of transverse nodes and a longer distal part with alternate thecate internodes terminated by transverse nodes and thecate internodes terminated by more distinct steeply oblique nodes. Athecate intermediate internodes normally with one median nematotheca. Thecate internodes with five nematothecae, one median inferior and two pairs laterals, one large and one small.

Hydrotheca cup-shaped, with more or less parallel sides, adnate for about half adcauline length, 0,19–0,3 mm in adcauline height and 0,2–0,3 mm in marginal diameter. Margin forming an angle of 50–60° with internode.

Median inferior nematotheca seated well below hydrotheca and not reaching its base, movable, two-chambered; distal chamber scoop-shaped with low adcauline wall. The larger lateral nematotheca seated on a finger-shaped pedicel arising below top of adnate part of hydrotheca, not reaching thecal margin, movable, two-chambered; distal chamber funnel-shaped, with wall emarginated on two sides resulting in a bivalved appearance with a large lateral valve and a small median valve. The smaller lateral nematotheca seated in axil of pedicel of larger one, of approximately the same length as pedicel, of the same structure as larger one.

Gonothecae borne immediately below hydrothecae, singly or in pairs, male and female either on separate hydrocladia, or on the same one with the male more distal than the female. Female gonotheca large, pear-shaped, with wide operculate distal aperture, bearing two large, two-chambered nematothecae on basal region, with a pedicel of two segments. Male gonotheca smaller, spindle-shaped and curved, with small distal aperture, bearing one large, two-chambered nematotheca on basal region, with a pedicel of one segment.

**Variation.** The intermediate thecate internodes are of variable length and may be longer than the thecate ones (usually the case in the proximal region) or shorter (usually the case in the distal region). The number of nematothecae on the intermediate thecate internodes is usually one in this species, though sometimes two and rarely three. In the closely related *Antennella quadriaurita*
Ritchie from the Atlantic the number is *usually* two or three and rarely four. It is possible that these two species should be combined.

**Distribution outside South Africa.** Tropical West Africa and New Zealand. Type material from Setté Cama, Congo, and from Lüderitz Bay, South West Africa.

**Distribution in South Africa.** Abundant round the west and south coasts from Lüderitz Bay to Natal, littoral to 450 m. 26/15 (s), 32/18 (s), 33/17 (s), 33/18 (l, s), 34/18 (l, s), 34/20 (s), 34/21 (s), 34/22 (s), 34/23 (s, d), 34/24 (d), 33/25 (s), 34/25 (s, d), 33/26 (s, d), 33/27 (s), 32/28 (s), 32/29 (d), 28/32 (d), 27/32 (d)

*Antennella secundaria* (Gmelin, 1791)

Fig. 107F–L

*Sertularia secundaria* Gmelin, 1791: 3854.

**Diagnosis.** Hydrocladia reaching 12 mm in height, consisting of a short basal athecate part with a variable number of transverse nodes and a longer distal part with alternate thecate internodes terminated by transverse nodes (often indistinct) and athecate internodes terminated by steeply oblique nodes, the first oblique node forming a hinge-joint. Athecate intermediate internodes with one or two median nematothecae. Thecate internodes with four nematothecae, one median inferior, one pair laterals and one median superior.

Hydrotheca cup-shaped, with more or less parallel sides, adnate for about half adcauline length, 0,15–0,2 mm in adcauline height and 0,15–0,3 mm in marginal diameter. Margin forming an angle of 35–50° with internode.

Median inferior nematotheca seated below hydrotheca and not, or only just, reaching its base, probably movable, two-chambered; distal chamber scoop-shaped with reduced adcauline wall. Lateral nematotheca seated on a finger-shaped pedicel arising on a level with top of adnate part of hydrotheca, usually not reaching thecal margin, movable, two-chambered; distal chamber funnel-shaped with low wall on medial side, somewhat variable in structure. Median superior nematotheca seated behind free adcauline part of thecal wall and not reaching margin, minute, one- or indistinctly two-chambered.

Gonothecae borne immediately below hydrothecae, singly or in pairs, curved, pear-shaped, bearing two large, two-chambered nematothecae on basal region, with a pedicel of two segments, male and female on the same hydrocladium, with the male more proximal than the female. Female gonotheca large, with a wide operculate distal aperture. Male gonotheca smaller, rounded distally.

**Variation.** *Antennella secundaria* can on occasion produce upright pinnate colonies similar to *Halopteris*, in which the internodes of the stem are similar to those of the hydrocladia. The hydrocladia are given off alternately, except
Fig. 107.

*Antennella africana.* A, hydrocladium with male gonothecae; B, female gonotheca; C–E, lateral nematothecae.

*Antennella secundaria.* F and G, hydrocladia, F with a proximal male and a distal female gonotheca; H–L, lateral nematothecae.

Scale in mm/10.
for the first two which are opposite. It can also produce branches from the posterior surface of the hydrocladium as does Monostaechas. Only the latter type has been seen in South Africa; there are never more than two branches to a hydrocladium, and these arise from the basal athecate region. The main axis is formed by the first hydrocladium and not by the bases of successive hydrocladia as in Monostaechas. The length of the athecate internodes is variable and may or may not exceed that of the thecate internodes in length.

A form with extra long nematothecae (about double the height of the hydrotheca) and shallow hydrothecae (0.11 mm abcauline height) also occurs.

**Distribution.** Cosmopolitan. Type locality: Mediterranean Sea.

**Distribution in South Africa.** Cape Agulhas on the south coast to Moçambique, littoral to 164 m. Not common in any one locality. 35/19 (s), 35/20 (d), 34/22 (s), 34/24 (d), 33/25 (s), 34/25 (s), 33/26 (s), 33/27 (s), 32/28 (s), 33/28 (s), 30/30 (l, s), 30/31 (d), 29/31 (s), 28/32 (s), 26/32 (l, s), 24/34 (s), 24/35 (s), 21/35

**Genus Corhiza Millard, 1962**

**Diagnosis.** An erect fascicled stem present, which may be branched or unbranched, and is composed of intercommunicating tubes of equal diameter and importance, these tubes giving rise irregularly to hydrocladia or to branches which bear hydrocladia. Branches, if present, bearing cauline hydrothecae and pinnately arranged hydrocladia. Hydrocladia unbranched, occasionally (as a secondary growth-form) arising independently from hydorhiza. Hydrotheca cup-shaped, with untoothed, though sometimes sinuated, margin.

**Type species:** Antennopsis scotiae Ritchie, 1907.

**KEY TO SPECIES**

1. Only one pair of lateral nematothecae
   - More than one pair of lateral nematothecae
   2.

2. Stem and branches giving rise directly to hydrocladia. Lateral nematothecae not reaching thecal margin
   - Stem and branches giving rise to sub-branches which bear hydrocladia. Lateral nematothecae overreaching thecal margin
   - *C. mortenseni*
   - *C. valdiviae*

3. Stem branching in lower region only. Branches very long. Lateral nematothecae with funnel-shaped distal chamber which is not emarginated
   - Branching irregular, colony short and bushy
   4.

4. Two pairs of lateral nematothecae, with wineglass-shaped distal chamber which is emarginated on mesial wall. One nematotheca below base of hydrotheca
   - *C. pannosa*
   - More than two pairs lateral nematothecae, with distal chamber cut away on two sides, giving a bivalve appearance. Three nematothecae below base of hydrotheca
   - *C. bellicosa*

**Corhiza bellicosa Millard, 1962**

Fig. 108A–D

*Corhiza bellicosa* Millard, 1962: 275, fig. 2A–E.

**Diagnosis.** Colony branching irregularly, reaching a maximum height of 50 mm.
Component tubes of stem and branches diverging from one another to form hydrocladia in an irregular fashion.

Hydrocladium with a proximal region consisting of a variable number of athecate internodes bearing a double series of nematothecae and terminated by transverse nodes, except for the last which is terminated by an oblique node, then thecate internodes only, separated by oblique nodes. Each thecate internode bearing one hydrotheca and 11–18 nematothecae, one median inferior, four pairs laterals and two to nine superior.

Hydrotheca deep-campanulate, almost completely adnate, deeper than wide, with no intrathecal septum, 0.2–0.3 mm in height (in centre) and 0.16–0.2 mm in marginal diameter. Margin even, at right angles to internode.

Nematothecae all large, two-chambered and movable; distal chamber emarginated on two sides forming a bivalve structure with a large acauline valve and a smaller acauline valve. Median inferior nematotheca seated well below hydrotheca and not reaching its base. Lateral nematothecae: first pair seated below hydrotheca at a slightly higher level than median inferior and just reaching base of hydrotheca; second pair borne on finger-shaped pedicels at sides of hydrotheca and not quite reaching thecal margin; third pair borne in the axils of the pedicels of the second pair; fourth pair borne at the sides of the hydrotheca between the pedicels of the second pair and the thecal margin, overtopping thecal margin. Superior nematothecae most commonly including two pairs, one pair seated behind free part of thecal wall and overtopping its margin, and the other at a higher level and more laterally placed, but number and arrangement very variable.

Gonothecae unknown.

*Distribution*. Endemic to South Africa. Type locality: Agulhas Bank, 33°3'S/27°55'E, 27 m.

*Distribution in South Africa*. Agulhas Bank, between Port Elizabeth and East London, 27–84 m, rare. 34/25 (s), 33/27 (s)

*Corhiza mortensi* Millard, 1968

Fig. 108E–H

*Corhiza mortensi* Millard, 1968: 274, fig. 5A–D.

*Diagnosis*. Colony branching in a subdichotomous manner, reaching a maximum height of 47 mm. Component tubes of stem and branches giving rise to hydrocladia irregularly and on all sides. Hydrocladia forming almost a right angle with stem.

Hydrocladium bearing hydrothecae on upper surface, consisting of up to two long athecate and anematothecate internodes terminated by straight nodes, one long athecate internode bearing two to four median nematothecae and terminated by a steeply oblique node, then alternate short thecate and longer athecate internodes terminated by straight and steeply oblique nodes respectively.
Corhiza bellicosa. A and B, hydrocladia in lateral and anterior view respectively; C, stems; D, lateral nematothecae.

Corhiza mortensi. E, stem; F, part of fascicled stem showing origins of hydrocladia; G and H, hydrothecae.

Scale: C and E in cm, the rest in mm/10.
Each thecate internode bearing one hydrotheca and four nematothecae, one median inferior, one pair laterals and one median superior. Each intermediate thecate internode bearing two median nematothecae.

Hydrotheca cup-shaped, with parallel walls flaring slightly at margin, adnate for about half adcauline height, with no intrathecal septum, 0,14–0,2 mm in adcauline height and 0,19–0,2 mm in marginal diameter. Margin even, forming an angle of 20–40° with internode.

Nematothecae all two-chambered and movable; distal chamber funnel-shaped, with adcauline wall lower than adcauline. Median inferior nematotheca not reaching base of hydrotheca. Lateral nematotheca borne on finger-shaped pedicel at side of hydrotheca and not quite reaching thecal margin. Median superior nematotheca borne behind free part of adcauline thecal wall and not reaching thecal margin.

Gonothecae unknown.

Distribution. Endemic to South Africa. Type locality: off Natal, 29°48,5′S/31°18′E, 219 m.

Distribution in South Africa. East London to Natal, 88–219 m, rare. 33/27 (s), 30/31 (d), 29/31 (d)

*Corhiza pannosa* Millard, 1962

Fig. 109F–K

*Corhiza pannosa* Millard, 1962: 278, fig. 3A–B, D–G.

Diagnosis. Colony capable of producing two growth-forms, one in which hydrocladia arise from an erect stem, and one in which hydrocladia arise independently from the hydrorhiza, the latter often epizooct on other hydroids. Stem branching irregularly, reaching a maximum height of 53 mm, its component tubes giving rise to hydrocladia in an irregular fashion.

Hydrocladium consisting of two or more thecate internodes bearing a double series of nematothecae and terminated by transverse nodes except for the last which is terminated by an oblique node, then normally thecate internodes terminated by oblique nodes. Each thecate internode bearing one hydrotheca and six to eight nematothecae, one median inferior, two pairs laterals and one to three median superior. In some regions the distal part of the thecate internode cut off by a transverse node taking with it the superior nematothecae.

Hydrotheca cup-shaped, with almost parallel sides, adnate for about half height, with no intrathecal septum, 0,3–0,5 mm in adcauline height and 0,3–0,4 mm in marginal diameter. Margin even, forming an angle of about 50° with internode.

Nematothecae all two-chambered and movable. Median inferior nematotheca seated below hydrotheca and not reaching its base; distal chamber scoop-shaped with very low adcauline wall. First pair lateral nematothecae seated on finger-shaped pedicels at sides of hydrotheca and not reaching thecal
margin; distal chamber wineglass-shaped and deeply emarginated on mesial side. Second pair lateral nematothecae seated in axils of pedicels of first pair; distal chamber wineglass-shaped, with mesial wall lower than lateral wall.

Gonothecae borne on the hydrocladia below the hydrothecae, singly or in pairs, male and female on the same colony, the male more distal than the female. Female gonotheca (described as male by Millard 1962) curved pear-shaped, with a broad distal and operculate aperture, bearing two large nematothecae near base; pedicel of one segment. Male gonotheca spindle-shaped, smaller than female, with bluntly pointed distal end; pedicel of one segment.

**Distribution.** Endemic to South Africa. Type locality: Agulhas Bank, 34°15'S/25°5'E, 11 m.

**Distribution in South Africa.** From Dassen Island to East London, 11–120 m. 33/18 (s), 34/18 (s), 34/23 (s), 34/24 (d), 34/25 (s), 32/28 (s)

*Corhiza scotiae* (Ritchie, 1907)

Fig. 109A–E

*Antennopsis scotiae* Ritchie, 1907b: 543, pl. 3 (fig. 3). Ritchie, 1909: 90, fig. 8.

*Corhiza scotiae*: Millard, 1962: 281, fig. 3C.

**Diagnosis.** Colony consisting of clusters of very long stems usually branching irregularly near the base, reaching a maximum height of 330 mm. Stem and branches thick and fascicled, the superficial tubes giving rise to hydrocladia irregularly and on all sides. Hydrocladia close-set and forming an acute angle with the stem.

Hydrocladium bearing hydrothecae on upper surface, consisting of two to six thecate internodes of variable length and bearing a variable number of nematothecae, these internodes terminated by straight nodes except for the last which is terminated by a steeply oblique node; then alternate thecate and athecate internodes terminated by straight and steeply oblique nodes respectively. No internodal septa. Each thecate internode with one hydrotheca and five nematothecae, one median inferior and two pairs laterals. Each intermediate thecate internode normally with one median nematotheca.

Hydrotheca cup-shaped, with parallel walls flaring slightly at margin, adnate for about half adcauline height, with no intrathecal septum, 0,16–0,25 mm in adcauline height and 0,17–0,25 mm in marginal diameter. Margin even, forming an angle of 40–60° with internode.

Nematothecae two-chambered, movable; distal chamber funnel-shaped, not emarginated but with slightly lower adcauline wall. Median inferior nematotheca not reaching base of hydrotheca. One pair lateral nematothecae borne on finger-shaped pedicels at sides of hydrotheca and not quite reaching thecal margin; the second pair smaller and seated in the axils of the pedicels of the first pair. Nematothecae also abundant on tubes of larger stems.

Gonothecae borne on hydrocladia below hydrothecae, male and female on
Fig. 109.

Corhiza scotiae. A, hydrocladium with male gonothecae; B, the two lateral nematothecae in medial (adcauline) view; C, part of fascicled stem showing origins of hydrocladia; D, hydrocladium with female gonothecae; E, colony.

Corhiza pannosa. F, hydrocladium; G, colony; H, hydrocladium with female gonothecae; J, the two lateral nematothecae in medial (adcauline) view; K, hydrocladium with male gonothecae.

Scale: E and G in cm, the rest in mm/10.
separate colonies. Female gonotheca compressed, ovate in broad view, with truncated, operculate distal end, bearing two large nematothecae near base; pedicel of one segment. Male gonotheca smaller, not compressed, elongate, slightly curved, with bluntly pointed distal end; pedicel of one segment.

Variation. The intermediate athecate internodes of the hydrocladia are usually very short and overlapped, sometimes completely, by the free part of the preceding hydrotheca, but rarely they are longer than the thecate internodes and may then bear two median nematothecae instead of one.

In young colonies solitary hydrocladia may occur, arising directly from the hydorhiza.

Distribution. Endemic to South Africa. Type locality: entrance to Saldanha Bay, 46 m.

Distribution in South Africa. From Saldanha Bay on the west coast to East London on the south coast, particularly common in False Bay, 18–120 m. 33/17 (s), 33/18 (s), 34/18 (s), 34/20 (s), 35/21 (d), 34/22 (s), 35/22 (d), 34/23 (s, d), 34/24 (d), 33/25 (s), 34/25 (s), 33/26 (s, d), 33/27 (s)

Corhiza valdiviae (Stechow, 1923)

Fig. 110

Heteroplon valdiviae Stechow, 1923a: 15.
Theocaulus(?) valdiviae Stechow, 1925a: 495, figs 42–43.
Halopteris valdiviae Millard, 1957: 228, fig. 14B. Millard, 1962: 290, fig. 41H–J.

Diagnosis. Colony branching irregularly, reaching 370 mm. Stem and branches stiff, thick and fascicled throughout and reaching 10 mm in diameter at base, the component tubes diverging irregularly and on all sides to form hydrocladia-bearing sub-branches (pinnae), without hydrothecae or nematothecae.

Sub-branches (pinnae) unfascicled or lightly fascicled; consisting of a short basal part and a long distal thecate and hydrocladia-bearing part, the two separated by an oblique hinge-joint; a second hinge-joint present after the first hydrotheca. Basal part with a variable number of transverse nodes and nematothecae. Distal part usually divided by oblique nodes into thecate internodes, each bearing one hydrotheca on anterior face. An opposite pair of hydrocladia arising by short apophyses at the sides of the first hydrotheca (i.e. between the hinge-joints) and sometimes the second hydrotheca; remaining hydrocladia alternate, one to each hydrotheca. Each internode with five nematothecae, one median inferior, one pair laterals and one pair minute superior behind hydrotheca; one or more extra nematothecae between hinge-joints.

Hydrocladium bearing hydrothecae on anterior surface, consisting of one very short athecate and anematothecate internode terminated by a slightly oblique node, one longer athecate internode bearing one median nematotheca and terminated by an oblique node, then up to nine thecate internodes terminated by oblique nodes. Towards tips of hydrocladia distal ends of internodes
sometimes cut off by transverse nodes to form intermediate athecate internodes. No internodal septa. Each thecate internode with four nematothecae, one median inferior, one pair laterals and one median superior.

Hydrotheca cup-shaped, deep, with depth normally greater than diameter, with straight walls, adnate for about $\frac{3}{4}$ height, with no intrathecal septum, 0.17–0.2 mm in abcauline height and 0.14–0.2 mm in marginal diameter. Margin sinuata, with high lateral walls and low adcauline wall, forming an angle of about 60° with internode.

Median inferior nematotheca well below hydrotheca and not reaching its base, two-chambered, possibly slightly movable; distal chamber scoop-shaped with low adcauline wall. Lateral nematotheca borne on a triangular pedicel, large, reaching well above thecal margin, two-chambered, movable; distal chamber funnel-shaped, not emarginated. Superior nematotheca seated behind free part of adcauline thecal wall and just reaching margin, minute, one-chambered, immovable.

Male and female gonothecae borne on same colony, the female on the sub-branches (pinnae) and the male on the hydrocladia, arising immediately below hydrotheca, with a pedicel of one segment. Female gonotheca large, flattened anterio-r-posteriorly, round to oval in front view with truncated distal end; with three to four large nematothecae on basal part. Male gonotheca elongate-pear-shaped, curved; with two large nematothecae on basal part.

Variation. The number of hinge-joints on the sub-branches may occasionally be as many as four, and the hydrocladia arising between them are always in opposite pairs. Beyond this level the normal oblique nodes may be indistinct at first, becoming more distinct in the distal regions. The paired hydrocladia on the first segments of the sub-branch may have three athecate internodes instead of two at the base, of which the second and third both bear a median nematotheca.

Remarks. Due to the characteristic stem, it is necessary to transfer this species from Halopteris to Corhiza. The appearance of the colony is very similar to C. scotiae, differing from it in the fact that the diverging tubes of the stem form sub-branches instead of hydrocladia.

Distribution. Endemic to South Africa. Type locality: Plettenberg Bay, 100 m.

Distribution in South Africa. Sparsely distributed round the west and south coasts of the Cape Province, with one record from Moçambique, 4–201 m. 30/15 (d), 34/18 (s), 34/22 (s), 34/23 (s, d), 33/25 (s), 33/26 (s), 32/28 (s), 24/35 (d)

Genus Gattya Allman, 1886

Syn Paragattya Warren, 1908.

Diagnosis. An erect stem present, which may be branched or unbranched, fascicled or unfascicled; if fascicled, with one main axial tube which bears hydrocladia or branches. Hydrocladia pinnately arranged and borne on stem or its branches, or (as a secondary growth-form) independently on hydrorhiza.
Corhiza valdiviae. A, stem; B, hydrotheca; C, anterior view of sub-branch (pinna), showing cauline hydrothecae and origins of hydrocladia; D, male gonothecae; E, female gonotheca.

Scale: A in cm, the rest in mm/10.
Hydrocladia-bearing stem or branch with cauline hydrothecae. Hydrocladia normally unbranched. Hydrotheca cup-shaped, with toothed margin.

Type species: *Gattya humilis* Allman, 1886.

**KEY TO SOUTH AFRICAN SPECIES**

1. Hydrocladia confined to branches (pinnae), which arise from a long, lightly fascicled stem. Hydrotheca with straight abcauline wall. ... G. heurtelii
   - Hydrocladia borne directly on short, unfascicled and unbranched stem, or arising independently from hydrothiza. Abcauline wall of hydrotheca not straight. ... 2

2. Hydrotheca with four distinct marginal teeth, one adcauline, one abcauline and two lateral... G. humilis
   - Hydrotheca with two distinct marginal teeth, one adcauline and one abcauline, lateral edges sinuate... G. multithecata

3. Abcauline marginal tooth of hydrotheca curved inwards. Stem and hydrocladia usually heteromeros... G. conspecta
   - Abcauline marginal tooth of hydrotheca more or less straight. Stem and hydrocladia usually homomeros... G. conspecta

*Gattya conspecta* (Billard, 1907)

Fig. 111A–C

*Plumularia conspecta* Billard, 1907b: 81, fig. 3. Billard, 1907a: 362, fig. 11.

**Diagnosis.** Stem unfascicled, unbranched, reaching 11 mm in height, consisting of a short basal part and a long distal hydrocladia-bearing part, the two separated by an oblique hinge-joint. Basal part with a few transverse nodes and nematothecae. Distal part divided into thecate internodes by oblique nodes. The first internode longer and broader than the rest, terminated by a more distinct node and bearing one pair of opposite hydrocladia; the second internode also bearing a pair of opposite hydrocladia; remaining internodes bearing alternate hydrocladia, one to each. Each internode with one cauline hydrotheca and six to eight nematothecae, one median inferior, one pair laterals, one median superior and one or two pairs superior. Hydrocladal apophysis arising from process supporting lateral nematotheca. The two rows of hydrocladia not in one plane but set on the anterior surface of the stem.

Hydrocladium bearing hydrothecae on anterior surface, consisting of one short athecate and anematothecate internode terminated by a straight node, one short athecate internode bearing one median nematotheca and terminated by an oblique node, then up to six long thecate internodes terminated by oblique nodes. Thecate internodes without septa, with four to six nematothecae, one median inferior, one pair laterals, one median superior and usually one pair superior.

Hydrotheca cup-shaped and indented in middle of abcauline wall which is markedly thickened, expanding to margin, adnate for a little over half adcauline length, with no intrathecal septum, 0,16–0,20 mm in abcauline depth and 0,19–0,2 mm in marginal diameter. Margin forming an angle of about 40° with internode, with one strong abcauline tooth, one smaller abcauline tooth.
and sinuated margins which are deeply indented next to the abcauline tooth.

Median inferior nematotheca borne immediately below hydrotheca and overreaching thecal base; two-chambered, immovable, distal chamber scoopshaped with no abcauline wall. Lateral nematotheca borne on long finger-shaped pedicel which reaches to level of thecal margin, two-chambered, movable; distal chamber beaker-shaped and emarginated right to the base on medial side. Median superior nematotheca situated behind free part of abcauline thecal wall and usually pressed close against it, not reaching thecal margin, two-chambered, with very short basal chamber and beaker-shaped distal chamber which is deeply emarginated on adthecal side. Paired superior nematothecae seated above median superior; those of hydrocladium smaller than median superior, curved away from hydrotheca, situated behind free part of thecal wall; those of stem larger, less curved and sometimes overreaching thecal margin; two-chambered, movable.

Gonotheca (described here for the first time) borne on stem below hydrotheca, whelk-shaped, with oblique aperture directed away from stem, with up to five nematothecae on basal part, sex unknown.

Variation. Very rarely the distal part of an internode may be cut off by a transverse node to form a single athecate intermediate internode. This may occur on the stem or on the hydrocladia and the athecate internode takes with it a pair of superior nematothecae. The last internode of a hydrocladium always terminates at the level of the transverse node and lacks paired superior nematothecae.

Distribution outside South Africa. Madagascar. Type locality: Fort Dauphin.

Distribution in South Africa. One record only, off Scottburgh, Natal in 6–12 m.

Gattyia heurteli (Billard, 1907)

![Figure 111J-L](image)

Plumularia Heurteli Billard, 1907a: 360, figs 9–10.
Plumularia quadridentata Jarvis, 1922: 348, p. 26 (fig. 22).
Paragattyia heurteli: Millard, 1958: 208, fig. 10E.

Diagnosis. Main stem lightly fascicled at base, long and flexuous, reaching 180 mm, branching sparsely and irregularly. Axial tube of stem and branches divided into internodes of irregular length by transverse nodes, giving rise to alternate sub-branches (pinnae) at irregular intervals, without hydrothecae or nematothecae.

Sub-branches (pinnae) unfascicled, consisting of a short basal part and a long distal and hydrocladia-bearing part, the two separated by an oblique hinge-joint. Basal part bearing 1–3 median nematothecae, often not sharply demarcated from apophysis of stem. Distal part divided into internodes by oblique nodes. The first internode thicker than the rest, terminated by a more distinct node and bearing one pair of opposite hydrocladia; remaining internodes bearing alternate hydrocladia, one to each. Each internode of distal part with one cauline
Fig. 111.

Gattyia conspecta. A, stem in anterior view, including first internode and hinge-joint; B, hydrocladium; C, gonotheca.

Gattyia hamulis. D and E, male and female gonophores respectively, the latter with planula; F, pinnate stem in anterior view; G, hydrothecae; H, colony with pinnate and simple stems.

Gattyia heurtelii. J, colony; K, anterior view of sub-branch (pinna); L, hydrothecae.

Scale: H and J in cm, the rest in mm/10.
hydrotheca and four nematotheca, one median inferior, one pair laterals and one median superior. Hydrocladial apophysis arising from process supporting lateral nematotheca. The two rows of hydrocladia not in one plane but set on the anterior surface of the pinna.

Hydrocladium bearing hydrotheca on anterior surface, consisting of one short athecate internode, then up to five thecate internodes terminated by oblique nodes. Thecate internodes without internodal septa, with four nematotheca, one median inferior, one pair laterals and one median superior.

Hydrotheca deep cup-shaped, expanding slightly to margin, adnate for over half adcauline length, adcauline wall straight, with no intrathecal septum, 0.12–0.3 mm in adcauline depth and 0.16–0.2 mm in marginal diameter. Margin forming an angle of 50–60° with internode, with four marginal teeth, one median adcauline, one median adcauline and one pair laterals, the lateral teeth closer to the adcauline side.

Median inferior nematotheca well below hydrotheca, with margin not, or only just, reaching thecal base; two-chambered, but basal chamber small, immovable and not distinctly demarcated from internode, distal chamber scoop-shaped, with no adcauline wall. Lateral nematotheca borne on a finger-shaped pedicel, overtopping thecal margin, two-chambered, movable; distal chamber flattened and deeply cut away at the narrow ends giving a bivalved appearance. Median superior nematotheca seated behind free part of adcauline thecal wall and not reaching margin, one-chambered, hook-shaped, immovable. Median nematotheca on basal part of pinna similar to median inferior, but movable and with longer basal chamber.

Gonophores unknown.

Variation. The two rows of sub-branches (pinnae) may be in one plane on the stem, or the whole may be twisted in a loose spiral giving an irregular effect. The basal part of the pinna may have 1–4 indistinct nodes, the last internode being the longest and bearing the nematotheca.

Distribution outside South Africa. Tropical East Africa. Type locality: Macalonga in Moçambique, 22 m.

Distribution in South Africa. Natal and Moçambique, 22–66 m, with one doubtful record from Cape Town. ?33/18, 30/30 (s), 29/31 (s), 28/32 (s), 25/33 (s), 24/34 (s)

Gattya humilis Allman, 1886

Fig. 111D–H

Paragattya intermedia Warren, 1908: 323, fig. 16, pl. 47 (fig. 27).

Diagnosis. Hydrorhiza creeping, usually on weed. Colony capable of producing two growth-forms, one in which hydrocladia arise from an erect stem, and one in which hydrocladia arise independently from the hydrorhiza. Stem unfascicled, unbranched, reaching 30 mm in height, consisting of a short basal part and a
long distal and hydrocladia-bearing part, the two separated by an oblique hinge-joint. Basal part with 1–4 transverse nodes and sometimes one median nematotheca. Distal part divided into internodes by oblique nodes. The first internode thicker than the rest, terminated by a more distinct node and bearing one pair of opposite hydrocladia; remaining internodes bearing alternate hydrocladia, one to each. Each internode with one caulline hydrotheca and four nematothecae, one median inferior, one pair laterals and one median superior. Hydrocladial apophysis arising from process supporting lateral nematotheca. The two rows of hydrocladia not in one plane but set on the anterior surface of the stem.

Hydrocladium bearing hydrothecae on anterior surface, consisting of one or two short athecate internodes, then up to three thecate internodes terminated by oblique nodes. Thecate internodes without septa, with four nematothecae, one median inferior, one pair laterals and one median superior.

Hydrotheca cup-shaped and deep, expanding to margin, adnate for about half adcaulline length, abcaulline wall with a slight, but distinct, double curvature, with no intrathecal septum, 0.19–0.3 mm in abcaulline depth and 0.18–0.3 mm in marginal diameter. Margin forming an angle of 50–60° with internode, with four marginal teeth, one median adcaulline, one median abcaulline and one pair laterals, the lateral teeth closer to the abcaulline side.

Median inferior nematotheca immediately below hydrotheca, with margin overreaching thecal base; two-chambered, but basal chamber small and immovable, distal chamber scoop-shaped, with no adcaulline wall. Lateral nematotheca borne on a finger-shaped pedicel, overtopping thecal margin, two-chambered, movable; distal chamber flattened, and deeply cut away at the narrow ends giving a bivalved appearance. Median superior nematotheca seated behind free part of adcaulline thecal wall and not reaching margin, one-chambered, similar in shape to the laterals.

Gonotheca borne on stem, and rarely on hydrocladium, immediately below hydrotheca and on one side, pear-shaped, with two large nematothecae on basal part, male and female on same stem but male more distal than female. Female truncated distally and with a large terminal operculate aperture, containing one egg which develops into a planula in situ. Male rounded distally, with a small apical pore.

Variation. The species occurs commonly on coralline algae, but has also been found on a sponge and on the crab, Dehaamius dentatus (M. Edw.).

Examples have been seen in which the hydrocladia branch in a similar way to the stem. Other minor variations include the occurrence of intermediate athecate internodes in the hydrocladia (Stechow 1925a), and a secondary point to the lateral marginal tooth of the hydrotheca (Warren 1908).

Distribution. Endemic to South Africa. Type locality: Port Elizabeth.

Distribution in South Africa. Northern South West Africa on the west to Natal,
littoral to 70 m. [19/12 (l)], 32/18 (s), 33/17 (l), 33/18 (l, s), 34/18 (l, s), 34/22 (s), 34/23, 33/25, 34/25 (s), 33/26 (s), 33/27 (l, s), 32/28 (s), 31/29 (l), 31/30 (l), 30/30 (l)

*Gattya multithecata* (Jarvis, 1922)

Fig. 112A–B

*Plumularia multithecata* Jarvis, 1922: 346, pl. 25 (fig. 19).

*Diagnosis.* Stem unfascicled, unbranched, reaching 14 mm in height, consisting of a short basal part and a long distal hydrocladia-bearing part, the two separated by an oblique hinge-joint. Basal part with a few transverse nodes and scattered nematothecae. Distal part divided by oblique nodes into thecate internodes, of which the terminal part is often cut off by a transverse node to form an intermediate atethecate internode. The first thecate internode longer and broader than the rest and bearing one pair of opposite hydrocladia; the second thecate internode also bearing one pair of opposite hydrocladia; remaining thecate internodes bearing alternate hydrocladia, one to each. Five to nine nematothecae to each hydrotheca, one median inferior, one pair laterals, and one to three pairs of superior; the last pair of superior seated on the following atethecate internode when this is present. Hydrocladal apophysis arising from process supporting lateral nematotheca. The two rows of hydrocladia not in one plane but set on the anterior surface of the stem.

Hydrocladium bearing hydrothecae on anterior surface, consisting of one short atethecate and anematothecate internode terminated by a straight node, one short atethecate internode bearing one median nematotheca and terminated by an oblique node, then usually alternate long thecate internodes terminated by straight nodes and short atethecate intermediate internodes terminated by oblique nodes. Up to nine hydrothecae to a hydrocladium. Thetheate internodes without septa, with four nematothecae, one median inferior, one pair laterals and one median superior. Atethecate intermediate internodes with one pair of nematothecae.

Hydrotheca cup-shaped and deep, expanding to margin, adnate for a little over half adcauline length, with no intrathecal septum, 0.2–0.3 mm in adcauline depth and 0.18–0.2 mm in marginal diameter. Margin forming an angle of about 40° with internode, with one strong inturned adcauline tooth, one smaller adcauline tooth and sinuated lateral margins.

Median inferior nematotheca borne immediately below hydrotheca and overreaching thecal base; two-chambered, immovable, distal chamber scoop-shaped with no adcauline wall. Lateral nematotheca borne on long, curved, pedicel which reaches to level of thecal margin, two-chambered, movable; distal chamber beaker-shaped; the whole emarginated to base of proximal chamber on mesial side. Median superior nematotheca situated behind free part of adcauline thecal wall, minute, two-chambered, with very short basal chamber. Paired superior nematothecae of stem and nematothecae of atethecate
internodes larger than median superior, curved, two-chambered, movable.
   Gonothecae unknown.

Variation. The presence or absence of athecate intermediate internodes is
variable within the single colony known from the country. They are often present
on the stem, almost invariably on the hydrocladia. They are reported as present
in the type material.

Distribution outside South Africa. Tropical East Africa. Type localities: Zanzibar
and Wasin.

Distribution in South Africa. One record only, off Scottburgh, Natal in 6–12 m.
30/30 (s)

Genus Halopteris Allman, 1877

   Acladia Marktaner-Turneretscher, 1890.
   Theocanulus Bale, 1915.

Diagnosis. An erect stem present, usually (always, in South African species)
unfascicled and unbranched, if fascicled with one main axial tube, usually with
hinge-joints in basal region, bearing pinnately arranged hydrocladia and cauline
hydrothecae. Hydrocladia alternate or in opposite pairs, but usually with at
least the first one or two pairs opposite, sometimes (as a secondary growth-form)
arising independently from hydorhiza, normally unbranched. Hydrotheca
cup-shaped, with untoothed margin.

Type species: Halopteris carinata Allman, 1877.

KEY TO SPECIES
(For simple forms see also under Antennella, p. 330)

1. Stem heteromerous, with alternate thecate, hydrocladiate internodes and athecate,
   ahydrocladiate internodes                   ... ... ... ... ... ... ... ... ... ... ... ... ... ... 2
   Stem normally homomerous, with all internodes thecate and hydrocladiate; may be
   unsegmented ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... 3

2. Hydrotheca with even margin; free part of adcauline wall concave   H. pseudoconstricta
   Hydrotheca raised into a beak-like process on adcauline edge; free part of adcauline
   wall straight ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... H. rostrata

3. All hydrocladia in opposite pairs. Lateral nematothecae one-chambered   H. gemellipara
   Hydrocladia alternate (except for the first one or two pairs which may be opposite).
   Lateral nematothecae two-chambered ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... 4

4. Lateral nematotheca with distal chamber wineglass-shaped and deeply emarginated
   on mesial side ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... H. glutinosa
   Lateral nematotheca with distal chamber funnel-shaped and not deeply emarginated,
   though the mesial edge may be lower than the lateral edge ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... 5

5. No superior nematotheca on hydrocladiate internodes ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... H. tuba
   Two superior nematotheca on hydrocladiate internodes, one behind hydrotheca and
   one above it, the latter sometimes cut off on a separate athecate internode H. polymorpha
Fig. 112.

*Gattyia multithecata*. A, stem in anterior view; B, hydrothecae.

*Halopteris gemellipara*. C, hydrothecae; D, stem in anterior view; E, lateral nematotheca; F, stem.

*Halopteris polymorpha*. G and H, lateral nematothecae; J, stem; K, hydrothecae; L, stem in anterior view.

Scale: F and J in cm, the rest in mm/10.
Halopteris gemellipara Millard, 1962

Fig. 112C–F

*Halopteris gemellipara* Millard, 1962: 283, fig. 4A–F.

**Diagnosis.** Stem reaching 60 mm in height, consisting of an athecate basal part and a distal thecate and hydrocladia-bearing part. No hinge-joints. Basal part with a variable number of transverse nodes and median nematotheca. Distal part divided into long thecate internodes by oblique nodes. Cauline hydrothecae in one row on front of stem, one on the proximal part of each internode. Hydrocladia in opposite pairs, one pair to each internode, arising from the sides of the hydrothecae by short apophyses. Each internode with five to seven nematothecae, one median inferior, one pair laterals and two to four median superior.

Hydrocladium bearing hydrothecae on upper surface, consisting of one short athecate internode bearing one median nematotheca and then up to 11 thecate internodes terminated by oblique nodes. No internodal septa. Each thecate internode with three to four nematothecae, one median inferior, one pair laterals, and sometimes one median superior.

Hydrotheca cup-shaped, adnate for $\frac{1}{2} - \frac{3}{4}$ height (usually about $\frac{2}{3}$), with parallel walls flaring slightly to margin, with no intrathecal septum, 0.2–0.5 mm in abcauline height and 0.2–0.3 mm in marginal diameter. Margin forming an angle of 50–70° with internode.

Median inferior nematotheca not reaching base of hydrotheca, two-chambered, immovable; basal chamber smaller than distal and not distinctly demarcated from internode; distal chamber scoop-shaped, with no abcauline wall. Lateral nematotheca borne on low protuberance of internode, not reaching thecal margin, minute, immovable, one-chambered, with emarginated mesial wall. Median superior nematotheca, when present, seated above level of thecal margin, similar to median inferior but with more convex abcauline wall, those of stem larger than those of hydrocladium.

Gonothecae unknown.

**Variation.** Occasionally the distal end of a thecate internode may be cut off by a transverse node to form an intermediate athecate internode. This is more common near the distal ends of the hydrocladia. One stem has been seen bearing a pair of hydrocladia on the posterior surface in addition to those on the anterior surface.

The hydrotheca may have a diameter more or less equal to the height and be set at a comparatively wide angle to the internode, or it may have a diameter of about half the height and be set almost parallel to the internode.

**Distribution.** Endemic to South Africa. Type locality: Agulhas Bank, 33°54′S/26°51′E, 120 m.

**Distribution in South Africa.** South-east coast, from Port Elizabeth to Durban, 49–120 m. 34/25 (s), 33/26 (d), 33/27 (s), 32/28 (s), 29/31 (s)
Halopteris glutinosa (Lamouroux, 1816)

Fig. 113

Aglaophenia Glutinosa Lamouroux, 1816: 171.
Heteroplum pluma Allman, 1883: 32, pl. 8 (figs 1–3).
Plumularia glutinosa: Billard, 1910: 36, fig. 16.
Plumularia alternata: Jarvis, 1922: 345, pl. 25 (fig. 16).
Plumularia (Heteroplum) glutinosa: Stechow, 1925a: 502.

Diagnosis. Stem capable of reaching 180 mm though more commonly 10–40 mm, consisting of an athecate basal part and a distal thecate and hydrocladia-bearing part, the two sometimes separated by an oblique hinge-joint, a second hinge-joint sometimes present after the first hydrotheca. Basal part with a variable number of transverse nodes and nematothecae. Distal part usually divided into thecate internodes by oblique nodes. Cauline hydrothecae usually in one row on front of stem, one to an internode. One or two pairs of opposite hydrocladia arising by short apophyses at the sides of the first one or two hydrothecae; remaining hydrocladia alternate, one to each hydrotheca. At least four nematothecae to each internode, one median inferior, one pair laterals, one median superior; one to three extra pairs of laterals and one to two extra median superior sometimes present.

Hydrocladium bearing hydrothecae obliquely (intermediate between upper and anterior surface), consisting of one very short thecate and anematothecate internode terminated by a slightly oblique node, one longer thecate internode bearing one median nematotheca and terminated by a steeply oblique node, and then up to 15 thecate internodes terminated by oblique nodes. No internodal septa. Each thecate internode with three to six nematothecae, one median inferior, one pair laterals, up to two, or rarely three, median superior.

Hydrotheca cup-shaped, adnate for $\frac{1}{2}$–$\frac{3}{4}$ height, with walls straight or flaring slightly to margin, with no intrathecal septum, 0.15–0.3 mm in abcauline height and 0.19–0.4 mm in marginal diameter. Margin forming an angle of 30–60° with internode.

Median inferior nematotheca not, or only just, reaching base of hydrotheca, two-chambered, with basal chamber immovable and not sharply demarced from internode, distal chamber scoop-shaped, with no adcauline wall. Lateral nematotheca borne on finger-shaped pedicel, not quite reaching thecal margin, two-chambered, movable; distal chamber wineglass-shaped and deeply emarginated on mesial side. Superior nematotheca seated behind free part of adcauline thecal wall, variable in structure and size, one- or two-chambered.

Male and female gonothecae borne on same colony, the female on the stem and the male on the hydrocladia, arising immediately below hydrotheca. Female gonotheca large, flattened antero-posteriorly, elongate-oval in front view, with broad distal aperture; with two to five large nematothecae on basal part; pedicel of one segment. Male gonotheca spindle-shaped.

Variation. This is one of the most variable species of Halopterinae, and its
Halopteris glutinosa. A, stem in anterior view; B, lateral nematotheca; C, stems; D, female gonotheeca; E, male gonotheeca; F, hydrocladium.

Scale: C in cm, the rest in mm/10.
most useful diagnostic character is the structure and size of the lateral nematotheca.

The stem varies greatly in length and thickness, and in the older, thicker stems nodes may be absent and the hydrothecae may be displaced alternately to left and right. In some stems nodes occur after every two hydrothecae. Sometimes extra hinge-joints, probably due to regeneration after injury, occur in the basal part of the stem.

In the distal region of both stem and hydrocladia the distal ends of the internodes may be cut off by transverse nodes above the level of the hydrotheca to form intermediate athecate internodes. These may carry one median nematotheca. Several examples of branched hydrocladia have been observed.

The hydrothecae are also extremely variable in size, though their shape and proportion remains constant.

Distribution outside South Africa. Bass Strait, South Australia; Gulf of Aqaba; tropical East Africa. Type locality: ‘Mers des Indes et de l’Australasia’.

Distribution in South Africa. Fairly common on south and east coasts, from off Still Bay to Inhaca in Moçambique, littoral to 411 m. 34/21, 35/21 (d), 34/22 (s), 34/24 (d), 33/25 (s), 34/25 (s, d), 33/26 (s), 33/27 (s), 32/28 (s), 33/28 (s), 31/29 (s), 30/30 (s), 29/31 (l, s, d), 28/32 (s, d), 26/32 (l, s)

Halopteris polymorpha (Billard, 1913)

Fig. 112G–L


Diagnosis. Stem reaching 82 mm in height, consisting of an athecate basal part and a distal thecate and hydrocladia-bearing part, the two separated by an oblique hinge-joint, a second hinge-joint usually present after the first hydrotheca. Basal part with a variable number of transverse nodes and nematothecae. Distal part divided into thecate internodes by oblique nodes. Cauline hydrothecae in one row on front of stem, one to each internode. Hydrocladia alternate, one arising by a short apophysis at the side of each hydrotheca; usually a pair of opposite hydrocladia on the first and second thecate internodes. At least five nematothecae to each internode one median inferior, one pair laterals and two median superior; one or more extra pairs often present above level of hydrotheca.

Hydrocladium bearing hydrothecae on anterior surface, consisting of one short athecate and anematothecate internode terminated by a straight node, one long athecate internode bearing one median nematotheca and terminated by a steeply oblique node, then up to nine thecate internodes terminated by oblique nodes. No internodal septa. Each thecate internode with five nematothecae, one median inferior, one pair laterals and one or two median superior. The distal part of the thecate internode often cut off as a separate athecate
intermediate internode, carrying with it the second median superior nematotheca.

Hydrotheca cup-shaped, adnate for $\frac{1}{3}$–$\frac{2}{3}$ height, with straight walls widening slightly to margin, with no intrathecal septum, 0.17–0.3 mm in adcauline height and 0.18–0.3 mm in marginal diameter. Margin forming an angle of about 50° with internode.

Median inferior nematotheca not, or only just, reaching base of hydrotheca, two-chambered, immovable; distal chamber scoop-shaped, with no adcauline wall. Lateral nematotheca borne on finger-shaped pedicel, reaching approximately to thecal margin or above it, two-chambered, movable; distal chamber funnel-shaped, with lower mesial wall. First superior nematotheca behind free part of adcauline thecal wall, minute, one-chambered, immovable. Second superior nematotheca seated behind or above thecal margin, two-chambered, movable; distal chamber scoop-shaped with low adcauline wall.

Gonothecae arising immediately below hydrothecae, with curved pedicel of one segment. Female large, flattened, pear-shaped in broad view, bearing two nematothecae, containing one egg. Male smaller, curved-oval, bearing one nematotheca.

**Variation.** Billard has commented on the variability of this species and this is substantiated by the few samples known from South Africa. The most obvious variation is the presence or absence of a node separating off an intermediate internode from the distal end of a thecate internode. Normally such nodes occur only in the hydrocladia, but rarely also in the distal end of the stem. The first thecate internode of the hydrocladium may not be distinctly demarcated from the second, as in Vervoort's material. Several branching hydrocladia have been seen. Up to five pairs of opposite hydrocladia may occur at base of stem.

The proportions of the hydrothecae vary, sometimes they are deeper than wide, and sometimes wider than deep, both shapes illustrated by Billard (fig. 14) occurring. The first superior nematotheca behind the thecal wall is sometimes absent on the hydrocladia.

**Distribution outside South Africa.** Indian Ocean: Borneo Bank and south of Island of Rotti (type locality), East Indies, Seychelles, Red Sea. Pacific Ocean: New Caledonia.

**Distribution in South Africa.** Natal to Moçambique, littoral to 495 m. 29/31 (s, d), 29/32 (s), 28/32 (s), 27/32 (d), 26/32, 25/32, 21/35

*Halopteris pseudoconstricta* sp. nov.

Fig. 114D–G


*non Halopteris constricta* Totton, 1930: 217, fig. 56a. Ralph 1961b: 43, fig. 6a–e.

**Type.** Designated holotype: SAM–H542: material from intertidal region at
Melkbostrand, Table Bay, collected 17/11/67. Numerous pinnate stems bearing female gonophores and reaching a maximum height of 7 mm. Simple forms also present and a few pinnate stems with branched hydrocladia.

**Diagnosis.** Colony capable of producing two growth-forms, one in which hydrocladia arise from an erect stem, and one in which hydrocladia arise independently from the hydrohriza. Stem reaching 9 mm in height, consisting of a short basal part and a long distal and hydrocladia-bearing part, the two separated by an oblique hinge-joint. Basal part with a variable number of transverse nodes and median nematothecae. Distal part divided into alternate thecate and athecate internodes terminated by straight and steeply oblique nodes respectively. Hydrocladia alternate, one to each thecate internode, with sometimes an opposite pair on the first and second thecate internodes, arising from the pedicels of the lateral nematothecae. Thecate internodes with three or four nematothecae, one median inferior, one pair laterals and sometimes one median superior; athecate internodes with one or two median nematothecae.

Hydrocladium bearing up to six hydrothecae on anterior surface, consisting of one or two short athecate and anematothecate internodes terminated by slightly oblique nodes, one longer athecate internode bearing one or two median nematothecae and terminated by a steeply oblique node, and then alternate long thecate and short athecate internodes terminated by straight and oblique nodes respectively. No internodal septa. Each thecate internode with three nematothecae, one median inferior and one pair laterals. Each athecate internode with one, and sometimes two median nematothecae.

Hydrotheca cup-shaped, adnate for \(\frac{1}{2} - \frac{3}{4}\) height, with straight abcauline wall and with distinct concavity in free part of abcauline wall, with no intrathecal septum, 0.14–0.20 mm in abcauline height and 0.09–0.17 mm in marginal diameter. Margin forming an angle of 40–60° with internode.

Median inferior nematotheca not reaching base of hydrotheca, two-chambered, with basal chamber immovable and not distinctly demarcated from internode, distal chamber scoop-shaped, with low abcauline wall. Lateral nematotheca borne on a short papilla-shaped pedicel, not quite reaching thecal margin, two-chambered, movable; distal chamber funnel-shaped, not emarginated but with a lower mesial wall. Median superior nematotheca, when present, seated behind free part of abcauline thecal wall, this and the nematotheca on athecate intermediate internodes two-chambered, movable.

Female gonothecae borne on stem or hydrocladia immediately below hydrothecae singly or in pairs, laterally compressed, curved-pear-shaped in side view, with broad distal aperture facing towards stem, containing one egg on side of blastostyle which develops into a planula in situ; with two large nematothecae on basal part; reaching 0.66 mm in length and 0.40 mm in maximum diameter. Pedicel of one segment. Male gonotheca unknown.

**Variation.** In addition to the variations included in the diagnosis, pinnate stems have been seen with hydrocladia which branch in a similar manner to the stem.
The margin of the hydrotheca is sometimes thickened on the abcauline side, and may also be narrowed.

In some cases the distal part of a thecate hydrocladal internode may be cut off as an extra thecate internode.

Remarks. This material was previously assigned to Halopteris constricta, a species first described by Totton from infertile material from New Zealand. The female gonophores were described by Ralph (1961b). These are curved in a sigmoid manner and have their apertures directed away from the stem. At this stage a paper was already in the press by the present author describing female gonophores in the South African material. These are pear-shaped and have their apertures directed towards the stem. On the basis of this difference in the gonophores it is now necessary to create a new species for the South African material. There is little to distinguish the trophosomes of the two species, but neither simple forms nor branched hydrocladia have been observed in the New Zealand material.

Distribution outside South Africa. Angola and Vema Seamount (South Atlantic).

Distribution in South Africa. Table Bay to Transkei coast, littoral to 19 m. 33/18 (l), 34/18 (l, s), 34/22 (s), 34/25 (s), 31/29 (l)

_Halopteris rostrata_ sp. nov.

Fig. 114A–C

Material. The holotype, SAM H543, consists of a colony of 11 complete stems and a number of damaged ones growing over the skeleton of an antipatharian coral. Position: off Natal, 29°11’S/32°02’E, 70 m, 30/7/1964.

Description. Hydrorhiza creeping and branching, giving rise to erect stems. Stems unfascielced, unbranched, the tallest 11 mm in height, with a short basal part devoid of hydrothecae and hydrocladia but sometimes with one or two nematothecae, and a longer distal part bearing hydrocladia and hydrothecae. No hinge-joints. Distal part divided into regularly alternate long thecate and short thecate internodes terminated by straight and oblique nodes respectively, the first thecate internode bearing a pair of opposite hydrocladia arising from the sides of the hydrotheca, remaining hydrocladia alternate, one from the side of each hydrotheca alternately on the left and the right. Stem geniculate in terminal part. Hydrothecae in one row on front of stem, but with their apertures directed alternately to left and right (to the same side as the corresponding hydrocladium). Each thecate internode with three nematothecae, one median inferior and one pair laterals, of which one is in the axil of the hydrocladium. Each thecate internode with one median nematotheca.

Hydrocladium bearing one to five hydrothecae on anterior face, with one short thecate and anematothecate internode terminated by a slightly oblique node, then alternate short thecate and long thecate internodes terminated by oblique and straight nodes respectively. Each thecate internode with one hydro-
Fig. 114.

*Halopteris rostrata* sp. nov., all from holotype. A, hydrothecae; B, lateral nematotheca in medial view; C, stem in anterior view (the basal pair of hydrocladia broken off).

*Halopteris pseudoconstricta* sp. nov. D, hydrocladium; E, stem in anterior view; F, lateral nematotheca; G, female gonothecae.

Scale in mm/10.
theca and three nematothecae, one median inferior and one pair laterals. Each athecate internode, other than the first, with one median nematotheca.

Hydrotheca cup-shaped in side view, with straight walls widening to margin, more or less conical in anterior view, adnate for about half height and with free part of adcauline wall overlapping subsequent athecate internode. Margin forming an angle of 50–60° with internode, more or less even on posterior and lateral edges, but rising into a beak-like lobe on anterior (adcauline) edge; adcauline edge sometimes thickened.

Median inferior nematotheca seated below hydrotheca and reaching approximately to the level of its base, though sometimes a little above or below, two-chambered, immovable; basal chamber small and inconspicuous; distal chamber scoop-shaped, with no adcauline wall. Lateral nematotheca seated on a short, rounded process applied to the lateral wall of the hydrotheca, just, or not quite, reaching thecal margin, two-chambered, movable; basal chamber shorter than distal; distal chamber wineglass-shaped, with very deep emargination on mesial surface. Lateral nematothecae of stem shorter than those on hydrocladia and not reaching thecal margin. Median nematotheca of athecate internode two-chambered, movable, often obscured by adcauline wall of hydrotheca, basal and distal chamber of approximately equal size; distal chamber scoop-shaped, with low adcauline wall.

Gonothecae absent.

Measurements (mm)

- Hydrocladium, thecate internode, length
- Athecate internode other than first, length
- Hydrotheca, depth adcauline diameter at margin
- Free part adcauline wall/adcauline height
- Lateral nematotheca, length

0.29–0.38
0.12–0.17
0.17–0.29
0.23–0.34
0.31–0.59
0.09–0.12

Remarks. The shape of the hydrotheca is reminiscent of that in *H. carinata* Allman, 1877, *Gattyia multithecata* (Jarvis, 1922) and *Gattyia trebileocki* Watson, 1973. All of these have lateral nematothecae overtopping the thecal margin and seated on long pedicels; that of *H. carinata* is one-chambered. There are also other differences in the complement of nematothecae and the margin of the hydrotheca of these three species.

*H. rostrata*, with its lobed thecal margin, shows tendencies towards the genus *Gattyia*.

Distribution. Endemic to South Africa.

*Distribution in South Africa*, off Natal, 70–100 m. 29/31 (s), 29/32 (s), 28/32 (d)

**Halopteris tuba** (Kirchenpauer, 1876)

Fig. 115

*Plumularia tuba* Kirchenpauer, 1876: 44, pl. 1 (fig. 2), pl. 4 (figs 2–2d).
*Heteroplon jaederholmi* Stechow, 1912: 366, figs F–G.
*Plumularia (Heteroplon) africana*: Stechow, 1925a: 500, figs 44–45.
*Halopteris tuba*: Millard, 1962: 286, fig. 5.
Diagnosis. Stem reaching 220 mm in height, consisting of an athecate basal part and a distal thecate and hydrocladia-bearing part, the two usually separated by an oblique hinge-joint, a second hinge-joint sometimes present after the first hydrotheca. Basal part with a variable number of transverse nodes and nematothecae. Distal part normally unsegmented, but with faint transverse or slightly oblique nodes sometimes visible near tip, bearing hydrothecae on anterior face, the first two median, the rest displaced alternately to left and right and forming two longitudinal rows. Two pairs of opposite hydrocladia arising by short apophyses at the sides of the first two hydrothecae; remaining hydrocladia alternate, one to each hydrotheca. Five nematothecae corresponding to each hydrotheca, one median inferior, one pair laterals, and one pair superior; the median inferior not directly below the hydrotheca, but displaced to the opposite side so that it lies above the previous hydrotheca; one or more extra nematothecae between hinge-joints.

Hydrocladium bearing hydrothecae on anterior surface, consisting of one short athecate internode bearing one median nematotheca and terminated by an oblique node and then up to 13 thecate internodes terminated by oblique nodes. Two internodal septa (one proximal and one distal) sometimes present in old colonies. Each thecate internode with three nematothecae, one median inferior and one pair laterals, and also one median superior naked sarcophore behind posterior wall of hydrotheca.

Hydrotheca cup-shaped, shallow, with depth usually less than diameter, with straight walls, almost completely adnate, 0.09–0.20 mm in abcauline height and 0.14–0.3 mm in marginal diameter on hydrocladium; cauline hydrotheca normally with thickened perisarc and eroded margin, thus shallower and with no free part. Margin forming an angle of 50–70° with internode.

Median inferior nematotheca well below hydrotheca and not reaching its base, two-chambered, immovable; basal chamber not distinctly demarcated from internode; distal chamber scoop-shaped, with no adcauline wall. Lateral nematotheca large, reaching well above thecal margin, two-chambered, movable; distal chamber funnel-shaped and not emarginated; those on hydrocladium seated on rounded pedicel, those of stem larger, not pedicellate. Superior nematothecae of stem seated above adnate part of thecal wall, minute, hook-shaped, one-chambered, immovable.

Gonothecae borne on hydrocladia below hydrothecae, male and female on same stem, but male more distal than female. Female gonotheca flattened anterior-posteriorly, oval in front view, containing one, or rarely two, eggs between the limbs of a bifurcating blastostyle, eggs developing into planulae in situ; with three large nematothecae on basal part; pedicel of one segment. Male gonotheca elongate-oval, curved.

Variation. Apart from variations included in the diagnosis there may occasionally be more than two pairs of opposite hydrocladia on the stem.

In some cases there may be an extra, short athecate internode at the base
Fig. 115.

*Halopteris tuba.* A, stem; B, proximal end of hydrocladium; C, lower part of stem in anterior view, with hinge-joints; D, male gonothecae; E, female gonotheca; F and G, cauline hydrothecae, F from a lower level on the stem, showing paired superior nematothecae (aperture for lateral nematotheca on left of hydrotheca).

Scale: A in cm, the rest in mm/10.
of the hydrocladium, representing part of the apophysis which has been cut off.

Rarely deeper hydrothecae occur, when the depth equals the marginal diameter.

**Distribution.** Endemic to South Africa. Type locality: Algoa Bay.

**Distribution in South Africa.** South and east coasts from False Bay to Natal, in 11–550 m. Fairly common. 34/18 (s), 34/19 (s), 35/20 (d), 34/21 (s), 34/22 (s), 35/22 (d, vd), 34/23 (s, d), 34/24 (d), 33/25 (s), 34/25 (s, d), 33/26 (s), 33/27 (s), 33/28 (s), 32/28 (s), 30/31 (s), 29/31 (s, d)

**Genus Monostaechas Allman, 1877**

**Diagnosis.** An erect stem present or absent. If present and fascicled, stem composed of intercommunicating tubes of equal diameter and importance which give rise irregularly to hydrocladia. If stem absent, hydrocladia arising directly from hydorhiza. Hydrocladia branching in the form of a sympodium, either dichotomous or helicoid, in the latter case branching from the posterior surface. Hydrotheca cup-shaped, with untoothed margin.

Type species: **Monostaechas dichotoma** Allman, 1877 (= Plumularia quadridens McCrady, 1857).

**KEY TO SPECIES**

(For simple forms, see also under Antennella, p. 330)

1. Hydrotheca completely adnate, margin at right angles to hydrocladium      *M. faurei*
   - Hydrotheca not completely adnate, margin directed obliquely outwards  ... ... 2

2. Subsidiary hydrocladium adnate to previous one for a short distance and then forming a small angle with it (under 30°)  ... ... ... ... ...  *M. natalensis*
   - Subsidiary hydrocladium not adnate to previous one and forming a large angle with it (over 30°)  ... ... ... ... ...  *M. quadridens*

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**Monostaechas faurei** Millard, 1958

Fig. 116A–D

*Monostaechas faurei* Millard, 1958: 204, fig. 11. Millard, 1968: 277, fig. 5E.

**Diagnosis.** Stem fascicled, reaching 142 mm, branching in a roughly dichotomous manner, its component tubes diverging from one another to form hydrocladia in an irregular fashion.

Hydrocladia branching sympodially from the posterior surface, the whole sympodium curved backwards in one plane. Hydrocladium consisting of a short basal athecate part terminated by an oblique node and a long distal thecate part divided into thecate internodes by oblique nodes. The basal part of a subsidiary hydrocladium very characteristic: originating from previous hydrocladium immediately below the first oblique node of the latter; its first internode almost entirely adnate to posterior surface of the first thecate internode of the previous hydrocladium and communicating with it by a pore near the distal end, then free for a short distance and terminated by a transverse node; second internode free, bearing a double series of nematothecae, termi-
nated by an oblique node. Each thecate internode bearing one hydrotheca and nine nematothecae, one median inferior and four pairs laterals.

Hydrotheca deep-campanulate, completely adnate, 0.18–0.3 mm in height and 0.11–0.15 mm in marginal diameter. Margin at right angles to internode.

Nematothecae all large, two-chambered and movable; distal chamber funnel-shaped, with adcauline edge lower than abcauline. Median inferior nematotheca not, or only just, reaching base of hydrotheca. Lateral nematothecae: first pair borne on long finger-shaped pedicels at sides of hydrotheca but not reaching thecal margin, second pair borne in axils of pedicels of first pair, third pair arising at sides of hydrotheca and overtopping thecal margin, fourth pair arising above level of hydrotheca and overreaching next oblique node.

Gonothecae borne on hydrocladia below hydrothecae, male and female on the same colony, the male more distal than the female, curved-pear-shaped, pedicel of one segment. Female gonothece with wide and operculate distal aperture, bearing 2–5 large nematothecae near base, containing one or two planulae. Male gonothece smaller than female, with rounded distal end, bearing two large nematothecae near base.

*Variation.* The first hydrotheca of a hydrocladium is distinctly shallower than the rest. Occasionally the distal end of a hydrocladial internode may be cut off by a transverse node to form an intermediate thecate internode, causing some irregularity in the nematothecae.

*Distribution.* Endemic to South Africa. Type locality: off Natal, approximately 28°41'S/32°22'E, 62 m.

*Distribution in South Africa.* On the east coast, from East London to St. Lucia, 49–219 m. 33/28 (s), 30/31 (s), 29/31 (s, d), 28/32 (s, d)

*Monostaechas natalensis* Millard, 1958

Figs 116E–G, 117A–C


*Diagnosis.* Colony reaching a maximum height of 76 mm, though more often under 30 mm, consisting of either numbers of hydrocladia arising in tufts from a short fascicled stem or separate hydrocladia arising independently from the hydrorhiza. The component tubes of the stem diverging to form branches and hydrocladia.

Hydrocladium unbranched or branching sympodially once or twice from posterior surface; consisting of a short basal thecate part terminated by an oblique node and a long distal thecate part divided into thecate internodes by oblique nodes. Basal part containing one or two transverse nodes and bearing a double series of nematothecae. A subsidiary hydrocladium arising from previous one at any level and forming an acute angle with it, adnate to it for a short distance and with or without a second communicating pore. Each thecate
**Monostaechas faurei.** A, branching hydrocladium; B, stem; C, hydrocladium with male gonotheca; D, hydrocladium with female gonotheca.

**Monostaechas natalensis.** E, hydrocladium; F, branching hydrocladia; G, lateral nematothecae.

Scale: B in cm, the rest in mm/10.
internode bearing one hydrotheca and six to ten nematothecae, one median inferior, two pairs laterals and one to five superior.

Hydrotheca campanulate, generally adnate for over half height, with no intrathecal septum, 0.16–0.6 mm in height and 0.15–0.4 mm in marginal diameter. Margin forming an angle of about 65° with internode.

Nematothecae all two-chambered and movable. Median inferior nematotheca not reaching base of hydrotheca. Lateral nematothecae: first pair borne on long finger-shaped pedicels at sides of hydrotheca but not reaching thecal margin; second pair borne in axils of pedicels of first pair; in both distal chamber funnel-shaped and deeply emarginated on two sides forming a bivalve structure with a large abcauline and a very small adcauline valve. Superior nematothecae variable in number and position, sometimes one or a pair arising behind free part of thecal wall and overtopping margin, sometimes one to three median arising above level of thecal margin.

Gonothecae borne on hydrocladia below hydrothecae, male and female on same colony, the male more distal than the female, curved pear-shaped, pedicel of one segment, bearing two nematothecae near base. Female gonotheca with wide and operculate distal aperture. Male gonotheca smaller than female, with rounded distal end.

Variation. This species is very variable in its growth-form, the larger colonies possessing rugged stems which branch irregularly and give rise to spectacular sprays of hydrocladia; the smaller colonies consisting of low tufts of hydrocladia arising from an agglomeration of stem-tubes, and many solitary hydrocladia.

The tendency for the hydrocladia to branch sympodially is not as strong as in M. faurei and the species appears to be intermediate between the genera Monostaechas and Corhiza. Its ability to produce solitary hydrocladia indicates affinity with Antennella.

Occasionally the distal end of a thecate internode may be cut off by a transverse node to form an intermediate atethecate internode, taking with it one or two of the superior nematothecae.

Distribution. Endemic to South Africa. Type locality: off Natal, 30°32'S/30°38.5'E, 46 m.

Distribution in South Africa. On the south and east coasts, from Port Elizabeth to Inhambane, 18–150 m. 34/25 (s, d), 33/28 (s), 31/29 (s), 30/30 (s), 29/31 (s), 28/32 (s), 24/34 (s), 24/35 (s)

Monostaechas quadridens (McCray, 1858)

Fig. 117D–F

Plumularia quadridens McCray, 1858: 97.
Monostaechas dichotoma Allman, 1877: 37, pl. 22 (figs 1–5).
Monostaechas fisheri var. simplex Billard, 1913: 16, fig. 7.
*Diagnosis.* Colony reaching a maximum height of 15 mm, consisting of hydrocladia which arise separately from the hydrorhiza and branch sympodially. Larger colonies branching first in the form of a dichotomous sympodium, in which two subsidiary hydrocladia of equal diameter arise from opposite sides of the primary one; later branching in the form of a helicoid sympodium, in which each subsidiary hydrocladium arises from the posterior surface of the previous one. Smaller colonies branching as a helicoid sympodium only. Subsidiary hydrocladia always facing towards the previous one, thus all hydrocladia of a helicoid sympodium in one plane, but not those of a dichotomous sympodium. False axis of helicoid sympodium straight or curved backwards, formed by the bases of successive hydrocladia.

Each hydrocladium consisting of a basal unsegmented athecate part bearing a variable number of nematothecae, and a distal thecate part, the two separated by an oblique node; with a distinct forward bend of 140–160° just below the oblique node, from which region the next hydrocladium arises. Distal part of hydrocladium consisting of alternate thecate and athecate internodes terminated by transverse and oblique nodes respectively, though the transverse nodes may be very poorly defined in certain areas. Each thecate internode bearing one hydrotheca and four nematothecae, one median inferior, one pair laterals and one median superior. Each athecate internode bearing two median nematothecae.

Hydrotheca cup-shaped, adnate for about half height, with no intrathecal septum, 0.2–0.3 mm in height and 0.2–0.3 mm in marginal diameter. Margin forming an angle of 30–60° with internode.

Median inferior nematotheca not quite reaching base of hydrotheca, possibly movable, two-chambered; distal chamber scoop-shaped, with low adcauline wall. Lateral nematothecae borne on finger-shaped pedicels at sides of hydrotheca and not quite reaching thecal margin, two-chambered, movable; distal chamber funnel-shaped. Median superior nematotheca seated behind free part of thecal wall, minute, one-chambered. Nematothecae of athecate internodes similar to median inferior, movable.

Gonothecae borne on hydrocladia below hydrothecae, male and female on same colony, curved pear-shaped, pedicel of two segments, bearing two nematothecae near base. Female with wide operculate distal aperture, containing a single egg. Male smaller than female and with smaller aperture.

*Variation.* Most of the South African stems have the helicoid sympodium only, but a few show the dichotomous sympodium at the base. The ‘dichotomy’ is not as regular as in the type area (West Indies) as figured by Allman, and the two subsidiary hydrocladia may arise side by side from the posterior surface of the previous one, or one from the lateral surface and one from the posterior surface.

*Distribution outside South Africa.* Circumglobal in tropical and temperate waters. Type locality: Charleston, U.S.A.
Monostaechas natalensis. A, male gonotheca; B, stem; C, part of hydrocladium with female gonotheca.

Monostaechas quaeirdens. D, male gonotheca; E, two stems, the one on the left branching first dichotomously and then in a helicoid manner, the one on the right branching as a helicoid sympodium only; F, hydrocladium with female gonotheca.

Scale: B in cm, the rest in mm/10.
Distribution in South Africa. Natal to Moçambique, littoral and 0–70 m. 31/30 (l), 30/30 (s), 29/31 (s), 29/32 (s), 28/32 (s), 26/32, 25/32, 21/35

Genus Schizotricha Allman, 1883

Diagnosis. An erect stem present, which may be branched or unbranched, fascicled or unfascicled; if fascicled with one main axial tube bearing pinnately arranged hydrocladia; with cauline hydrothecae. Hydrocladia alternate, at least some of them branching sympodially from anterior or lateral surface immediately below hydrothecae. Hydrotheca cup-shaped, with untoothed margin.

Type species: Schizotricha unifurcata Allman, 1883.

KEY TO SPECIES
1. Hydrotheca not completely adnate, one to each thecate internode. Stem unfascicled
   S. simplex
   - Hydrotheca completely adnate, more than one to each internode. Stem fascicled
     S. frutescens

Schizotricha frutescens (Ellis & Solander, 1786)

Sertularia frutescens Ellis & Solander, 1786: 55, pl. 6 (figs a, A).

Diagnosis. Stem fascicled, branching irregularly, reaching 200 mm, bearing alternate hydrocladia in the distal regions. Axial tube in its distal region divided into internodes each bearing one to three hydrothecae and one hydrocladium from the side of each hydrotheca, alternately on the left and the right.

Hydrocladium consisting of thecate internodes separated by transverse or slightly oblique nodes; each internode bearing one to five hydrothecae. Hydrocladium normally branched, giving rise to a secondary branch from one side of the first hydrotheca; the secondary branch sometimes rebranching in a similar manner; secondary and tertiary branches similar to primary in structure. No internodal septa. Three nematothecae corresponding to each hydrotheca, one median inferior and one pair laterals.

Hydrotheca deep cup-shaped, completely adnate. Margin tilted slightly towards internode.

Nematothecae all two-chambered and movable, with funnel-shaped distal chamber. Median inferior seated well below hydrotheca and not reaching its base. Lateral nematotheca overreaching thecal margin.

Male and female gonothecae (not reported from South Africa) borne on different colonies, arising from below hydrothecae on the hydrocladia, (?female) pear-shaped, with wide operculate distal aperture, bearing two nematothecae near base.

Distribution outside South Africa. North Atlantic, Mediterranean, Kerguelen Island. Type locality: Scarborough, U.K.
Distribution in South Africa. One record only, by Krauss (1837) from Algoa Bay. Needs confirmation. 33/25

Schizotricha simplex Warren, 1914

Fig. 118A–C

Schizotricha simplex Warren, 1914: 83, figs 1–4, pl. 6.

Diagnosis. Stem unfascicled, unbranched, reaching a maximum height of 14 mm, consisting of an athecate basal part, and a distal thecate and hydrocladia-bearing part, the two separated by two oblique hinge-joints. Basal part with a variable number of transverse nodes. Distal part divided into thecate internodes by oblique nodes. First thecate internode bearing a pair of opposite hydrocladia arising from the sides of the hydrotheca; remaining hydrocladia alternate, one to each internode. Three nematothecae to each internode, one median inferior and one pair laterals.

Hydrocladium bearing hydrothecae on anterior surface, consisting of one very short athecate and anematothecate internode terminated by a transverse node and not always sharply demarcated from apophysis, then alternate athecate and thecate internodes terminated by distinctly and slightly oblique nodes respectively, usually two or three (rarely four) thecate internodes in all. Hydrocladium giving rise to a subsidiary branch from one side of the first hydrotheca. Subsidiary branch similar to primary one in structure and forming an angle of about 30° with it, bearing one or two hydrothecae. No internodal septa. Each thecate internode with three nematothecae, one median inferior and one pair laterals. Each athecate internode other than the first with one median nematotheca.

Hydrotheca cup-shaped, with walls flaring slightly to margin, adnate for a little over half height, with no intrathecal septum, 0.12–0.16 mm in abcauline height, and 0.16–0.2 mm in marginal diameter. Margin forming an angle of 30–40° with internode.

Median inferior nematotheca not reaching base of hydrotheca, two-chambered, probably movable, distal chamber scoop-shaped with low adcauline wall. Lateral nematotheca borne on a short pedicel, not, or only just, reaching thecal margin, two-chambered, movable, emarginated on both adcauline and abcauline walls but more deeply on adcauline. Nematotheca of athecate internode similar to median inferior.

Male and female gonothecae borne on same colony, the female on the stem and the male on the first thecate internodes of the primary hydrocladia, arising immediately below hydrothecae. Female gonotheca large, flattened antero-posteriorly, pear-shaped in broad view, with wide distal operculate aperture, with two large nematothecae on basal part, containing a single ovum which develops into a planula in situ; pedicel of one segment. Male gonotheca cylindrical or somewhat flattened, with bluntly pointed distal end.

Variation. Branching hydrocladia are found only in the older proximal part of
a colony, and the last hydrocladia of a stem are usually unbranched.

Distribution. Endemic to South Africa. Type locality: near mouth of St. John’s River, littoral.

Distribution in South Africa. Sparsely distributed from Still Bay to the Cape/Natal border, littoral only. 34/21 (l), 34/22 (l), 33/27 (l), 31/29 (l)

Subfamily Kirchenpaueriinae

Diagnosis. Stem erect, branched or unbranched, fascicled or unfascicled, giving rise to alternate hydrocladia. Hydrocladia arising from a single axial tube in fascicled stems. No cauline hydrothecae. Hydrothecae small (usually under 0.2 mm in depth). Nematothecae reduced: laterals absent; medians poorly developed, seldom two-chambered, often rudimentary and sometimes represented by naked sarcostyles only. Gonothecae unprotected, not aggregated, not bearing nematothecae.

KEY TO GENERA
[Genera not represented in South Africa are bracketed]

1. Hydrothecal margin toothed 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
   – Hydrothecal margin not toothed

2. Hydrotheca with abcauline intrathecal septum 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
   – Hydrotheca without intrathecal septum

3. At least some of the hydrocladia forked 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
   – No hydrocladia forked

Genus Kirchenpaueria Jickeli, 1883

Diagnosis. Stem branched or unbranched, bearing hydrocladia. Rarely with simple forms where the hydrocladia arise directly from the hydrorhiza. Hydrocladia unbranched. Hydrotheca cup-shaped, without intrathecal septum, with untoothed margin.

Type species: Sertularia pinnata Linnaeus, 1758.

KEY TO SPECIES

1. One median superior nematotheca present 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
   – Median superior nematotheca replaced by a naked sarcostyle

2. Stem internode with at least one nematotheca on proximal region and one on apophysis. Hydrotheca seated on proximal half of internode. Gonotheca triangular in section 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
   – Stem internode with one nematotheca in axil of hydrocladium, none on apophysis. Hydrotheca seated on distal half of internode. Gonotheca round in section

Kirchenpaueria irregularis (Millard, 1958)

Fig. 118D–G

Plumularia irregularis Millard, 1958: 211, fig. 13A–C.

Diagnosis. Hydrorhiza creeping. Stem fascicled at base, unbranched or sparsely branched, reaching a height of 13 mm, bearing alternate hydrocladia.
Fig. 118.

*Schizotricha s.* A, anterior view of stem with female gonophores; B, male gonotheca; C, hydrocladium with branch.

*Kirchenpaueria irregularis.* D and F, parts of hydrocladia; E, stem and origins of hydrocladia; G, stem.

Scale: G in cm, the rest in mm/10.
divided into regular internodes by transverse nodes. Each internode bearing one hydrocladal apophysis near distal end, one mamelon on upper surface of apophysis and one nematotheca immediately above apophysis. No internodal septa. The two rows of hydrocladia in one plane.

Hydrocladium bearing hydrothecae on upper surface, very irregularly segmented, normally consisting of only thecate internodes terminated by transverse nodes, but often with intermediate athecate internodes. Each thecate internode with two nematothecae, one median inferior not reaching base of hydrotheca and one median superior. No internodal septa. Hydrotheca seated on distal half of internode.

Hydrotheca cup-shaped, not completely adnate, widening to margin, 0.07–0.11 mm in abcauline depth and 0.10–0.12 mm in marginal diameter. Margin oblique.

Nematotheca two-chambered, with very small basal chamber, flask-shaped, with convex abcauline wall.

Gonothecae unknown.

Variation. The hydrocladal internodes vary greatly in length though generally very long and slender. Athecate internodes may occur in almost any position on the hydrocladia, as many as three at the base and up to two between consecutive thecate internodes. Usually these are bounded by straight nodes and carry no nematothecae. Occasionally, however, the distal part of a thecate internode is cut off behind the hydrotheca by an oblique node, carrying with it the median superior nematotheca.

The hydrothecae are adnate for about $\frac{1}{4}$–$\frac{3}{8}$. Those with an oblique node behind them have a long free portion.

Distribution. Endemic to Southern Africa.

Distribution in South Africa. Natal and Moçambique, rare; type locality: Salisbury Island, Durban Bay. 29/31 (1), 21/35

Kirchenpaueria pinnata (Linnaeus, 1758)

Fig. 119A–D

Sertularia pinnata Linnaeus, 1758: 813.
Plumularia pinnata: Hincks, 1868: 295, pl. 65 (fig. 1). Ritchie, 1907b: 541.
?Plumularia Gaywardi: Kirchenpauer, 1876: 27, pl. 1 (fig. 6), pl. 3 (fig. 6).
Plumularia unilateralis Ritchie, 1907b: 541, pl. 2 (fig. 1).

Diagnosis. Hydrorhiza creeping. Stem unfissicled, unbranched, usually reaching a height of 10–30 mm (maximum 75 mm), bearing alternate hydrocladia, divided into internodes by transverse or slightly oblique nodes. Each internode bearing a variable number of hydrocladia on short apophyses and two naked sarcostyles in the axil of each, one on upper surface of apophysis and one on stem
just above apophysis. No internodal septa. No mamelon. The two rows of
hydrocladia in one plane or displaced towards the anterior surface.

Hydrocladium bearing hydrothecae on upper surface, consisting of one
very short athecate and anematothecate internode, then all thecate internodes
terminated by oblique nodes. Each thecate internode with one median inferior
nematotheca and one median superior naked sarcostyle. Internodal septa
absent, or two in each thecate internode, one proximal and one distal, and one
in the thecate internode. Hydrotheca seated in centre of internode.

Hydrotheca cup-shaped, almost completely adnate ($\frac{3}{4}$), with straight
abcauline wall, 0,07-0,12 mm in abcauline depth and 0,12-0,17 mm in marginal
diameter. Margin oblique, reaching approximately to next node.

Median inferior nematotheca minute, scoop-shaped, one-chambered, with
no abcauline wall. All others reduced to naked sarcostyles emerging through
foramina in the perisarc.

Gonothecae borne on stem (but not on the hydrocladial apophyses) or
hydrorhiza, without nematothecae, elongate-oval, with longitudinal ridges
which often bear spines.

Variation. This is a very variable species, in which features such as the number
of hydrocladia to a stem internode, presence or absence of thecate internodes
in the hydrocladia, shape of hydrotheca and presence or absence of spines on
the gonotheca have been used in the past for the separation of species, varieties
or forms. South African material conforms most nearly to the typical form as
described by Hincks.

The length of the stem internodes varies, and each may bear one to four
hydrocladia, depending on the length. The most common number is two, with
a tendency for more near the base and only one near the tip. In some stems all
internodes bear one hydrocladium each.

The hydrocladia lack regular thecate internodes (other than the first).
Occasional ones do, however, occur sporadically, with 0, 1, or 2 median
nematothecae each.

Ritchie (1907b) has reported a colony from Saldanha Bay (as Plumularia
unilateralis) with branching hydrocladia, but no further examples have been
seen. Rare examples of solitary hydrocladia arising separately from the
hydrorhiza occur.

Gonothecae vary in the development of the spinous processes. In general,
young ones are practically smooth, older ones ribbed longitudinally, and fully
mature ones provided with spines. Female gonothecae appear to be more
spinous than male.

Distribution. Cosmopolitan. Type locality: U.K.

Distribution in South Africa. From South West Africa on the west to Natal on
the east; the most common littoral hydroid in the south-western Cape; also
common on ships’ hulls and in shallow water, extending down to 64 m. 22/14,
Fig. 119.

*Kirchenpaueria pinnata*. A, hydrocladium; B, part of stem with origins of hydrocladia; C, fertile stems; D, gonothecae, arising from hydorhiza.

*Kirchenpaueria triangulata*. E, colony with pinnate stem bearing gonothecae and several simple stems; F, nematotheca; G, part of stem showing nematothecae and origins of hydrocladia; H, hydrocladium.

Scale: C in cm, E in mm, the rest in mm/10.
Kirchenpaueria triangulata (Totton, 1930)

Fig. 119E–H

Plumularia triangulata Totton, 1930: 225, fig. 61. Ralph, 1961b: 41, fig. 5f–g.

Diagnosis. Hydrorhiza creeping, giving rise to both pinnate stems and, as a secondary growth-form, separate hydrocladia. Pinnate stem unfascicled, unbranched, reaching 10–35 mm in height, bearing alternate hydrocladia, divided into regular internodes by straight nodes which may be indistinct in parts. Each internode bearing one hydrocladial apophysis at distal end, one mamelon on upper surface of apophysis and two to four nematothecae, including one on proximal end immediately above last apophysis and one on upper surface of apophysis distal to mamelon. No internodal septa. The two rows of hydrocladia in one plane or displaced slightly to the anterior surface.

Hydrocladium bearing hydrothecae on upper surface, consisting of thecate internodes only, terminated by straight or slightly oblique nodes. Each internode with two nematothecae, one median inferior and one median superior. No internodal septa. Hydrotheca seated in proximal half of internode.

Separate hydrocladium borne on long apophysis of hydrohiza, about 4 mm in height, exactly similar to those borne on the stem except that the measurements of individual parts are slightly less.

Hydrotheca cup-shaped, completely adnate or with a very short free par., widening slightly to margin, 0,07–0,10 mm in abcauline depth and 0,10–0,12 mm in marginal diameter. Margin slightly oblique and very slightly everted.

Nematotheca one-chambered, movable, flask-shaped, with convex abcauline wall and practically straight abcauline wall.

Gonothecae borne on hydrocladial apophysises of stem, large (reaching 3 mm in length), without nematothecae, increasing in diameter to truncated distal end, triangular in section, with short pedicel of two segments.

Variation. In South Africa this species grows epizootically on other hydroids.

In pinnate stems there is a tendency for the nodes to be indistinct or completely absent. This is most common in the proximal part and sometimes only the last few nodes are visible. Occasionally the node between the hydrocladial apophysis and the first thecate internode is also indistinct.

Athetic internodes of variable length (possibly due to regeneration) commonly occur in the hydrocladia. They may be present in any position, but are most common at the proximal ends.

Although the nematothecae are one-chambered a very thin septum is sometimes visible near the base. The number of cauline nematothecae is variable, although the two mentioned in the diagnosis always occur.
Distribution outside South Africa. New Zealand. Type locality: off Three King’s Island in 550 m.

Distribution in South Africa. A deep-water species occurring at scattered localities from off the Cape Peninsula to Moçambique in 111–1 207 m. 34/17 (d), 34/23 (d), 29/31 (d), 28/32 (a), 25/35 (vd)

Genus Oswaldella Stechow, 1919

Diagnosis. Stem unfascicled, unbranched or sparingly branched, bearing hydrocladia. Rarely with a simple form where the hydrocladia arise direct from the hydorhiza. At least some of the hydrocladia forking once or several times in a plane at right angles to the hydrocladium. Hydrotheca cup- or jug-shaped, without intrathecal septum, with untoothed margin.

Type species: Schizotricha bifurca Hartlaub, 1904.

One species in South Africa.

Oswaldella nova (Jarvis, 1922)

Fig. 120A–C

Plumularia nova Jarvis, 1922: 347, pl. 26 (fig. 20).
Kirchenpaueria adhaerens Millard, 1958: 203, fig. 13F–G.

Diagnosis. Hydorhiza epizootic on other hydroids (Plumulariidae, Halopterinae), giving rise, so far as is known, to simple stems (hydrocladia) only.

Hydrocladia borne on long apophyses of hydorhiza, reaching a maximum height of 7 mm, often forked dichotomously once or twice. The two limbs of a fork of equal length and thickness and bearing hydrothecae on the same surface as the undivided part. Hydrocladium consisting of thecate internodes only, terminated by oblique nodes. Each internode with one median inferior nematotheca and one median superior naked sarcostyle situated behind abcauline wall of hydrotheca. One median nematotheca on apophysis of hydorhiza. No internodal septa. Hydrotheca seated approximately in centre of internode.

Hydrotheca cup-shaped, either completely adnate or with a very short free part, with straight or slightly concave abcauline wall, 0.05–0.12 mm in abcauline depth and 0.07–0.14 mm in marginal diameter. Hydranth with about 16 tentacles.

Median inferior nematotheca minute, one-chambered, saucer-shaped, often missing.

Male gonothecae borne singly immediately below hydrothecae, elongated, with truncated distal end and curved base, reaching 0.90 mm in length and 0.27 mm in maximum diameter. Female gonothecae unknown.

Variation. The hydrocladia may be undivided and very short, bearing only two or three hydrothecae. At the other extreme are long hydrocladia forked twice, reaching 7 mm and bearing up to 15 hydrothecae. The hydorhizal apophysis
may be separated off by a node, and the distal end of an internode may be separated off by a straight node to form an athecate intermediate internode. Internodes of very variable length.

Remarks. It is possible that this is a stunted epizootic form of a species with a pinnate stem such as *O. bifurca* (Hartlaub, 1904) or *O. antarctica* (Jäderholm, 1904). Both the latter are antarctic forms.

**Distribution outside South Africa.** Tropical East Africa. Type locality: Zanzibar.

**Distribution in South Africa.** From the west coast of the Cape Peninsula to Moçambique in 10–110 m. 34/18 (s), 35/21 (d), 34/22 (s), 34/23 (s), 33/26 (s), 33/27 (s), 30/30 (s), 28/32 (s), 21/35

**Genus Pycnotheca** Stechow, 1919

*Syn. Diplocheilus* Allman, 1883.

**Diagnosis.** Stem unbranched or sparsely branched, bearing hydrocladia. Hydrocladia unbranched. Hydrothece cup-shaped, with strong abcauline intrathecal septum and untoothed margin.

Type species: *Diplocheilus mirabilis* Allman, 1883.

One species only in South Africa.

**Pycnotheca mirabilis** (Allman, 1883)

Fig. 120D–G


**Diagnosis.** Hydrorhiza creeping. Stem unfascicled, unbranched, reaching 30 mm in height, bearing alternate hydrocladia, divided into internodes by very oblique nodes which are successively more distinct towards the base where they resemble hinge-joints. Each internode bearing one or two hydrocladiad apophyses, the two rows of hydrocladia not in one plane but displaced onto anterior surface. No internodal septa. Mamelon present on upper surface of apophysis. One nemathotheca on each hydrocladiad apophysis and one on the anterior surface of the distal end of each stem internode.

Hydrocladium bearing hydrothecae on anterior surface, consisting of thecate internodes only, terminated by oblique nodes. Each internode with one median inferior rematotheca close below base of hydrotheca and one median superior naked sarcostyle behind abcauline wall of hydrotheca. Internodes short and hydrothecae close-set, with margin of one almost reaching the base of the next. No internodal septa. Hydrotheca seated in centre of internode.

Hydrotheca cup-shaped, widening slightly to a circular aperture, adnate for about two-thirds height, with strong abcauline intrathecal septum reaching about half-way across cavity and triangular in side view, 0.2–0.3 mm in depth
Oswaldella nova. A, epizootic colony on Halopteris glutinosa (hydrocladia of host cut off short); B, hydrocladium; C, hydrocladium with male gonothecae. 
Pvenotheca mirabilis. D, fertile colony; E, anterior view of stem showing origins of hydrocladia; F, hydrocladium; G, gonotheca.

Scale: D in cm, A in mm, the rest in mm/10.
and 0.18–0.3 mm in marginal diameter. Margin oblique. Hydranth with about
18 tentacles.

Median inferior and cauline nematothecae scoop-shaped, one-chambered,
immovable, with no adcauline wall. Median superior naked sarcostyle seated
in a funnel-shaped depression of the perisarc.

Gonothecae borne on hydorhiza or on basal part of stem replacing
hydrocladia, without nematothecae, elongate-oval, transversely annulated,
with truncated distal end, containing one or two gonophores.

Variation. Minor differences in structure have led to the establishment of
separate varieties, geographical races or subspecies (Stechow 1925b; Totton
1930). The features used include the thickness of the stem and hydrocladia,
the number of hydrocladia to a stem internode (one or two), the size of the
hydorhiza, the distance between consecutive hydrothecae, the thickness of the
intrathecal septum, the proportion of the free part of the adcauline thecal wall
and the plane of the basal opening of the median inferior nematotheca. In
general there seems little justification for subdivision of the species. In South
African material the longer stem internodes near the base tend to bear two hydro-
cladia, the shorter ones near the tip one. The measurements of the False Bay
material are on the whole greater than those of the east coast material.

Distribution outside South Africa. South-east Madagascar, Australia, New
Zealand, Japan, India, Pacific coast of North America, Vema Seamount (South
Atlantic). Type locality: Bass Strait in 69–73 m.

Distribution in South Africa. False Bay and the coasts of Natal and Moçambique,
littoral to 49 m. 34/18 (s), 30/30 (l, s), 29/31 (s), 28/32 (s), 26/32 (l, s)

Subfamily Plumulariinae

Diagnosis. Stem erect, branched or unbranched, fascicled or unfasicled, giving
rise to hydrocladia alternately or in alternating verticils. Hydrocladia arising
from a single axial tube in fascicled stems. No cauline hydrothecae. Hydоро-
thecae small (usually under 0.2 mm in depth). Nematothecae generally two-
chambered and movable, not fused to hydrotheca, at least three associated with
every hydrotheca (one median inferior and one pair laterals). Gonothecae
unprotected, not aggregated, generally without nematothecae.

KEY TO GENERA

1. Mature stem and branches bearing verticils of hydrocladia, those of one verticil
normally alternating with those above and below forming double the number of
longitudinal rows ................................. Nemertesia p. 381
   - Stem and branches bearing alternate hydrocladia which form two longitudinal rows ................................. 2

2. Hydrotheca with untoothed margin ................................. Plumularia p. 388
   - Hydrotheca with toothed margin ................................. Dentitheca p. 380
Genus *Dentitheca* Stechow, 1919

*Diagnosis.* Stem pinnate, giving rise to alternate hydrocladia. Hydrotheca cylindrical to cup-shaped, margin with a large lobe on each side.

Type species: *Plumularia hertwigi* Stechow, 1909

One species only from South Africa.

*Dentitheca bidentata* (Jäderholm, 1920)

Fig. 121A–C

*Plumularia bidentata* Jäderholm, 1920: 7, pl. 2 (figs 5–6).

*Plumularia crosslandi* Jarvis, 1922: 346, pl. 25 (fig. 18).

*Dentitheca crosslandi* Vannucci, 1949: 250, pl. 3 (figs 49–50).

*Dentitheca bidentata* Millard & Bouillon, 1973: 78, fig. 11C.

*Diagnosis.* Stem unfasci cled, unbranched, reaching a maximum height of 32 mm, bearing alternate hydrocladia, divided into internodes by oblique nodes, those near the base forming hinge-joints. Each internode bearing a variable number of hydrocladia. Three nematothecae to each apophysis (one on apophysis, one in axil, one on stem next to origin), one on anterior surface of base of internode and sometimes one on distal end of internode. Mamelon present on upper surface of apophysis. The two rows of hydrocladia not in the same plane but displaced towards the anterior surface.

Hydrocladium bearing hydrothecae on anterior surface, consisting of thecate internodes separated by oblique nodes and bearing the hydrotheca on the basal half. Each internode with one long median inferior nematotheca reaching about half-way up length of hydrotheca, one pair shorter laterals not reaching level of lateral thecal teeth and one median superior. Up to six perisarcal thickenings on anterior surface which may be developed as internodal septa.

Hydrotheca completely adnate, with the perisarca usually strongly thickened and projecting into the interior near the distal end of the abcauline side and sometimes the adcauline side as well. Margin with two large, triangular lateral lobes and an abcauline lobe which is bent out at an angle to the axis. Hydrotheca 0,10–0,13 mm in abcauline height and 0,07–0,14 mm in marginal diameter.

Nematothecae all two-chambered and movable, the median inferior with an extra long basal chamber.

Gonothecae (not reported from South Africa) arising from axils of hydrocladia, cylindrical, with two longitudinal ridges on anterior surface and four irregular distal expansions (Jarvis).

*Variation.* The structure of the lower part of the stem is variable and as many as five of the basal nodes may be in the form of hinge-joints. One stem was seen with four branches. The number of hydrocladia to an internode varies from one to four.

The perisarca of the hydrotheca varies in thickness. In young hydrothecae
the abcauline wall is only slightly thickened. In older ones this thickening projects into the cavity as a large triangular tooth and there is a second smaller projection into the cavity from the abcauline wall.

**Distribution outside South Africa.** Brazil (type locality: south of Pernambuco, 9°S, 33 m); tropical western Indian Ocean: Wasin, Madagascar, Seychelles.

**Distribution in South Africa.** Durban to Inhaca, littoral to 48 m. 28/32 (s), 26/32 (l)

Genus *Nemertesia* Lamouroux, 1812

Syn. *Antennularia* Lamarck, 1816.

**Diagnosis.** Hydrocladia arranged in verticils in mature colonies, the number to a verticil typically increasing with age, and members of one verticil typically alternating with those above and below forming double the number of longitudinal rows. Hydrotheca cup-shaped, with untoothed margin.

Type species: *Sertularia antennina* Linnaeus, 1758.

**KEY TO SPECIES**

1. All hydroclial internodes normally thecate ........... . N. ramosa
   - Hydroclial internodes alternately thecate and athecate ....... . 2

2. Stem unbranched and unfascicled ................. . N. antennina
   - Stem branched and fascicled .............. . 3

3. Branching in one plane, stiff. Each stem internode bearing more than one whorl of hydrocladia. First hydroclial internode thecate ........... . N. ciliata
   - Branching irregular, flexuous. Each stem internode bearing only one whorl of hydrocladia. First hydroclial internode athecate ........... . N. cymodocea

_Nemertesia antennina* (Linnaeus, 1758)

Fig. 121D–E

*Sertularia antennina* Linnaeus, 1758: 811.
*Antennularia irregularis* Quechel, 1885: 8, pl. 2 (fig. 4).
*Antennularia antennina*: Billard, 1904a: 211, figs 80–86. Hincks, 1868: 280, pl. 61.
*Nemertesia antennina irregularis*: Vervoort, 1966b: 140, fig. 42.

**Diagnosis.** Stems thread-like, unfascicled, unbranched or rarely with one or two branches, reaching 55 mm. Hydrocladia borne in whorls of 2–10. Stem divided by transverse nodes (which may be obscure) into internodes each bearing one whorl of hydrocladia. Mamelon present on upper surface of hydroclarial apophysis. A variable number of nematothecae corresponding to each apophysis but always one pair in axil.

Hydrocladium consisting of alternate short athecate and long thecate internodes. Athecate internodes with one or two median nematothecae. Thecate internodes with three nematothecae, one median inferior and one pair laterals overreaching thecal margin.
Fig. 121.

*Denticula bidentata*. A, hydrocladium; B, part of stem in lower region showing origin of hydrocladium; C, stems.

*Nemertesia antennina*, redrawn from Vervoort (1966b). D, gonotheca; E, hydrocladium.

*Nemertesia ciliata*. F, hydrocladium from old region of stem; G, more typical hydrocladium; H, stem; J and K, parts of stem with two and three hydrocladia per whorl respectively, J with gonothecae (nematothecae omitted).

Scale: C and H in cm, the rest in mm/10.
Hydrotheca cup-shaped, completely adnate, widening to margin, 0.07 mm in abcauline depth and 0.08–0.09 mm in marginal diameter.

Nematothecae all two-chambered and movable.

Gonothecae borne on hydrocladal apophyses, without nematothecae, smooth, pear-shaped, with wide, oblique aperture tilted towards stem. Male and female similar, on same colony. Female containing one egg, rarely two, which develops into a planula in situ.

Variation and remarks. The general appearance of this species with its unbranched, thread-like stems is very characteristic. It is recognized as being extremely variable in structure and several varieties and/or subspecies have been described. Variations involve:

(i) The number of hydrocladia to a whorl, which probably increases with age.
(ii) The presence or absence of nodes on the stem.
(iii) The segmentation of the hydrocladia, where extra intermediate athecate internodes may occur.
(iv) The number of nematothecae to an athecate internode. One appears to be normal, but two may occur or, on extra intermediate internodes, none at all.

Stechow (1912) reports the species from South Africa without locality or depth. Since his material was dry, without hydrocladia and without gonothecae, this record is subject to doubt.

Vervoort (1966b) reports subspecies irregularis from off Durban, and the measurements given above are from this work. Vervoort reports that the whorls of hydrocladia do not alternate as is usual for the species.

Because of the variability within the species, and because it is so poorly known in South Africa, I prefer not to be categorical about subdivision into subspecies and/or varieties. There is also a possibility of confusion with young colonies of Nemertesia cymodoceae.

Distribution outside South Africa. Atlantic Ocean from Greenland to tropical West Africa and from North America to Europe. Mediterranean. Pacific. Type locality: U.K.

Distribution in South Africa. Off Durban in 425–430 m. 29/31 (d)

Nemertesia ciliata Bale, 1914

Fig. 121F–K


Nemertesia ciliata var. cruciata Bale, 1915: 300.

Diagnosis. Hydrorhiza matted and thick. Stem thick and fascicled, reaching 245 mm, branching and rebranching in an irregularly alternate fashion and always in one plane. Branches forming an acute angle with stem, larger ones fascicled, smaller ones unincised. Hydrocladia borne in whors of 2–4 on long apophyses of stem and branches, the whole often compressed in one plane. Axial tube of stem and branches, where exposed, with irregular transverse
nodes, usually after every two or three whorls of hydrocladia. Mamelon present on upper surface of hydrocladal apophysis. Three or four nematotheca corresponding to each apophysis, two in the axil and one or two medians on upper surface distal to the mamelon, none on main axial tube. Scattered nematotheca on peripheral tubes.

Hydrocladium bearing hydrotheca on upper surface, consisting of alternate long thecate and short athecate internodes separated by oblique nodes. All internodes with at least two internodal septa, one proximal and one distal. Athecate internodes with one median nematotheca on proximal end. Thecate internodes with three nematotheca, one median inferior on proximal end and well below base of hydrotheca and one pair laterals overreaching thecal margin. Hydrotheca seated approximately in centre of internode.

Hydrotheca cup-shaped, completely adnate, widening to margin, 0.02–0.07 mm in abcauline depth and 0.06–0.09 mm in marginal diameter. Margin perpendicular to hydrocladium.

Nematotheca all two-chambered and movable. Distal chamber funnel-shaped, deeply emarginated on abcauline side in medians, slightly so in laterals.

Gonotheca borne on hydrocladal apophyses, without nematothecae, smooth, often curved, widening from base to truncated distal end, with broad terminal aperture.

Variation. As is usual in this genus there is variation in the number of hydrocladia to a whorl. At the base of a stem or branch the arrangement is either alternate or quite irregular. Further up there is a rough grouping into whorls, though the members of a whorl are not all at the same level, until finally the regular whorls are established.

Distribution outside South Africa. Tasmania, Japan. Type locality: Oyster Bay, Tasmania.

Distribution in South Africa. From the west coast to off Port Elizabeth in 11–392 m. 31/16 (d), 34/17 (d), 34/18 (d), 35/21 (d), 26/21 (d), 34/22 (s), 34/23 (d), 34/25 (s)

Nemertesia cymodocea (Busk, 1851)

Fig. 122A–C

Antennularia Cymodocea Busk, 1851: 119.
Nemertesia (Antennularia) decussata Kirchenpauer, 1876: 52, 54, pl. 2 (fig. 24), pl. 3 (fig. 24), pl. 7 (fig. 24).
?Nemertesia (Antennularia) Johnstoni Kirchenpauer, 1876: 52, 54, pl. 8 (fig. 26).
Antennularia decussata: Marktanner-Turneretscher, 1890: 258, pl. 6 (fig. 7).
Antennularia hartlaubi Ritchie, 1907b: 542, pl. 3 (fig. 4).

Diagnosis. Hydorhiza matted and spreading. Stem thick and fascicled, reaching 100 mm or more (maximum 492 mm), dividing irregularly and usually close to the base into long flexuous branches, which may be fascicled in basal region.
Hydrocladia in whorls of two or three. Branches divided into regular internodes by transverse nodes, each internode bearing two or three hydrocladial apophyses near distal end. Mamelon present on upper surface of apophysis. Nematothecae present on peripheral tubes of fascicled stem. Three nematothecae corresponding to each apophysis, two seated side by side on its upper surface and one on the next internode immediately above it.

Hydrocladium bearing hydrothecae on upper surface, consisting of alternate short athecate and long thecate internodes separated by slightly oblique nodes. All internodes with at least two internodal septa, one proximal and one distal. Athecate internodes with one median nematotheca. Thecate internodes with three nematothecae, one median inferior reaching approximately to base of hydrotheca and one pair laterals overreaching thecal margin. Hydrotheca seated approximately in centre of internode.

Hydrotheca cup-shaped, completely adnate, widening to margin, 0.06–0.11 mm in abcauline depth and 0.08–0.14 mm in marginal diameter. Margin perpendicular or slightly oblique to hydrocladium.

Nematothecae all two-chambered and movable; distal chamber funnel-shaped and with abcauline wall lower than abcauline.

Gonothecae borne on hydrocladial apophyses, without nematothecae, smooth, compressed, flask-shaped and often slightly curved in side view, with terminal aperture on a short tubular neck, held parallel to branch.

Variation. The most obvious variation is in the number of hydrocladia to a whorl, two (decussate arrangement) and three (hexastichous arrangement) being the most common, but there may also be only one (alternate arrangement) and Kirchenpauer (1876) reports four. It appears that generally, though possibly not always, this is a factor of age, for very young colonies have alternate hydrocladia and develop the decussate arrangement only at the tips of the branches; mature colonies have normally lost the hydrocladia in the older fascicled part of the stem and have the decussate arrangement in the proximal regions of the branches and the hexastichous arrangement more distally. Some colonies are entirely decussate and some entirely hexastichous.

Occasionally a secondary hydrocladium arises from the apophysis of the primary. This is not a regular occurrence and appears to be an abnormal condition in which the secondary hydrocladium replaces a gonophore.

The number and strength of the internodal septa in the thecate internodes is also variable, and in addition to the basic two (proximal and distal) there may be one opposite the base of the hydrotheca, another immediately above this and another below it.

Other minor variations include the presence of extra athecate regeneration internodes, of which there may be as many as six at the base of the hydrocladium, and the presence of an extra nematotheca on the hydrocladial apophysis.

Distribution outside South Africa. New Zealand, south-western Atlantic.
Distribution in South Africa. From Saldanha Bay to East London in 5–170 m. Type locality: 'South Africa'. 33/17 (s), 33/18 (s), 34/18 (s), 34/19 (s), 34/20 (s), 35/21 (d), 34/22 (s), 35/22 (d), 34/23 (s, d), 33/25 (s), 34/25 (s, d), 33/26 (s), 33/27 (s), 32/28 (s)

*Nemertesia ramosa* Lamouroux, 1816

Fig. 122D–H


**Diagnosis.** Hydrorhiza thick and matted. Stem thick and fascicled, generally reaching 40–160 mm (maximum 282 mm), unbranched or branching irregularly, bearing hydrocladia in whorls of two to five. Nodes either absent altogether or transverse and quite irregular. Hydrocladial apophyses stout, bearing a mamelon on upper surface. Four to seven nematothecae corresponding to each apophysis, one or two on stem above apophysis, one pair on the apophysis in the axil and one to three distal to mamelon.

Hydrocladia bearing hydrothecae on upper surface, normally consisting of only thecate internodes separated by slightly oblique nodes. Internodal septa present or absent. Each internode with three or four nematothecae, one median inferior not reaching base of hydrotheca, one pair laterals overreaching thecal margin and generally one median superior. Hydrotheca seated in proximal half of internode.

Hydrotheca cup-shaped, completely adnate, widening to margin, 0,06–0,14 mm in abcauline depth and 0,07–0,14 mm in marginal diameter. Margin perpendicular or slightly oblique to hydrocladium.

Nematothecae all two-chambered and movable; distal chamber funnel-shaped with abcauline wall slightly lower than abcauline.

Gonothecae borne on hydrocladial apophyses, without nematothecae, smooth. Male elongate-oval, symmetrical and with rounded distal end when young, slightly curved and with oblique aperture when mature. Female curved, widening to distal end, with broad oblique aperture usually facing towards stem. Eggs developing into planulae in situ.

**Variation.** This is an extremely variable species, both in the arrangement of hydrocladia and in the segmentation within them.

In young stems the hydrocladia are alternate, but as development proceeds whorls of two, three, four, five, or even six are produced, with the result that whorls with a larger number of hydrocladia occur at the distal end of the stem. In time the lower (alternate) hydrocladia fall off or are obscured by the fasciculation. Sometimes the arrangement is quite irregular in parts.

Though the normal condition seems to be hydrocladia with only thecate internodes, athecate internodes may occur either below the first thecate one or between any two thecate ones. This, however, is not a regular occurrence as in *N. cymodoce*a.
Fig. 122.

*Nemertesia cymodocea*. A, stem; B, part of stem with three hydrocladia per whorl and female gonothecae (nematothecae omitted); C, hydrocladium.

*Nemertesia ramosa*. D, part of stem with three hydrocladia per whorl and female gonothecae (nematothecae omitted); E, typical hydrocladium with no median superior nematotheca; F, hydrocladium with small hydrothecae and with median superior nematothecae; G, hydrocladium from old stem and with median superior nematothecae; H, stem.

Scale: A and H in cm, the rest in mm/10.
In the hydrocladial internodes septa commonly occur, including one at the proximal end and one at the distal end, the number increasing with age, so that in old colonies as many as 12 may be present.

The median superior nematotheca is not invariably present in the thecate internodes. It is sometimes absent altogether, or may be cut off on an athecate internode.

Variation also occurs in the gonothecae. Female gonothecae normally have the aperture facing towards the stem, but examples have been seen where the gonothecae, containing embryos, are quite symmetrical and with terminal apertures.

**Distribution.** Cosmopolitan. Type locality: ‘European Ocean’. Syntype from Dieppe and Calvados (Redier 1967).

**Distribution in South Africa.** From off Table Bay, round the south coast and up the east coast to Moçambique, in 11–700 m. 33/18 (s), 34/18 (s), 35/21 (d), 34/22 (s), 35/22 (d), 34/23 (d), 33/25, 34/25 (s, d), 30/31 (d), 29/31 (d, v), 27/32 (d), 25/35 (v), 24/35 (d)

**Genus Plumularia** Lamarck, 1815

**Diagnosis.** Stem branched or unbranched (always unbranched in South Africa), bearing hydrocladia. Rarely with simple forms where the hydrocladia arise directly from the hydrorhiza. Hydrocladia alternate, sometimes with the whole plume spirally twisted (though not in South Africa), unbranched.

Type species: *Sertularia setacea* Linnaeus, 1758

**KEY TO SPECIES**

1. Hydrocladium bearing one hydrotheca only  
   - Hydrocladium bearing more than one hydrotheca  
     2

2. Hydrotheca with adcauline intrathecal septum. Hydrocladium ending in spine *P. spinolosa*  
   - Hydrotheca without intrathecal septum. Hydrocladium broadly rounded distally  
     3

3. Hydrotheca with concave adcauline wall. Two nematotheca in axil of hydrocladium  
   - Hydrotheca with convex to straight adcauline wall. One nematotheca in axil of hydrocladium  
     4
     5

4. Hydrotheca adnate for half or less of adcauline height  
   - Hydrotheca completely adnate or practically so  
     6

5. Hydrotheca with adcauline intrathecal septum. Gonotheca flat on substratum *P. filicaulis*  
   - Hydrotheca without intrathecal septum. Gonotheca borne on stem  
     7

6. Each stem internode with three nematotheca, two in axil of hydrocladium and one on opposite surface. Hydrotheca with free part of adcauline wall concave *P. pennycuikae*  
   - Stem with numerous nematotheca in two longitudinal rows. Hydrotheca with free part of adcauline wall straight  
     8

7. Adcauline wall of hydrotheca markedly convex  
   - Adcauline wall of hydrotheca more or less straight  
     9

8. One nematotheca on each hydrocladial apophysis. Hydrotheca seated more or less in centre of internode  
   - Two nematotheca on each hydrocladial apophysis. Hydrotheca usually not in centre of internode  
     10

9. hydrotheca seated more or less in centre of internode  
   - hydrotheca not in centre of internode
9. Gonotheca transversely annulated, borne on base of stem only
   - Gonotheca smooth, borne at any level on stem
   P. strictocarpa
   ... ... ... ... 10

10. Female gonotheca with external marsupium, without neck
    - Female gonotheca without marsupium, with curved tubular neck
    P. setacea
    ... ... P. warreni

11. Athecate internodes, when present, cut off from proximal end of thecate internodes,
    when not present hydrotheca seated on distal half of internode. First hydrocladal
    internode very short (less than ⅓ normal thecate internode)
    P. antonbruuni
    - Athecate internodes, when present, cut off from distal end of thecate internodes,
      when not present hydrotheca seated on proximal half of internode. First hydrocladal
      internode not very short (about ⅓ normal thecate internode)
      P. mossambicae

Plumularia antonbruuni Millard, 1967

Fig. 123A–D

Plumularia antonbruuni Millard, 1967: 185, fig. 5.

Diagnosis. Hydrorhiza penetrating into soft substratum, branching and filamentous. Stem unfascicled, reaching 51 mm, bearing alternate hydrocladia, indistinctly divided into internodes in upper region only, by straight nodes. Where demarcated each internode bearing one hydrocladal apophysis in distal half and three nematothecae, one on opposite side to apophysis and two on apophysis. No internodal septa. Mamelon present on upper surface of apophysis. The two rows of hydrocladia in one plane.

Hydrocladium bearing hydrothecae on upper surface, consisting of one very short athecate internode, then either all long thecate internodes or alternate athecate and thecate internodes, the latter condition being more common towards the distal end and the athecate internodes being cut off from the proximal ends of the thecate internodes. Nodes slightly oblique. First internode without nematothecae, with one internodal septum. Other athecate internodes with 0–2 median nematothecae and two internodal septa, one proximal and one distal. Thecate internodes with 0–3 median inferior nematothecae, the uppermost not reaching base of hydrotheca, one pair laterals overreaching thecal margin and sometimes one median superior; with two internodal septa, one proximal and one distal. Hydrotheca seated in distal half of internode in regions where no athecate internodes occur and in centre of internode in regions with athecate internodes.

Hydrotheca cup-shaped, completely adnate, widening to margin, with no intrathecal septum, with more or less straight abcauleine wall and convex abcauleine wall, 0.08–0.10 mm in abcauleine depth and 0.11–0.12 mm in marginal diameter. Margin oblique.

Nematothecae all two-chambered and movable, with funnel-shaped distal chamber.

Gonothecae borne on hydrocladal apophyses of stem. Only the male known: without nematothecae, smooth, elongated, with terminal aperture, held at a small angle (10–15°) to stem.

Distribution. Endemic to South Africa.
Distribution in South Africa. Type locality and only record: off Natal in 440 m, 29/31 (d)

*Plumularia filicaulis* Kirchenpauer, 1876


Diagnosis. Hydrorhiza creeping on weed, flattened and ribbon-shaped, with very thick perisarc and internal projections, giving rise to both pinnate and simple stems.

Pinnate stem unfascicled, reaching a height of 6 mm, bearing alternate hydrocladia, divided into regular internodes by distinct nodes. Lowest nodes very strong and very oblique, resembling hinge-joints, becoming less marked and less oblique distally. Each internode bearing one hydrocladal apophysis in centre or in distal half and two median nematothecae, one near the base and one next to the apophysis. Mamelon present on upper surface of apophysis. The two rows of hydrocladia not in the same plane, but displaced towards the anterior surface.

Hydrocladium bearing up to six hydrothecae on anterior surface, with perisarc of anterior surface greatly thickened around origins of hydrothecae and nematothecae; consisting of one short, athecate, anematothecate internode; sometimes a second short athecate internode with one nematotheca; then alternate long thecate and short athecate internodes terminated by transverse and oblique nodes respectively. Athecate internodes other than the first with one median nematotheca. Thecate internodes with three nematothecae, one median inferior reaching to base of hydrotheca and one pair laterals not reaching to thecal margin.

Simple stem arising from apophysis of hydrorhiza, reaching 5 mm in height, representing an independent hydrocladium and exactly similar to a hydrocladium in structure except that the first two nodes (bounding the first athecate internode) are very strongly developed and resemble hinge-joints.

Hydrotheca cup-shaped, adnate for only a small part of adcauline wall, with an adcauline intrathecal septum and a curved adcauline wall, 0,09–0,15 mm in height and 0,18–0,3 mm in marginal diameter. Margin forming an angle of about 45° with hydrocladium, produced to form a peak on the adcauline and on the adcauline side.

Median nematotheca immovable, two-chambered, with very small basal chamber and large curved distal chamber in which the adcauline wall is almost completely cut away. Lateral nematotheca movable, two-chambered, with very small basal chamber and long, funnel-shaped distal chamber.

Gonothecae borne on hydrorhiza and firmly applied to substratum, flattened, with very thick perisarc, irregularly ovate in outline, with a circular aperture on upper surface near one end and a variable number of minute pores on upper surface.
Fig. 123.

*Plumularia antonbruuni*. A and B, hydrocladia, A with only thecate internodes, B with alternate atecate and thecate internodes; C, part of stem with gonothecae and origins of hydrocladia; D, stem.

*Plumularia massambicae* sp. nov., from holotype. E, stem; F, part of stem showing origins of hydrocladia; G, hydrocladium.

*Plumularia flicicaulis*. H, hydrocladium; J, stem in anterior view showing origins of hydrocladia; K, male gonophore; L, fertile colony growing on weed, with pinnate stems, simple stems and gonothecae.

Scale: D, E and L in cm, the rest in mm/10.
Variation and remarks. This species shows considerable variation in its method of branching. Apart from its ability to exist in a pinnate and a simple form in the same colony, the simple stem occasionally produces a few irregular branches, and in one case a branch was seen to arise from within a hydrotheca. Further, in some cases the terminal part of a pinnate stem, after the origin of the last hydrocladium, may bear hydrothecae and is thus continued as a hydrocladium.

Thus, in its ability to bear cauline hydrothecae and also in the closely packed hydrothecae and the immovable median nematothecae, the species shows relationships with the subfamily Halopterinae.

Distribution outside South Africa. Chile (type locality), south-east Madagascar, Australia. (var. japonica from Japan.)

Distribution in South Africa. From South West Africa to Hermanus; Moçambique: littoral to 27 m. 26/15 (I), 33/18, 34/18 (s), 34/19, 26/32 (s), 24/35 (s), 23/35 (I)

Plumularia lagenifera Allman, 1886

Fig. 124A–D

?Aglaophenia Gaimardi Lamouroux, 1824: 611, pl. 95 (figs 9–10).

Diagnosis. Hydorhiza creeping, with or without internal perisarcal thickenings, flattened, bearing nematothecae. Stem unfascicled, reaching 45 mm in height, bearing alternate hydrocladia, divided into regular internodes by straight or slightly oblique nodes. Each internode bearing one hydrocladial apophysis in distal half and two nematothecae, one near base and one in axil of apophysis. Three or four internodal septa, including one near base, one near distal end and one in apophysis. Mamelon present on upper surface of apophysis. The two rows of hydrocladia not in one plane but displaced towards the anterior surface.

Hydrocladium bearing hydrothecae on upper surface, consisting of alternate short athecate and long thecate internodes terminated by oblique and transverse nodes respectively. First athecate internode without nematothecae, with one internodal septum. Other athecate internodes with one median nematotheca and one or two internodal septa. Thecate internodes with three nematothecae, one median inferior seated well below hydrotheca or just reaching its base and one pair laterals overreaching thecal margin, and with at least two internodal septa including one near base and one near distal end.

Hydrotheca cup-shaped, completely adnate, narrowing to margin, with no intrathecal septa, with abcauline wall distinctly convex and thickened, at least at margin, 0.06–0.17 mm in abcauline depth and 0.07–0.14 mm in marginal
diameter. Margin perpendicular to hydrocladium or almost so. Hydranth with about 17 tentacles.

Nematothecae all two-chambered and movable, with adcauline wall slightly lower than abcauline.

Gonothecae borne on hydrocladal apophyses of stem, dimorphic, male and female on separate colonies, without nematothecae, compressed, ovate in outline, with terminal aperture. Female about twice as long as broad, with aperture mounted on slender curved neck. Male about three times as long as broad, with shorter and less obviously curved neck.

Variation. A form described by Torrey as var. septifera occurs, in which the perisarc is in general much thicker and all internodes and hydrothecae are shorter. Thus the internodal septa are stronger, the whole abcauline wall of the hydrotheca is thickened, and the hydrotheca is wider than deep in contrast to the normal form which is deeper than wide. Internal thickenings of perisarc also occur in the hydrorhiza. This appears to be a growth-form only and all intermediate stages occur between it and the normal form.

Minor variations occasionally encountered include stolonization from the distal end of the stem, extra cauline internodes without hydrocladia, extra athecate internodes in the hydrocladia, extra cauline nematothecae (though not in axils) and branching hydrocladia. The curvature in the neck of the gonotheca varies considerably from almost straight to so strongly curved that the aperture faces downwards.

Remarks. This species is closely related to P. setacea, differing only in the shape of the hydrotheca. Discovery of intermediate forms may necessitate the combination of the two.

Distribution outside South Africa. West coast of America from Chile to Alaska. Type locality: Vancouver Island.

Distribution in South Africa. South West Africa to Hermanus; Knysna Estuary; littoral to 51 m. 26/15 (l, s), 28/16 (s), 32/17 (l), 32/18 (s), 33/17 (s), 33/18 (l, s), 34/18 (s), 34/19, 34/23 (s)

Plumularia mossambicae sp. nov.

Fig. 123E–G


Description. Hydrorhiza branching and filamentous for penetration of substratum. Stem unfascicled, bearing alternate hydrocladia, the two rows in one plane. Nodes transverse, not very distinct, irregular. Each internode bearing 1–5 hydrocladia (of which the first two are opposite, though broken off short, and the rest alternate). No internodal septa in main axis. Hydrocladal apophysis with a mamelon on upper surface and a weak internodal septum. Cauline
Plumularia lagenifera. A and B, hydrocladia, both from same sample; C, colony; D, stem in anterior view showing female gonothecae and origins of hydrocladia.

Plumularia setacea. E, colony; F, part of stem showing male gonotheca and origins of hydrocladia; G, hydrocladium; H, female gonotheca; J and K, stem and hydrocladium of epizootic form.

Scale: C and E in cm, the rest in mm/10.
nematothecae: two in axil of each apophysis, none on main axis of stem.

Hydrocladium very slender, with one athecate internode of moderate length, generally followed by long thecate internodes only, but sometimes with intermediate athecate internodes present towards the distal end. First athecate internode without nematothecae, with two internodal septa, one proximal and one distal. Thecate internode with two poorly defined internodal septa, one proximal and one distal; with one median inferior nematotheca well below the hydrotheca, one pair of laterals overtopping thecal margin and with or without one median superior nematotheca. Intermediate internode, when present, with two poorly defined internodal septa, one proximal and one distal, and one median nematotheca. When no athecate internodes occur the hydrotheca is seated in the proximal half of the internode. When intermediate internodes occur, they appear to be formed by cutting off the distal end of a thecate internode together with the median superior nematotheca. The previous thecate internode is then shorter than normal with the hydrotheca seated more or less in the centre and there is no median superior nematotheca. In one case the proximal end of the first thecate internode is cut off, taking with it the median inferior nematotheca.

Hydrotheca completely adnate, with more or less straight abcauline wall and slightly convex abcauline wall. Width at margin exceeding depth.

Nematothecae all two-chambered and movable, very large, especially the laterals which may be nearly twice the length of the hydrotheca.

Gonothecae absent.

**Measurements (mm)**

<table>
<thead>
<tr>
<th>Measurement Description</th>
<th>Measurement Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stem internode, length</td>
<td>0.59–2.10</td>
</tr>
<tr>
<td>diameter at node</td>
<td>0.08</td>
</tr>
<tr>
<td>Hydrocladium, first athecate internode, length</td>
<td>0.22–0.24</td>
</tr>
<tr>
<td>normal thecate internode, length</td>
<td>0.72–0.84</td>
</tr>
<tr>
<td>diameter in centre</td>
<td>0.04</td>
</tr>
<tr>
<td>athecate internode, other than first, length</td>
<td>0.31–0.44</td>
</tr>
<tr>
<td>Hydrotheca, depth abcauline</td>
<td>0.06–0.075</td>
</tr>
<tr>
<td>diameter at margin</td>
<td>0.08–0.085</td>
</tr>
<tr>
<td>Lateral nematotheca, length</td>
<td>0.09–0.11</td>
</tr>
</tbody>
</table>

**Remarks.** This species is closely related to *Plumularia antonbr unimaginily. It differs from it in the following characters:

(i) The stem internodes bear more than one hydrocladium each.
(ii) There are no cauline nematothecae on the main axis.
(iii) The first internode of the hydrocladium is not particularly short.
(iv) The hydrotheca is seated on the proximal half of the internode, and intermediate athecate internodes, when present, are cut off from the distal parts of the thecate internodes.

The species is also close to *P. ventriculiformis* Marktanner-Turneretscher, 1890, resembling it in the arrangement of the stem internodes (though Marktanner mentions an occasional cauline nematotheca) and in the position of the
hydrotheca on the thecate internode. It differs in the constant presence of an
athecate internode at the base of each hydrocladium.

Distribution. Endemic to South Africa.

Distribution in South Africa. The only record is the type material recorded
above. 24/35 (d).

Plumularia obliqua (Johnston, 1847)

Fig. 125A–B

Laomedea obliqua Johnston, 1847: 106, pl. 28 (fig. 1).
Plumularia obliqua: Bale, 1884: 138, pl. 12 (figs 1–3). Hincks, 1868: 304, fig. 36, pl. 67 (fig. 1).
Pennycook, 1959: 180. Millard & Bouillon, 1974: 34, fig. 8A–D.
?Monotheca posidoniae Picard, 1951: 341, fig. 2B.

Diagnosis. Hydrorhiza creeping on weed, with internal projections of perisarc.
Stem unfascicled, reaching a maximum height of 5 mm, bearing up to 13
alternate hydrocladia, divided into internodes by straight nodes, each bearing
one hydrocladal apophysis in distal half. The two rows of hydrocladia in one
plane. Each internode bearing two nematothecae (one in axil of apophysis and
one on opposite side of internode). Mamelon present on upper side of apophysis.
At least three internodal septa, one proximal, one distal and one in apophysis.

Hydrocladium bearing one hydrotheca only, consisting of two internodes,
one short and athecate, and one long and thecate. Athecate internode with one
or two internodal septa and no nematothecae. Thecate internode bearing the
hydrotheca on the anterodistal surface, narrowed and curved round the thecal
wall, then widening to a broad, rounded distal end terminating very slightly
below thecal margin. Three nematothecae: one median inferior reaching
approximately to thecal base and one pair laterals above thecal margin.

Hydrotheca slightly compressed, cup-shaped, completely adnate, with a
smoothly convex to straight abcauline wall, abcauline wall with margin everted
over end of internode, with no intrathecal septum, 0.17–0.2 mm in abcauline
height and 0.12–0.17 mm in marginal diameter.

Nematothecae all two-chambered and movable. Median and cauline
nematothecae with abcauline wall lower than abcauline. Lateral nematotheca
deply cut away on upper face.

Gonotheca (not reported from South Africa) very large, ovate, truncated
distally (Hincks).

Variation. Extra regenerative nodes often appear in the stem. The thickness of
the perisarc is variable, and young hydrocladia have no internodal septa behind
the hydrotheca while old ones have two strong septa.

Distribution outside South Africa. North Atlantic, Mediterranean, Australia,
Japan. Type locality: Brighton, England.

Distribution in South Africa. Inhaca and Transkei coast, littoral to 15 m.
31/29 (1), 26/32 (1, s)
Fig. 125.

*Plumularia obliqua*. A, stem; B, hydrocladium.

*Plumularia pulchella*. C, hydrocladium; D, stem with gonothecae.

*Plumularia spinulosa*. E, stem with gonotheca; F-J, different views of hydrocladium, F from the side (lateral nematotheca removed), G, oblique view showing opening of funnel into septum, H, from behind, and J from above looking onto septum.

Scale in mm/10.
Plumularia pennycuikiae Millard & Bouillon, 1973

Fig. 126A–C

Plumularia sp. Pennycuik, 1959: 183, pl. 3 (fig. 7).
Plumularia pennycuikiae Millard & Bouillon, 1973: 85, fig. 10N, P. Hirohito, 1974: 39, fig. 18.

Diagnosis. Stem unfascicled, branched or unbranched, reaching 13 mm in height, bearing alternate hydrocladia, divided into internodes by transverse nodes. Each internode bearing one hydrocladiad apophysis at distal end and three nematothecae, two in axil and one on opposite surface, usually with one internodal septum at proximal end. Mamelon present on upper surface of apophysis. Branches, when present, arising next to hydrocladium from same apophysis, similar to stem. The two rows of hydrocladia in same plane.

Hydrocladium bearing hydrothecae on upper surface, consisting of one very short athecate and anemotheca internode terminated by an oblique node, then alternate long thecate and shorter athecate internodes terminated by transverse and oblique nodes respectively. First internode with two internodal septa, one proximal and one distal. Other athecate internodes with one median nemathotheca, with or without septa. Thecate internodes with three nematothecae, one median inferior reaching approximately to base of hydrotheca and one pair laterals not reaching thecal margin, without septa. Hydrotheca seated more or less in centre of internode.

Hydrotheca cup-shaped, adnate for about half adcauline length or a little more, with no intrathecal septum, with straight adcauline wall and with adcauline wall distinctly concave in free section, 0.13–0.15 mm in adcauline length and 0.12–0.15 mm in marginal diameter. Margin oblique.

Nematothecae all two-chambered and movable, with funnel-shaped distal chamber. Adcauline wall lower than adcauline in median nematothecae.

Gonothecae (not reported from South Africa) borne on apophyses of stem; female small, oval to spherical, containing one egg which develops into a planula in situ. Male gonotheca unknown.

Distribution outside South Africa. Seychelles, Queensland, Australia, and Japan. Type locality: Silhouette Island, Seychelles.

Distribution in South Africa. Santa Carolina in Moçambique only. 21/35

Plumularia pulchella Bale, 1882

Fig. 125C–D

Plumularia pulchella Bale, 1882: 30, pl. 15 (fig. 6). Bale, 1884: 140, pl. 12 (fig. 6), pl. 19 (fig. 37). Totton, 1930: 221, fig. 58. Ralph, 1961b: 39, fig. 5c–e.
Plumularia flexuosa Bale, 1894: 115, pl. 5 (figs 6–10).
Plumularia (Monotheca) flexuosa: Stechow, 1925a: 499.

Diagnosis. Hydrorhiza creeping, with or without internal projections of perisarc. Stem unfascicled, reaching a height of about 10 mm, bearing up to 29 alternate hydrocladia. Divided into regular internodes by distinct nodes, each bearing one hydrocladiad apophysis in distal half. The two rows of hydrocladia in the
same plane or displaced very slightly towards the anterior surface. Each inter-
node bearing three nematothecae (one in basal half, two in axil of apophysis). 
Mamelon present on upper surface of apophysis.

Hydrocladium bearing one hydrotheca only. Consisting of two internodes, 
one short and athecate and one long and thecate. Athecate internode with two 
internodal septa and no nematothecae. Thecate internode bearing the hydrotheca 
on the upper surface, with its distal end narrowed and curved round the adcauline 
theocal wall, then widening to a broadly rounded distal end terminating just 
below the thecal margin. Three nematothecae: one median inferior reaching 
above base of hydrotheca to about a third of its height, and one pair laterals 
overlapping thecal margin.

Hydrotheca cup-shaped, completely adnate, widening distally and curved 
away from hydrocladium, with concave abcauline wall, with no intrathecal 
septa, 0.09–0.13 mm in depth and 0.10–0.14 mm in marginal diameter. Margin 
almost perpendicular to hydrocladium.

Nematothecae all two-chambered, movable and funnel-shaped.

Gonothecae borne on hydrocladial apophyses, usually smooth, ovate, 
tapering below to slender, curved base, truncated distally, with wide terminal 
aperture.

Variation. The stem occasionally gives off 1–3 branches. These replace hydro-
cladia and are quite irregular in arrangement. At the base of the stem there may 
be up to four irregular internodes, occasionally with nematothecae.

The presence or absence of internodal septa is variable. Usually there is 
one in each hydrocladial apophysis, two in the thecate internode of the 
hydrocladium and up to two in the thecate internode behind the hydrotheca.

Regeneration after injury may result in extra irregular internodes in the 
stem or in the hydrocladia. Thus the latter may have two thecate internodes 
at the base, of which one may bear a nematotheca.

The gonothecae are variable in appearance, being sometimes smooth and 
sometimes irregularly corrugated. The aperture is usually at right angles to 
the axis, but it may be slightly oblique. Some of the gonothecae have a raised 
collar around the opening.

Distribution outside South Africa. Australia (type locality), New Zealand, Vema 
Seamount (South Atlantic), Japan.

Distribution in South Africa. West coast of Cape Peninsula to Natal, littoral to 
100 m. 33/18 (l), 34/18 (l, s), 35/19 (s), 35/20 (d), 34/22 (s), 34/23 (s, h), 33/25 
(s), 34/25 (s), 33/27 (s), 32/28 (s), 29/31 (s), 28/32 (d)

Plumularia setacea (Linnaeus, 1758)

Fig. 124E–K

Sertularia setacea Linnaeus, 1758: 813.
Plumularia setacea: Hincks, 1868: 296, fig. 34, pl. 66 (fig. 1). Broch, 1914: 25, pl. 1 (fig. 1).
Ralph, 1961b: 33, figs 3e, 4a, e–d. Vervoort, 1966b: 142, fig. 43. Millard, 1968: 278, 
fig. 5F–H. Millard, 1973: 27, fig. 3.
**Diagnosis.** Hydrorhiza creeping. Stem unfascicled, generally 10–20 mm in height (maximum 40 mm), bearing alternate hydrocladia, divided into regular internodes by transverse or slightly oblique nodes. Each internode bearing one hydrocladial apophysis in distal half and two nematothecae, one near base on side opposite to apophysis and one on apophysis. Internodal septa present or absent; when present including one in proximal region, one in distal region and one in apophysis. Mamelon present on upper surface of apophysis. The two rows of hydrocladia not in one plane but displaced towards the anterior surface.

Hydrocladium bearing hydrothecae on upper surface, consisting of one very short athecate internode, then alternate long thecate and shorter athecate internodes terminated by transverse or slightly oblique nodes. First internode without nematothecae, with one internodal septum. Other athecate internodes with one median nematotheca and two internodal septa, one proximal and one distal. Thecate internodes with three nematothecae, one median inferior not reaching base of hydrotheca and one pair laterals overreaching thecal margin, and with at least two internodal septa including one near base and one near distal end. Hydrotheca generally seated in centre of internode.

Hydrotheca cup-shaped, completely adnate, widening to margin, with no intrathecal septum, with straight abcauline wall, 0.06–0.12 mm in abcauline depth and 0.08–0.12 mm in marginal diameter. Margin slightly oblique.

Nematothecae all two-chambered and movable, with funnel-shaped distal chamber.

Gonothecae borne on hydrocladial apophyses of stem, dimorphic, male and female on separate colonies, without nematothecae, elongated, with terminal aperture. Male very slender, with small aperture. Female larger, compressed, with larger aperture on tubular neck, which may be curved slightly to one side, containing about eight eggs which develop into planulae in situ.

**Variation.** The hydrotheca of this species is known to vary in size. Normally it is $\frac{2}{3}$ length of the internode, but Broch (1914) distinguished a forma microtheca in which it is only $\frac{4}{5}$ length of the internode. In South Africa there are all variations between these limits.

An epizootic form of the species commonly occurs on other hydroids (e.g. on Nemertesia cymodocea and Salacia articulata), which is characterized by a greater or lesser degree of stunting. The stem is usually under 10 mm in height, and the hydrocladia are short, bearing one, or at most, four hydrothecae. The nematothecae are also reduced in size, especially the laterals which may be minute.

Less important variations include branching of the stem, variation in length of stem internodes, the placing of the two rows of hydrocladia in one plane, extra internodal septa and extra nematothecae (e.g. on the stem internodes and on the thecate hydrocladial internodes).

Because of the possibility of confusion between this species and *P. warreni* and *P. strictocarpa*, only records with mature gonophores have been quoted below.
**Distribution.** Cosmopolitan. Type locality: U.K.

**Distribution in South Africa.** All round the coast, common in the littoral region and shallow water, rare in deeper water to 430 m. 26/15 (l), 32/18 (l, s), 33/17 (s), 33/18 (l, s), 34/18 (l, s, h), 35/19 (s), 34/20 (l), 34/22 (s), 34/23 (s), 33/25 (s, h), 34/25 (s) 33/27 (l), 31/29 (l), 31/30 (l), 30/30 (l), 29/31 (l, s, d), 28/32 (s), 25/32 (s)

*Plumularia spinulosa* Bale, 1882

Fig. 125E–J


*Monotheca spinulosa* var. *obtusa* Stechow, 1923e: 224.


*Plumularia spinulosa* var. **typica**: Millard, 1958: 212.

*Plumularia spinulosa* var. *spinulosa*: Ralph, 1961b: 37, fig. 4i–j.

**Diagnosis.** Hydrorhiza creeping, strengthened by internal projections of perisarc.

Stem unfascicled, reaching a height of about 5 mm, bearing up to 18 alternate hydrocladia; divided into regular internodes by distinct nodes, each bearing one hydrocladal apophysis. The two rows of hydrocladia in the same plane or displaced slightly towards the anterior surface. Each internode usually with three internodal septa (one near base, one near distal end and one in apophysis) and bearing two nematotheca (one near base and one in axil of apophysis). Mamelon present on upper surface of apophysis.

Hydrocladium bearing one hydrotheca only. Consisting of two internodes, one short and athecate and one long and thecate. Athecate internode with one internodal septum and no nematotheca. Thecate internode bearing the hydrotheca on the upper surface and with its distal end curved round the adcauline thecal wall, ending in a short, bluntly pointed spine at or above the thecal margin. Usually one or two internodal septa behind adcauline thecal wall. Three nematotheca: one median interior reaching approximately to base of hydrotheca and one pair of laterals overtopping thecal margin.

Hydrotheca laterally compressed, completely adnate, with convex adcauline wall; with a strong adcauline intrathecal septum projecting about half-way across cavity and with a funnel-shaped opening into it on each side; with an adcauline intrathecal septum near base, so that expanded hydanth is twisted into an S-shape. Margin perpendicular to hydrocladium, somewhat sinuated in adcauline region. Hydrotheca 0.12–0.18 mm in depth and 0.10–0.17 mm in marginal diameter. Hydanth with about 13 tentacles.

Nematotheca all two-chambered and movable. Wall of distal chamber lower on adcauline side.

Gonothecae borne on hydrocladal apophyses, smooth, deep-campanulate and sometimes curved asymmetrically, with a wide terminal aperture, containing one or two gonophores.

**Variation.** The most obvious variations are in the length of the terminal hydrocladal spine, which may just reach the thecal margin or may be produced above
it, and in the position of the hydrocladal apophysis, which may arise either from the distal end of the stem internode or from its centre. Both variations may occur within the same colony.

Minor variations include the presence or absence of one or two irregular internodes without hydrocladia or nematothecae at the base of the stem, the position of the basal nematotheca on the stem internode, and the number of internodal septa which may be greater or less than the number given in the diagnosis depending on the strength of the perisarc in the colony as a whole. A few instances of a branching stem have been seen.

Distribution outside South Africa. Australia (type locality), New Zealand, Japan, Vema Seamount (South Atlantic).

Distribution in South Africa. False Bay to Natal, littoral to 56 m. 34/18 (s), 34/22 (s), 33/25 (s), 34/25 (s), 33/26 (s), 33/27 (l, s), 32/28 (s), 31/29 (l), 31/30 (l), 30/30 (l, s), 29/31 (l, s)

*Plumularia strictocarpa* Pictet, 1893

Fig. 126D-E

*Plumularia strictocarpa* Pictet, 1893: 55, pl. 3 (figs 47–49). Stechow & Uchida, 1931: 565, fig. 12, pl. 15 (fig. 6). Millard & Bouillon, 1973: 88, fig. 11A–B.

Diagnosis. Stem unfascicled, reaching 10 mm in height, bearing alternate hydrocladia, divided into regular internodes by transverse nodes. Each internode bearing one hydrocladal apophysis at distal end and two nematothecae, one in axil and one on opposite side of internode. Internodal septa usually absent. Mamelon present on upper surface of apophysis. The two rows of hydrocladia in one plane.

Hydrocladium bearing hydrothecae on upper surface, consisting of one very short athecate internode terminated by an oblique node, then alternate long thecate and shorter athecate internodes terminated by straight or slightly oblique nodes. First internode without nematothecae, with one internodal septum. Other athecate internodes with one median nematotheca and usually two internodal septa, one proximal and one distal. Thecate internodes with three nematothecae, one median inferior seated well below base of hydrotheca and one pair laterals overreaching thecal margin, and with at least one internodal septum at proximal end. Hydrotheca seated more or less in centre of internode.

Hydrotheca cup-shaped, almost completely adnate, widening to margin, with no intrathecal septum, with straight abcauline wall, 0,06–0,08 mm in abcauline depth and 0,08–0,11 mm in marginal diameter. Margin slightly oblique.

Nematothecae all two-chambered and movable, with funnel-shaped distal chamber.

Gonothecae borne on lower part of stem only, on apophyses of hydrocladia which have usually fallen off, elongate-oval, transversely annulated, with
Fig. 126.

*Plumularia pennycuikae*. A, stem; B, part of stem showing origins of hydrocladia; C, hydrocladium.

*Plumularia strictocarpa*. D, lower part of stem with female gonothecae; E, hydrocladium.

*Plumularia warreni*. F, hydrocladium; G, anterior view of stem with female gonothecae and their marsupia; H, stem with male gonothecae.

Scale: A in mm, the rest in mm/10.
terminal aperture and no neck, reaching 1,0 mm in length and 0,6 mm in maximum diameter. Young ones shorter and truncated.

Remarks. This species cannot be distinguished from *P. setacea* in the absence of gonothecae.

*Distribution outside South Africa*. Circumglobal in tropical and subtropical waters. Type locality: Bay of Amboine, East Indies.

*Distribution in South Africa*. Santa Carolina in Moçambique only. 21/35

*Plumularia warreni* Stechow, 1919

Fig. 126F–H

*Plumularia tenuis* Warren, 1908: 316, fig. 13.


*Diagnosis*. Hydorhiza creeping, usually on weeds, with internal projections of perisarc. Stem unbranched, reaching a maximum height of 22 mm, bearing alternate hydrocladia, divided into regular internodes by transverse nodes. Each internode bearing one hydrocladial apophysis in distal half and two nematothecae, one near the base on anterior surface and one on apophysis. Internodal septa present or absent; when present including one in proximal region, one in distal region and one in apophysis. Mamelon present on upper surface of apophysis. The two rows of hydrocladia usually not in one plane but displaced towards anterior surface.

Hydrocladium bearing hydrothecae on upper surface, consisting of one very short athecate internode, then alternate long thecate and shorter atethecate internodes terminated by transverse or oblique nodes. First internode without nematothecae, with one internodal septum. Other atethecate internodes with one medial nematotheca and usually two internodal septa, one proximal and one distal. Thethecate internodes with three nematothecae, one median inferior not reaching to base of hydrotheca and one pair laterals overreaching thecal margin, and usually with at least two internodal septa including one near base and one near distal end. Hydrotheca seated more or less in centre of internode.

Hydrotheca cup-shaped, completely adnate, widening to margin, with no intrathecal septum, with more or less straight abcauline wall, 0,06–0,11 mm in abcauline depth and 0,09–0,14 mm in marginal diameter. Margin slightly oblique. Hydranth with 18–20 tentacles.

Nematothecae all two-chambered and movable, with funnel-shaped distal chamber.

Gonothecae borne on hydrocladial apophyses of stem, dimorphic, male and female on separate colonies, without nematothecae, transverse-oval in section, with terminal aperture. Male elongated, often slightly curved, with irregular outline, reaching 0,8 mm in length. Female elongate-oval, smooth or with irregular outline, without neck, eggs extruded into an external marsupium, where they develop into planulae; young ones with truncated distal end.
Variation. Occasionally the stem branches near the base.

Remarks. This species cannot be distinguished from P. setacea in the absence of gonothecae. A form of the species occurs on the west coast of the Cape Peninsula in which the hydrocladia have only one or two thecate internodes and in which there is usually a deficiency in the nematotheca complement, in many stems only the laterals remaining. The female gonophores are also larger than those from the east coast.

Distribution outside South Africa. Queensland, Madagascar, Seychelles, and southern India. Type locality: Natal, South Africa.

Distribution in South Africa. Coast of Natal and Moçambique, littoral, with two records from the west coast of the Cape Peninsula. 33/18 (l), 34/18 (l), 29/31 (l), 27/32 (l), 26/32 (l), 24/35 (s), 23/25 (l), 21/35

Plumularia wasini Jarvis, 1922

Fig. 127

Plumularia wasini Jarvis, 1922: 349, fig. 1, pl. 26 (fig. 23). Millard, 1962: 301, fig. 8.

Diagnosis. Hydrorhiza creeping. Stem unfascicled, reaching 36 mm in height, bearing alternate hydrocladia, divided into internodes of irregular length by transverse nodes, of much greater diameter than hydrocladia. Each internode bearing 1–5 short hydrocladal apophyses, the two rows of hydrocladia in the same plane. No internodal septa. Nematostele numerous, in two longitudinal rows. No mamelon.

Hydrocladium bearing hydrothecae on upper surface, consisting of alternate short athecate and longer thecate internodes terminated by oblique and transverse nodes respectively. Each thecate internode with one or two median nematothecae. Each thecate internode with one median inferior nematotheca not quite reaching base of hydrotheca, one pair pedicellate laterals not quite reaching margin, and one or a pair of minute median superior behind adcauline wall of hydrotheca. No internodal septa.

Hydrotheca cup-shaped, wider than deep, adnate for about half height, then free, with no intrathecal septa, with more or less parallel adcauline and abcauline walls, 0,12–0,2 mm in abcauline height and 0,2 mm in marginal diameter. Margin forming an angle of about 40° with hydrocladium.

Nematostele two-chambered and movable, except the superiors, which are minute, one-chambered and immovable, all with the adcauline wall cut away to a certain extent.

Gonothecae borne on hydrocladia immediately below the hydrothecae, dimorphic, pedicellate, bearing two or three large nematothecae, female(?) flattened pear-shaped, large and on first thecate internode, male smaller and round in section and on thecate internodes other than the first, both with terminal aperture.
Variation. The most marked variation is in the length of the stem internodes and in the structures which they bear. Although the hydrocladia are spaced fairly evenly, the number borne on a stem internode varies from one to five and the length of the internode varies accordingly, as does the number of nematothecae (2–14). The latter are arranged in two fairly distinct longitudinal rows, which may lie along the lateral surfaces or on the anterior surface. Here and there nematothecae may be displaced from their rows.

The straight nodes on the hydrocladia are sometimes indistinct. One instance of a branching hydrocladium has been seen.

Distribution outside South Africa. Tropical East Africa (type locality).
Distribution in South Africa. Natal to Moçambique (Santa Carolina), 18–100 m.
31/29 (s), 29/31 (s), 29/32 (s), 28/32 (d), 21/35

Subfamily Aglaopheniinae

Diagnosis. Stem erect, branched or unbranched, fascicled or unclasped, bearing hydrocladia. No cauline hydrothecae. Hydrocladia arising from a single axial tube in fascicled stems, homomeros, bearing close-set hydrothecae generally on the anterior surface. Hydrothecae generally completely adnate and with toothed margin. Paired lateral nematothecae always present and fused to hydrothecae; generally (always, in South African species) at least three nematothecae to each hydrotheca, one pair laterals and one median inferior which may or may not be fused to hydrotheca. All nematothecae one-chambered and immovable, though often with more than one opening, of which one may communicate with cavity of hydrotheca. Gonothece unprotected, or protected by simple nematophore-bearing phylactocarps, or aggregated into a corbula.

KEY TO GENERA

[Genera not represented in South Africa are bracketed]

1. Gonothecae unprotected ... ... ... ... ... Gymnangium p. 432
- Gonothecae protected by accessory structures ... ... ... ... ... 2
2. Gonothecae aggregated in a corbula, which replaces a hydrocladium and bears secondary ribs ... ... ... ... ... ... ... 3
- No true corbula present, gonothecae solitary and protected by unbranched phylactocarps ... ... ... ... ... ... ... 4
3. Each corbula rib with a hydrotheca at its base ... ... ... ... Theococarpus p. 453
- Corbula ribs without hydrothecae at their bases ... ... ... ... Aglaophenia p. 407
4. Phylactocarp formed from a modified hydrocladium ... Lytocarpus p. 446
- Phylactocarp an appendage of a hydrocladium, which is itself unmodified ... ... ... 5
5. Hydrocladia arranged in a spiral around stem ... ... ... ... ... [Streptocaulus]
- Hydrocladia pinnately arranged in two longitudinal rows ... Cladocarpus p. 416

Genus Aglaophenia Lamouroux, 1812

Diagnosis. Stem branched or unbranched, bearing alternate hydrocladia. Hydrocladia unbranched. Hydrotheca sac-shaped to deep, usually with toothed margin and an adcauline intrathecal septum. Median inferior nematotheca at least partly adnate to hydrotheca, of variable length. Gonothecae in corbula formed by modified hydrocladium bearing secondary ribs. Ribs bearing nematothecae but no hydrothecae.

Type species: Sertularia pluma Linnaeus, 1758.

KEY TO SPECIES

(Doubtful species not included; for these see p. 415)

1. Stem strongly fascicled. Median inferior nematotheca adnate to hydrotheca for entire length ... ... ... ... ... ... ... ... ... ... ... A. cupressina
- Stem unclasped. Median inferior nematotheca not adnate to hydrotheca for entire length ... ... ... ... ... ... ... ... ... ... ... 2
2. Hydrotheca with a solid perisarcal keel on abcauline surface projecting as an 'outer point' beyond the abcauline marginal tooth \[ A. \text{latecarinata} \]
- Hydrotheca with no perisarcal keel, median abcauline tooth simple \[ A. \text{pluma} \]

*Aglaophenia cupressina* Lamouroux, 1816

Fig. 128A–C


*Aglaophenia magillivrayi*: Allman, 1883: 34, pl. 10, pl. 20 (figs 4-6).

*Diagnosis*. Stem robust, thickly fascicled, branching and rebranching irregularly up to the fourth order, reaching a maximum height of 230 mm, bearing alternate hydrocladia from an axial tube (though hydrocladia absent in basal parts). Final branches (pinnæ) arising from axial tube of stem at regular intervals in subopposite pairs, unfascicled or with one or two supplementary tubes derived from the accessory tubes of stem, bearing alternate hydrocladia. No hinge joints. Axial tube of pinna segmented, each internode bearing one hydrocladal apophysis, with two nematothecae and a mamelon on the apophysis.

Hydrocladia closely set, short (1–2 mm), bearing hydrothecae on anterior surface, divided into squarish thecate internodes by transverse nodes, proximal internodes larger than distal ones. Each internode with two powerful internodal septa converging towards one another anteriorly. Anterior wall of internode with thick perisarc.

Hydrotheca deep, obconical, completely adnate, 0.3 mm in height and 0.14–0.15 mm in marginal diameter, with an abcauline intrathecal septum arising above hydropore and running obliquely upwards across about two-thirds of cavity. A faint longitudinal line (visible only in macerated specimens) down centre of lateral surface. Margin smooth or sinuated, often with two or three pairs low rounded lobes.

Median inferior nematotheca completely adnate to hydrotheca, with a thick sigmoid intranematothecal septum arising from abcauline wall and passing obliquely downwards, with one large distal aperture sometimes bordered by two rounded lateral lobes; with no communication with hydrotheca. Lateral nematothecae tubular, curved, overreaching thecal margin, with one distal aperture.

Corbulae borne on pinnæ, replacing hydrocladia, with pedicel of onethecate segment and about six pairs of alternate ribs. Each rib bearing nematothecae along outer edge, the first two or three on a raised lobe, and with inner edge fused to rib behind (corbula closed). The first rib sometimes with a free branch on one side. Corbula reaching 2.8 mm in length and 1.1 mm in diameter.

Colour olive green to greenish black. 'Dreaded for its stinging powers' (Vervoort 1941).

*Distribution outside South Africa*. Tropical Indo-Pacific, from Zanzibar in East Africa to the Great Barrier Reef, extending northwards in the Pacific to the Sea of Okhotsk. Type locality: East Indies.
**Distribution in South Africa.** Santa Carolina in Moçambique, only. 21/35

*Aglaophenia latecarinata* Allman, 1877

Fig. 128D–F

*Aglaophenia latecarinata var. madagascariensis* Billard, 1907a: 387, pl. 26 (figs 18–19).
*Aglaophenia latecarinata:* Vervoort, 1968: 72, fig. 33.

**Diagnosis.** Stem unfascicled, unbranched, reaching a maximum height of 28 mm, with two hinge-joints separating a short basal part from a distal part bearing alternate hydrocladia. Basal part bearing a row of large median nematothecae only. Distal part generally unsegmented except in terminal region where oblique nodes separate short internodes bearing one hydrocladium each. Two or three nematothecae to each hydrocladial apophysis, one axillary anterior, one inferior anterior, and sometimes one axillary posterior. Mamelon present on anterior surface of apophysis. The two rows of hydrocladia not in one plane but shifted onto the anterior surface.

Hydrocladium bearing hydrothecae on anterior surface, consisting of thecate internodes separated by transverse nodes. Internodes with two distinct septa.

Hydrotheca sac-shaped, with a distinct adcauline intrathecal septum at about one-third of height, 0.2–0.4 mm in height and 0.12–0.16 mm in marginal diameter. Margin forming an angle of about 50° with internode, with nine marginal teeth, one median abcauline and four pairs laterals. Median abcauline tooth double, with an inner point, and a solid outer point continuous with a keel of perisarc down abcauline wall of hydrotheca.

Median inferior nematotheca adnate to abcauline thecal wall up to level of intrathecal septum, then free; not reaching thecal margin; with three apertures, one terminal, one on upper surface at base of free part (these two sometimes confluent), and one into hydrotheca; generally with a perisarcal thickening on abcauline surface. Lateral nematotheca sac-shaped, curved, not reaching thecal margin, with one distal aperture extending onto medial surface. Cauline nematotheca sac-shaped, with one wide, or two small, terminal aperture(s).

Corbula replacing hydrocladium; up to 3 mm in length; with a pedicel of one hydrotheca-bearing segment; bearing up to 10 pairs of alternate ribs. Each rib bearing a series of nematothecae along outer edge, the first on a spinous process, with inner edge fused to rib behind but leaving a series of openings into the interior.

**Variation.** The marginal teeth of the hydrotheca are variable. The four lateral teeth tend to be in two groups, with a more pronounced bay separating the first and second from the third and fourth. Generally this central bay is shallow and the two middle teeth are broad and rounded and the two outer ones narrow and pointed. A form also occurs with a very deep central bay, taller middle teeth and a reduced fourth (the most abcauline) tooth, which looks more like a
Fig. 128.

_Aglaophenia cupressina._ A, stem; B, hydrocladium; C, corbula.

_Aglaophenia latecarinata._ D, stems; E, hydrocladium; F, female corbula (apertures between ribs shaded).

Scale: A and D in cm, the rest in mm/10.
subsidiary point on the third (var. *madagascariensis* Billard). This form lacks the posterior axillary cauline nematotheca. The outer point of the median abcauline tooth is normally longer than the inner, but in the first hydrocladal internode it tends to be shorter than the inner and the median inferior nematotheca reduced, not reaching to the level of the intrathecal septum.

The thickening on the abcauline wall of the median inferior nematotheca is also variable, sometimes resembling a transverse septum and sometimes not developed at all.

*Distribution outside South Africa.* Atlantic Ocean from American to African coast and from the Azores in the north to Brazil and Angola in the south, very common in the tropical west Atlantic on Sargasso weed; Indian Ocean from Cargados and Madagascar. Type locality: Gulf of Mexico on floating weed.

*Distribution in South Africa.* Eastern Cape, Natal and Moçambique, in 6–55 m. 31/29 (s), 30/30 (s), 29/31 (s), 28/32 (s), 24/34 (s)

*Aglaoephnia plumula* (Linnaeus, 1758)

*Sertularia plumula* Linnaeus, 1758: 811.


*Diagnosis.* Stem unfascicled, branched or unbranched, with two (or occasionally three) hinge-joints separating a short basal part from a distal part bearing alternate hydrocladia. Basal part without hydrocladia or nematotheca, divided into irregular internodes by transverse nodes. Distal part divided into internodes by slightly oblique nodes, each internode bearing one hydrocladal apophysis and three nematotheca, one axillary anterior, one axillary posterior and one anterior inferior which may be seated on the base of the apophysis. Mamelon present on anterior surface of apophysis. The two rows of hydrocladia not in one plane but shifted on to anterior surface.

Hydrocladium bearing hydrothecae on anterior surface, consisting of thecate internodes separated by transverse or slightly oblique nodes. Internodes with two internodal septa.

Hydrotheca sac-shaped, expanding to margin, with an abcauline intrathecal septum at about one-third of the height, 0.17–0.4 mm in height and 0.12–0.3 mm in marginal diameter. Margin forming an angle of 60–70° with internode, with nine teeth, one median abcauline and four pairs laterals of which the second from the abcauline side may be double.

Median inferior nematotheca adnate to abcauline thecal wall for over two thirds of latter, then free; reaching to thecal margin or just below; with three apertures, one terminal, one on upper surface at base of free part (these two often confluent) and one into hydrotheca. Lateral nematotheca sac-shaped, reaching to thecal margin or just below, with one distal aperture extending onto median surface. Cauline nematotheca gutter-shaped.

Corbula replacing hydrocladium, consisting of a pedicel of one hydrotheca-
bearing segment, and then 4–9 alternate paired ribs, male and female on separate colonies. Female corbula closed; ribs, except for the first, bearing nematotheca along outer edge and fused to rib behind by inner edge; first rib free, giving off a branch on one side lying parallel to axis of corbula; both first rib and its branch bearing nematotheca on both edges. Male corbula partly or completely open; ribs, except for the first, fused in basal part and bearing nematotheca along outer edge, free in distal part and bearing nematotheca along both edges; first rib free and bearing nematotheca along both edges, normally unbranched. Corbula 2–3 mm in length.

Variation. One large median nematotheca occurs on the stem internode between the hinge-joints. The first internode beyond the hinge-joints may be longer than usual and give rise to two hydrocladia.

On the hydrocladial internodes the length of the median inferior nematotheca varies, though it tends to be longer in subspecies parvula.

In the corbula the branch of the first rib is occasionally absent in the female, and occasionally present, though small and stunted, in the male.

KEY TO SUBSPECIES

1. Stem long (usually over 100 mm) and straggling, with repeated dichotomous division .................................................. A. p. dichotoma
   – Stem short (usually under 100 mm) and unbranched or sparsely branched ........ 2

2. Hydrotheca with all marginal teeth simple and undivided .................................................. A. p. pluma
   – Hydrotheca with second paired tooth from abcauline side normally double  A. p. parvula

Aglaophenia pluma pluma (Linnaeus, 1758)

Fig. 129D

Aglaophenia pluma forma typica Bedot, 1919: 276.
Aglaophenia pluma var. typica: Millard, 1957: 238, fig. 15A.

Diagnosis. Stem short, reaching 97 mm, but usually much less, normally unbranched.

Marginal teeth of hydrotheca of approximately equal length and not divided. Median inferior nematotheca not reaching thecal margin.

Colour: Stem dark brown, hydrocladia light brown.

Variation. The stems may occasionally branch once or twice dichotomously, thus tending towards subs. dichotoma. Branches may also occur which replace hydrocladia; these resemble stems in their structure, with a basal part without hydrocladia separated from a distal hydrocladia-bearing part by two hinge-joints.

Rarely in the hydrotheca the second paired tooth from the abcauline side may have a small subsidiary point, thus tending towards subs. parvula.

Distribution. Cosmopolitan. Type locality: U.K.
Distribution in South Africa. South West Africa to Natal, not common, littoral to 49 m. 22/14 (l), 26/15 (s), 34/18 (s), 73/4/22, 34/23, 30/30 (l), 39/31 (l, s), 27/32 (l)

Aglaophenia plumula dichotoma (M. Sars, 1857)

Fig. 129A, C, E

Plumularia plumula var. dichotoma M. Sars, 1857: 164.
Aglaophenia dichotoma: Ritchie, 1907b: 539, pl. 3 (fig. 2). Stechow, 1925a: 516.
Aglaophenia heterodontia: Ritchie, 1909 (pp): 96.

Diagnosis. Stem long and straggling, reaching 300 mm, branching profusely in a dichotomous manner. The two limbs of a dichotomy of equal diameter and arising from two apophyses on a single broad stem internode, all internodes bearing hydrocladia.

Marginal teeth of hydrotheca sharply pointed and triangular, normally undivided. Median inferior nematotheca not, or only just reaching thecal margin.

Colour: Stem medium brown, hydrocladia cream.

Variation. In the hydrotheca the second paired tooth from the abcauline side may have a small subsidiary point as in subsp. parvula.

Distribution outside South Africa. Atlantic, from Europe to West Africa. Type locality: Mediterranean.

Distribution in South Africa. Northern South West Africa and Lambert’s Bay on west coast to East London on south coast, littoral to 119 m, but most common between 10 and 70 m, especially abundant in dredgings from False Bay and the Agulhas Bank. 20/13 (l), 32/18 (s), 33/18 (s), 34/18 (s, l), 34/20 (s), 34/21 (s), 34/22 (s), 35/22 (d), 34/23 (l, s, d), 33/25 (s), 34/25 (s, d), 33/26 (s), 33/27 (s)

Aglaophenia plumula parvula Bale, 1882

Fig. 129B, F

?Aglaophenia conferta Kirchenpauer, 1872: 32, pl. 1 (fig. 4), pl. 2 (fig. 4), pl. 3 (fig. 4).
Aglaophenia parvula Bale, 1882: 23, pl. 14 (fig. 3). Bale, 1884: 165, pl. 14 (fig. 3), pl. 17 (fig. 10). Stechow, 1925a: 516.

Diagnosis. Stems short, growing in thick clumps on rocks, reaching 116 mm but usually much less, unbranched or sparsely branched.

Hydrotheca with second paired tooth from abcauline side normally double, the two points either equal in size, or with the more abcauline one larger than the other. Median inferior nematotheca usually reaching to thecal margin or at least to bays between the teeth.

Colour: stem dark brown, hydrocladia light brown.
Fig. 129.


Scale: A and B in cm, the rest in mm/10.
Variation. The stem occasionally gives off one or two short branches, either dichotomously as in subsp. dichotoma, or replacing hydrocladia.

Rarely the subsidiary point of the second paired marginal tooth of the hydrotheca is very small or obsolete. This usually occurs towards the distal ends of hydrocladia, while the division is well marked towards the proximal ends.

Distribution outside South Africa. Australia, southern Indian Ocean (St. Paul), west coast of Africa. Type locality: Queenscliff, Australia.

Distribution in South Africa. Very common in littoral region and shallow water all round the coast from South West Africa to Natal, to a depth of 84 m. Characteristic of wave-washed areas. 26/15 (l), 29/16 (l), 32/18 (l, s), 33/17 (s), 33/18 (l, s), 34/18 (l, s), 33/25 (l, s), 33/27 (l), 32/28 (s), 31/29 (l, s), 31/30 (l), 30/30 (l), 29/31 (l)

Doubtful species

Aglaophenia alopecuroides Kirchenpauer, 1872

Aglaophenia alopecuroides Kirchenpauer, 1872: 33, pl. 3 (fig. 10). Marktanner-Turneretscher, 1890: 263, pl. 6 (fig. 20), pl. 7 (fig. 21). Stechow, 1912: 371.

Remarks. Kirchenpauer's description of this species is not sufficient for recognition, and unfortunately most of Kirchenpauer's collection no longer exists. Marktanner-Turneretscher's description of material from Algoa Bay would apply equally well to Thecocarpus flexuosus umbellatus, except that no mention is made of a hydrotheca at the base of each corbula rib, a feature which can easily be missed. Stechow's material (probably South African!) was fragmentary and does not help. It is recommended that the species be dropped from the records.

Aglaophenia attenuata Allman, 1883

Aglaophenia attenuata Allman, 1883: 37, pl. 11 (figs 7–9).

Remarks. The shape of the hydrotheca in this species resembles that of Thecocarpus brevirostris and that of Aglaophenia tubulifera. Allman says that the 'mesial' (median abcauline) tooth of the hydrotheca is bifid, but it is not clear whether he means that there is an inner and an outer point (as in Aglaophenia latecarinata), or whether the two points lie side by side.

Although Allman, in his diagrams, does not show hydrothecae at the bases of the corbula ribs, it is possible that he may have missed this feature.

Billard (1908) was unable to find Allman's type material in the British Museum. The position and nature of the species must thus remain doubtful.

Aglaophenia holubi Leloup, 1934

Aglaophenia (? holubi Leloup, 1934: 4, figs 4–6.

Remarks. This species was created for some admittedly badly preserved material, which can probably be included in A. pluma. The hydrotheca is missing the most abcauline pair of the marginal teeth, which is often very poorly developed in A. pluma. The corbula figured by Leloup would agree with a young corbula of A. pluma in which the ends of the ribs had been damaged and the gonophores broken off.
Aglaophenia pusilla Kirchenpauer, 1872

Aglaophenia pusilla Kirchenpauer, 1872: 32, pl. 1 (fig. 3), pl. 3 (fig. 3). Bedot, 1921: 335, Stechow, 1923c: 256.

Remarks. The presence of caulin hydrothecae and the toothed margin of the hydrotheca in this species suggest the genus Gattya (Halopterinae). Yet the presence of seven marginal teeth, of which the median abcauline is greatly elongated, is characteristic of no known South African species of the genus. Since Kirchenpauer’s type material is no longer available the presence of the species in the country must await confirmation and its systematic position remain doubtful.

Aglaophenia tubulifera (Hincks, 1861)

Plumularia cristata: Busk, 1851: 118.
Plumularia tubulifera Hincks, 1861: 256, pl. 7 (figs 1–2).
Aglaophenia filicula Allman, 1883: 36, pl. 11 (figs 1–6).

Remarks. The only South African record of this species is that of Busk (1851), a record which was quoted by Hincks (1868) and probably also by Kirchenpauer (1872). Though Busk’s material appears to belong to this species, the distinction between A. tubulifera and A. pluma is not clear since both species are very variable, and it is possible that all South African material should be included in A. pluma.

Genus Cladocarpus Allman, 1874

Syn. Dinotheca Stechow, 1911.
Cladocarpella Bale, 1915.
Aglaophenopsis Fewkes, 1881.
Nematotheca Broch, 1918.

Diagnosis. Stem branched or unbranched, bearing alternate hydrocladia. Hydrocladia usually unbranched. Hydrotheca deep, often bent into an S-shape, with or without intrathecal septa, usually with a median abcauline tooth, with or without lateral teeth. Nematotheca usually with more than one aperture; median inferior nematotheca short, usually below hydrotheca, never reaching thecal margin. Gonothecae protected by phylactocarps which arise as appendages of the hydrocladia. Phylactocarps branched or unbranched, usually without hydrotheca, bearing one or two rows of nematotheca.

Type species: Cladocarpus formosus Allman, 1874.

KEY TO SPECIES*

1. Abcauline wall of hydrotheca not sigmoidally curved and axis of hydrotheca more or less straight
   - Abcauline wall of hydrotheca markedly convex in lower part and axis of hydrotheca twisted into an S-shape which may be very pronounced
     2
2. Hydrothecal margin with three teeth, one median abcauline and two lateral C. lignosus
   - Hydrothecal margin with one median abcauline tooth only
     3
3. Hydrotheca with two intrathecal septa, one abcauline and one abcauline C. lelopi
   - Hydrotheca with no intrathecal septa
     4
4. Depth of hydrotheca 2–3 times marginal diameter. Phylactocarps with short nematotheca (under 0.1 mm) C. distomus

* See also Addendum, p. 483.
- Depth of hydrotheca 3\frac{1}{2}-5 times marginal diameter. Phylactocarps with long nematothecae (over 0.4 mm) ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... 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adcauline intrathecal septum present immediately above hydropore, curved upwards and projecting into bulging basal part.

Median inferior nematotheca short and free from hydrotheca, with two apertures, one terminal and one on upper surface. Lateral nematotheca tubular and overtopping thecal margin; with three apertures, either one terminal and two mesial or two terminal and one mesial.

Phylactocarps borne on hydrocladia below the first hydrotheca and to one side, reaching 1.4 mm in length and bearing five pairs of long nematothecae when mature. Nematothecae about 0.8 mm in length, with two apertures on a raised process close to the origin, one or two apertures along the length and one terminal. Both the main axis of the phylactocarp and the nematothecae with many septa. Each phylactocarp bearing 2–4 gonothecae between the origins of members of the first to fourth pairs of nematothecae. Gonothecae female, broad-oval in front view, slipper-shaped in side view with a broad subterminal aperture, each containing one planula larva.

**Measurements (mm)**

<table>
<thead>
<tr>
<th>Description</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydrocladium, internode length</td>
<td>0.80–0.98</td>
</tr>
<tr>
<td>Hydrotheca, depth including median tooth diameter at margin</td>
<td>0.55–0.70</td>
</tr>
<tr>
<td>Gonotheca, length maximum diameter</td>
<td>reaching 0.60</td>
</tr>
<tr>
<td></td>
<td>reaching 0.33</td>
</tr>
</tbody>
</table>

**Remarks.** The convexity of the basal part of the abcauline thecal wall is typical of a number of *Cladocarpus* species with a sigmoidally curved hydrotheca. In degree of curvature it lies between *C. sinuosus* Vervoort, 1966 and *C. unicornus* sp. nov.

It differs from *C. sinuosus* in the larger hydrothecae in which the basal part of the abcauline wall is more protuberant and the greatest concavity is at a lower level. The intrathecal septum is also at a lower level.

**Distribution.** Endemic to South Africa.

**Distribution in South Africa.** The only record is the holotype recorded above. 35/22 (d)

*Cladocarpus distomus* Clarke, 1907

Fig. 130D–F


*Cladocarpus sibogae* Billard, 1913: 71, figs 57–58, pl. 4 (fig. 39). Billard, 1918: 26, fig. 5.

*Cladocarpella multisepata* Bale, 1915: 304, pl. 47 (figs 1–5).

*Cladocarpus plumularioides* Jarvis, 1922: 352, fig. 3. Vervoort, 1966b: 152, fig. 51.


*Cladocarpus multitipertus* Billard, 1913: 73, fig. 59.

*Cladocarpus alatus* Jarvis, 1922: 351, fig. 2, pl. 26 (fig. 25). Vervoort, 1966b: 152, fig. 52.
Fig. 130.

*Cladocarpus crepidatus* sp. nov., from holotype. A, gonotheca and nematotheca from phylactocarp; B, part of stem in anterior view showing two phylactocarps and their gonothecae; C, hydrocladium.

*Cladocarpus distomus*. D, stem; E, hydrocladium; F, hydrocladium with phylactocarps bearing gonothecae.


Scale: D in cm, the rest in mm/10.
Diagnosis. Hydrorhiza forming a branching root-stock for penetration of mud. Stem weakly fascicled at base, unbranched, reaching about 100 mm in height, bearing alternate hydrocladia from an axial tube. Axial tube with or without irregular, oblique hinge-joints; with or without indistinct transverse nodes; without septa; bearing a row of nematothecae on anterior surface, of which one is seated in the axil of each hydrocladal apophysis.

Hydrocladium bearing hydrothecae on anterior surface, consisting of thecate internodes separated by slightly oblique nodes. Internodes straight or curved, with or without septa; with three or four nematothecae, one median inferior, one pair laterals and sometimes one median superior.

Hydrotheca deep; not sigmoidally curved; abcauline wall smoothly convex or with a slight concavity in distal half; widening to margin; without intrathecal septum; 0.5–1.0 mm in abcauline height including median tooth, and 0.2–0.3 mm in marginal diameter; with a delicate adcauline shelf of perisarc overarchign the hydropore. Margin perpendicular to hydrocladium, with one median abcauline tooth.

Median inferior nematotheca seated below hydrotheca and not reaching its base, with at least two apertures, one terminal in the form of a narrow transverse slit which may be subdivided, and one circular on upper surface near base. Lateral nematotheca tubular or spreading round lateral wall of hydrotheca even as far as median tooth; with one to many apertures, the first usually raised slightly above the level of the rest and overtopping thecal margin. Median superior nematotheca, when present, seated above hydrotheca, similar to median inferior. Cauline nematotheca similar to median inferior. Phylactocarps borne on hydrocladia, several to each, unbranched, with four or five pairs of short nematothecae (less than 0.1 mm), bearing one to three gonothecae on basal region. Gonotheca elongate, with terminal, transversely widened aperture. Nematothecae similar to median inferior.

Variation. This is a very variable species, thus accounting for the many synonyms under which it is known. Variation occurs in the following features:

(i) Branching. The stem is normally unbranched, but rare examples of branching have been reported from outside South Africa, and colonies have been observed where some hydrocladia continue as stems and give off secondary hydrocladia.

(ii) Stem segmentation. Some stems are completely unsegmented, others have oblique hinge-joints and/or indistinct transverse nodes. Hinge-joints are quite irregular in position and may occur in groups of three or four close together. Transverse nodes generally occur in the distal part of the stem and are more regular, one above each hydrocladium.

(iii) Number of internodal septa in hydrocladia. This varies from none at all to as many as 19 to an internode, in which case about 11 are behind the adcauline wall of the hydrotheca.

(iv) Cauline nematothecae. A variable number occurs between two consecutive hydrocladia, 2–14 have been reported in the literature and 2–12 observed in South Africa.

(v) Structure of nematothecae. The typical slit-like terminal aperture lends itself
to modification, for by widening of the nematotheca and approximation of
the margins the aperture may be subdivided. Thus, the median nematotheca
may have one to four terminal apertures, and the lateral nematotheca may
extend round the lateral margin of the hydrotheca as far as the abcauline
median tooth and have many terminal apertures.

(vi) Median superior nematothecae, which may be present or absent, and if
present may vary in number from one to three. The number appears to be
related to the length of the internode which also is variable. There is never
more than one inferior median nematotheca, but its distance from the base
of the hydrotheca varies.

**Distribution outside South Africa.** Eastern Pacific, 6°51'N/81°42,5'W, 1 012 m
(type locality), East Indies, Queensland, East Africa.

**Distribution in South Africa.** Off Cape Town, Natal and Moçambique, in 292
to 2 200 m. 34/17 (a), 30/31 (d, vd), 30/32 (a), 29/31 (d, vd), 24/36 (a), 23/37 (a)

*Cladocarpus dufleini* (Stechow, 1911)

Fig. 130G

*Dinotheca dufleini* Stechow, 1911: 194, fig. 1. Stechow, 1925a: 508, figs 49–52. Vervoort, 1966b:
162, figs 63–64.

**Diagnosis.** Hydrorhiza a tuft of branching tubes for penetration of mud. Stem
fascicled, unbranched, reaching a maximum height of 35 mm, bearing alternate
hydrocladia from an axial tube. Axial tube exposed on anterior surface, not
divided into internodes, without septa, bearing a row of nematothecae on
anterior surface, of which there are two to five between two consecutive
hydrocladia including one in the axil of hydrocladal apophysis.

Hydrocladium bearing hydrotheca on upper surface, consisting of slightly
curved and slender thecate internodes separated by oblique nodes. Each inter-
node bearing a hydrotheca in proximal half, with numerous septa of which all
except the first one or two and the last one or two are carried outwards by the
curvature of the hydrotheca and drawn away from the opposite side of the
internode. Each internode with three nematothecae, one median inferior and
one pair laterals.

Hydrotheca laterally compressed and with exaggerated double curvature;
abcauline wall grossly convex basally and bulging outwards and upwards above
thecaal margin, this part capped by a pointed spine, concave above this and
widening to margin; abcauline wall deeply but smoothly curved; basal part of
internode carried outwards with the base of the hydrotheca. Hydrotheca with
no intrathecal septum; 0,5–0,6 mm from upper abcauline wall to spine and
0,2 mm in marginal diameter; margin forming an angle of about 45° with
hydrocladium, slightly sinuous, with one median abcauline tooth; hydropore
surrounded by a low collar and a ring of minute teeth. Hydranth with 12–14
tentacles.

Median inferior nematotheca free from hydrotheca and not reaching its
base, with two apertures, one terminal, and one on upper surface. Lateral
nematotheca tubular, overtopping thecal margin, with one terminal aperture. Cauline nematotheca spindle-shaped, with two apertures, one terminal and one adcauline, containing an intranematothecal ridge.

Phylactocarps (not recorded from South Africa) borne as a pair on first internode of hydrocladium, unbranched, unsegmented, without hydrothecae, bearing a double row of nematothecae and one gonotheca between members of the first pair of nematothecae. Gonotheca lens-shaped with a slit-like terminal aperture (Stechow).

Variation. The measurements given above are from the South African material reported by Vervoort, which consisted of young colonies, some of them unfascicled. Stechow has described an older, fertile colony from East Africa, with a fascicled stem almost 1 mm thick at the base and 130 mm high.

Stechow reports an S-shaped septum in some of the median inferior nematothecae, a second aperture for the lateral nematothecae and only one aperture for the cauline nematothecae. Presumably these are variable characters.

Stechow also reports that in the first hydrotheca of a phylactocarp-bearing hydrocladium the curvature is less pronounced and the spine absent.

Distribution outside South Africa. Off East Africa. Type locality: probably Agulhas Bank, South Africa, on a crab.

Distribution in South Africa. Off Durban in 425 to 495 m. 29/31 (d)

*Cladocarpus inflatus* Vervoort, 1966

Fig. 131H


Diagnosis. Stem delicate, unfascicled, reaching a maximum height of 50 mm, unbranched, bearing short hydrocladia more or less spirally arranged, not divided into internodes but containing numerous straight septa, bearing a row of nematothecae, of which one is seated in the axil of each hydrocladal apophysis.

Hydrocladium consisting of three to five sigmoidally curved thecate internodes separated by slightly oblique nodes. Internodes containing numerous septa, of which three are carried outwards by the curvature of the hydrotheca and drawn away from the opposite side of the internode. Each internode with three nematothecae, one median inferior and one pair laterals.

Hydrotheca with double curvature; adcauline wall very strongly convex basally and with maximum convexity below $\frac{1}{2}$ height, strongly concave above this with maximum concavity at about $\frac{1}{2}$ height, then widening evenly to margin, not thickened; cauline wall strongly and evenly curved; with no intrathecal septum; 0.4 mm in height and 0.2 mm in marginal diameter; margin with one inturned median adcauline tooth and sinus, or crenulated lateral edges.

Median inferior nematotheca free from hydrotheca and well below its base, with two apertures, one terminal and one on upper surface near base. Lateral
nematotheca tubular, overtopping thecal margin, with three apertures, one terminal, one lateral and one mesial. Cauiline nematotheca with one terminal aperture and containing an intranematothecal septum.

Gonotheca unknown.

**Distribution.** Endemic to South Africa.

**Distribution in South Africa.** Type locality and only record; off Durban in 495 m. 29/31 (d)

*Cladocarpus leloupi* Millard, 1962

Fig. 131A–D

*Cladocarpus flexilis* Leloup, 1939: 14, fig. 10.


**Diagnosis.** Hydrorhiza forming a branching root-stock for penetration of mud or attachment to pebbles. Stem fascicled, flexible, reaching a maximum height of 237 mm, usually unbranched, bearing alternate hydrocladia. Axial tube without internodal septa, divided by oblique nodes (which may be invisible in older stems) into long internodes, each bearing one hydrocladial apophysis near distal end and a row of nematothecae on anterior surface.

Hydrocladium bearing hydrothecae on upper surface, consisting of straight thecate internodes separated by oblique nodes. Internodes containing five to eight well-marked septa, of which the first is oblique and the remainder transverse. Each internode with three nematothecae, one median inferior and two lateral.

Hydrotheca vase-shaped, not sigmoidally curved, with axis parallel to internode; with two intrathecal septa, one adcauline about half-way up and one abcauline about quarter way up; 0.5–0.6 mm in abcauline height and 0.19–0.3 mm in marginal diameter; margin with one median abcauline tooth.

Median inferior nematotheca seated below hydrotheca and not reaching its base, bifurcated, with two terminal apertures and one on upper surface near base. Lateral nematotheca just overtopping thecal margin, usually trifurcated, with three terminal apertures and one lateral. Cauiline nematotheca usually bifurcated, with two terminal apertures and one on upper surface.

One or two phylactecarps borne on first and sometimes on second internode of hydrocladium, unbranched, segmented, with two nematothecae on each segment, bearing gonothecae on first two or three segments. Gonotheca flattened distally and curled over the subterminal transverse aperture.

**Variation.** The stem occasionally bears one or two long branches. The number of nematothecae on the cauline internodes varies from three to six. The last one is always seated in the axil of the hydrocladial apophysis.

The intrathecal septa, so characteristic of the species, tend to disappear towards the distal ends of young hydrocladia.

The number of terminal apertures in the lateral and cauline nematothecae is variable (1–4 in the former and 1–3 in the latter).
Fig. 131.

Cladocarpus leloupi. A, stem; B, hydrocladium; C, hydrocladium bearing two phylactocarps, redrawn from Leloup (1939, as C. flexilis); D, anterior view of stem showing origins of hydrocladia.


Scale: A and E in cm, the rest in mm/10.
**Distribution.** Endemic to South Africa. Type locality: Cape Agulhas.

**Distribution in South Africa.** Agulhas Bank from Cape Agulhas to East London in 80 to 120 m. 34/20, 35/21 (d), 34/22 (s), 34/23 (s), 34/25 (s, d), 34/26 (d), 33/27 (s)

*Cladocarpus lignosus* (Kirchenpauer, 1872)

Fig. 132A–D

*Aglaophenia lignosa* Kirchenpauer, 1872: 28, 37, pl. 1 (fig. 13); pl. 4 (fig. 13).

**Diagnosis.** Hydrolriza a hard and thickened mat. Stem thick, strongly fascicled, very hard and woody, reaching a maximum height of 700 mm, branching profusely and in one plane, bearing alternate hydrocladia from an axial tube in the younger parts of the colony. Axial tube, where exposed, divided into regular internodes by transverse nodes. Each internode without septa, bearing one hydrocladal apophysis and two nematothecae, one on proximal region and the other in the axil. Each peripheral tube with two rows of nematothecae.

Hydrocladium bearing hydrothecae on upper surface, consisting of one short, atecate internode followed by longer straight thecate internodes. All nodes oblique. Two internodal septa in first internode, three to five in thecate internodes: three behind the hydrotheca and sometimes one proximal and one distal. First internode with one median nematotheca, remainder with one median inferior and one pair laterals.

Hydrotheca vase-shaped, not sigmoidally curved, with axis forming an angle of 20–30° with hydrocladium, widening slightly to margin, with no intrathecal septum, 0.2–0.3 mm in height and 0.15–0.19 mm in marginal diameter. Margin with three teeth, one median abcauline and two lateral.

Median inferior nematotheca seated below hydrotheca and reaching to just above its base, bifurcated, with two terminal apertures. Lateral nematotheca bifurcated, with one mesial and two terminal apertures, one of the latter overtopping thecal margin and one approximately level with it. Cauline nematotheca with two terminal openings.

Phylactocarps borne on first internode of hydrocladia, singly or in pairs, curved, unbranched, indistinctly segmented, bearing one to four gonothecae. Each 'segment' with two nematothecae. Gonotheca elongate, with distal rectangular aperture.

**Variation.** The method of branching is very irregular, sometimes alternate, sometimes opposite and sometimes unilateral, but the general result is usually a fan-shaped colony.

**Distribution.** Endemic to South Africa. Type locality: given only as Cape of Good Hope.

**Distribution in South Africa.** Fairly common from 10 to 120 m on the Agulhas
Bank, reaching Cape Agulhas in the west and Natal in the east. 34/19 (s), 34/20 (s), 34/21 (s), 34/23 (s), 34/24 (d), 33/25 (s), 34/25 (s, d), 33/26 (s, d), 33/27 (s), 32/28 (s), 33/28 (s), 29/31 (s)

*Cladocarpus millardae* Vervoort, 1966

*Fig. 131E–G*


**Diagnosis.** Hydrorhiza a branching root-stock for penetration of mud. Stem fascicled, unbranched, reaching a maximum height of 100 mm, bearing alternate hydrocladia from the anterior surface of an axial tube. Axial tube exposed on anterior surface, unsegmented, without septa, bearing a row of nematothecae, two to four between two successive hydrocladial apophyses, of which one is seated in the axil of the apophysis.

Hydrocladium bearing hydrothecae on anterior surface, consisting of sigmoidally curved thecate internodes separated by oblique nodes. Internodes with two to six incomplete septa, the two strongest behind basal part of hydrotheca; each with three nematothecae, one median inferior and two lateral.

Hydrotheca with double curvature; abcauline wall strongly convex basally and with maximum curvature at $\frac{1}{2} - \frac{2}{3}$ height; concave above this and with maximum concavity at about $\frac{3}{4}$ height, then widening to margin; adcauline wall following roughly the same curvature; a strong adcauline intrathecal septum projecting into bulging basal portion; 0.4–0.6 mm in abcauline depth and 0.2–0.3 mm in marginal diameter; margin smooth and without teeth.

Median inferior nematotheca seated below hydrotheca, with three or four tubular apertures. Lateral nematotheca broad and spreading round lateral wall of hydrotheca almost to abcauline side, with 4–9 apertures. Cauline nematotheca triangular, with four apertures, two lateral and two medial, with intranematothecal septum.

Phylactocarp borne on first or second internode of hydrocladium, slightly curved, unbranched, segmented at least in distal part, with two nematothecae on each segment, bearing gonothecae on the first one or two segments. Gonotheca globular, with truncated distal end and subterminal aperture.

**Variation.** The position of the median inferior nematotheca relative to the hydrotheca varies. In the proximal part of the colony it is immediately below the hydrotheca, but in the distal part it is separated from the hydrotheca by a distance approximately equal to its own length.

**Distribution outside South Africa.** North of Madagascar. Type locality: off Moçambique (25°20’S/35°17’E) in 575 to 595 m.

**Distribution in South Africa.** Still Bay on the south coast to Moçambique, from 200 to 595 m. 35/22 (d), 29/31 (d), 25/35 (vd)
Cladocarpus lignosus. A, stem; B, anterior view of stem showing origins of hydrocladia; C, hydrocladium; D, hydrocladium with phylactocarp bearing gonotheca.

Cladocarpus sinuosus. E, young phylactocarp bearing a gonotheca; F, stem; G, anterior view of stem showing young phylactocarps and origins of hydrocladia; H, hydrocladium.

Scale: A and F in cm, the rest in mm/10.
*Cladocarpus sinuosus* Vervoort, 1966

Fig. 132E–H


**Diagnosis.** Hydorhiza a tuft of fibres or a flat mat. Stem fascicled or unfa sacled, unbranched, reaching a maximum height of 53 mm, bearing hydrocladia on anterior surface directed alternately to left and right, not divided into internodes, without septa, bearing a row of nematothecae on anterior surface, of which there is one in the axil of each hydrocladal apophysis.

Hydrocladium consisting of sigmoidally curved thecate internodes separated by straight or oblique nodes. Internodes containing septa, with three nematothecae, one median inferior and one pair laterals.

Hydrotheca with double curvature; adcauline wall convex basally and with maximum convexity at about \( \frac{1}{3} \) height, concave above this and with maximum concavity at about \( \frac{1}{2} \) height, then widening to margin; adcauline wall following roughly the same curvature; an adcauline intrathecal septum at about \( \frac{1}{3} \) height projecting into bulging basal part; 0,3–0,5 mm in adcauline height and 0,13–0,2 mm in marginal diameter; margin with one median adcauline tooth and faintly sinuous lateral edges.

Median inferior nematotheca seated below hydrotheca and more or less reaching to its base, with two apertures, one terminal and one on upper surface near base. Lateral nematotheca tubular, overtopping thecal margin, with two apertures, one terminal and one mesial, with an intranematothecal septum. Caulesine nematotheca spindle-shaped, with two apertures, one terminal and one on upper surface, with an intranematothecal septum.

Phylactocarp borne on first internode of hydrocladium, curved, unbranched, segmented, with two very long, curved nematothecae on each segment. Nematotheca with up to four apertures, one terminal and the rest on the distal surface. Gonothecae borne below first pair of nematothecae, ovoid with truncated distal end, reaching 0,4 mm in length and 0,3 mm in maximum diameter (young).

**Variation.** This rare species is known only from a few stems. From these it is evident that there is variation in

(i) The number of caulesine nematothecae between two successive hydrocladia (1–5).

(ii) The number of septa in the hydrocladal internodes (3–8). There are one or two below the hydrotheca, 2–5 behind it and sometimes one above it.

(iii) The length of the hydrocladal internodes, particularly the distal part where evidence of regeneration may be present.

(iv) The size of the hydrotheca and the amount of curvature.

(v) The occasional absence of the adcauline marginal tooth of the hydrotheca.

Vervoort has established a separate variety *edentatus* for the form without a marginal thecal tooth and with a slender hydrotheca.

**Distribution.** Endemic to South Africa.
Distribution in South Africa. Off Durban (type locality) and on the Agulhas Bank, in 183 to 550 m. 35/22 (d, vd), 34/23 (d), 29/31 (d), 27/32 (d)

Cladocarpus tenuis Clarke, 1879

Fig. 133D


Diagnosis. Stem unfascicled, unbranched, reaching 40 mm in height, bearing alternate hydrocladia, containing some oblique nodes in basal region only, bearing a row of nematothecae on anterior surface, of which one is seated in the axil of each apophysis.

Hydrocladium consisting of weakly sigmoidal thecate internodes separated by slightly oblique nodes. Internodes containing numerous septa and bearing three nematothecae, one median inferior and two laterals.

Hydrotheca very deep and slender, not sigmoidally curved, narrowest in centre, then widening to margin; abcauline wall slightly concave in centre; adcauline wall straight; without intrathecal septum, 0.7–0.9 mm in height (without median tooth) and 0.19–0.2 mm in marginal diameter; margin with one median abcauline tooth and crenulated lateral edges.

Median inferior nematotheca free from hydrotheca, short and not reaching thecal base, with large, fan-shaped terminal aperture. Lateral nematotheca tubular, overtopping thecal margin, with terminal aperture. Cauline nematotheca similar to median inferior.

Phylactocarp borne on first internode of hydrocladium, unbranched, segmented, with two long nematothecae (over 0.4 mm) on each internode. Gonothecae unknown. Nematotheca with three apertures, one terminal and two lateral.

Variation. The number of cauline nematothecae between two successive hydrocladial apophyses varies from three to ten.

Distribution outside South Africa. Gulf of Mexico, 185 m (type locality), Virgin Islands, West Indies.

Distribution in South Africa. Off Durban in 495 m. 29/31 (d)

Cladocarpus unicornus sp. nov.

Fig. 133E–F

Holotype. SAM–H538: off Moçambique, 24°46’S/35°18’E, 110 m.

Description. A single stem in two parts, together 52 mm long. The stem bears alternate hydrocladia, but most of these, and all those in the basal region, have been broken off short. The longest are 6.5 mm in length and bear seven hydrothecae. At the base of the stem the component tubes separate from one another in such a way as to suggest that this is the beginning of the rootstock and the base of the colony.
Stem fascicled, consisting of a principal hydrocladia-bearing tube and a number of peripheral tubes applied to its posterior surface. The peripheral tubes terminate one by one until the distal part of the stem remains unfascicled. In no place is the anterior surface of the principal tube and its hydrocladia-bearing apophyses covered by peripheral tubes. Principal tube with no visible nodes, but with many septa (varying in number from four to ten between two consecutive apophyses, but usually five or six). Apophyses short, each containing one septum, directed alternately to the right and the left. A row of cauline nematothecae present on the anterior surface of the principal tube, 2–4 (usually two) between two consecutive apophyses. Of these one is always axillary and displaced to the corresponding side. Cauline nematotheca with two or three apertures, one or two terminal and one on upper surface.

Hydrocladia bearing up to seven straight thecate internodes separated by slightly oblique nodes. Each internode containing 8–12 septa, usually two below the hydrotheca, six or seven behind it and two above it.

Hydrotheca with double curvature: abcauline wall strongly convex basally and with maximum convexity at about 3/4 height, this part capped by a short solid horn of perisarc; strongly concave and indented above this, with maximum concavity at about 2/3 height; then widening evenly to margin. Adecauline wall strongly convex in basal 2/3, the convexity decreasing gradually beyond this. Margin with a single inturned abcauline tooth and the lateral edges cut away where they approach the internode. A strong adecauline intrathecal septum present, curved upwards and projecting into bulging basal portion.

Median inferior nematotheca short and free from hydrotheca, with two apertures, one terminal and one on upper surface near base. Lateral nematotheca tubular and overtopping thecal margin; with three apertures, one terminal, one in centre of lateral surface, and one on mesial surface near base.

Phylactocarps absent, though scars for their attachment present on some hydrocladia immediately below the first hydrotheca.

**Measurements (mm)**

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance between two consecutive hydrocladia</td>
<td>0.51–0.69</td>
</tr>
<tr>
<td>Hydrocladium, internode length</td>
<td>0.78–0.98</td>
</tr>
<tr>
<td>Hydrotheca, depth including median tooth diameter at margin</td>
<td>0.61–0.68</td>
</tr>
<tr>
<td></td>
<td>0.23–0.28</td>
</tr>
</tbody>
</table>

**Remarks.** In the degree of convexity of the basal part of the hydrotheca *C. unicornus* lies between *C. crepidatus* sp. nov. and *C. inflatus* Vervoort, 1966.

It differs from *C. crepidatus* in its straight hydrocladal internodes, in the cut-away adecauline edges of the hydrotheca and in the presence of a horn on the adecauline thecal wall.

In *C. inflatus* the curvature of the hydrotheca has involved three of the internodal septa, which have been drawn away from the opposite side of the hydrocladium. This has not occurred in *C. unicornus*.

**Distribution.** Endemic to South Africa.
Cladocarpus valdiviae. A, hydrocladium; B, anterior view of stem showing phylactocarps; C, male gonotheca and nematotheca from phylactocarp.

Cladocarpus tenuis, redrawn from Vervoort (1966b). D, hydrocladium and phylactocarp. Cladocarpus unicornus sp. nov., from holotype. E, anterior view of stem showing origins of hydrocladia; F, hydrocladium.

Scale in mm/10.
Distribution in South Africa. The only record is the holotype recorded above. 24/35 (d)

**Cladocarpus valdiviae** Stechow, 1923

Fig. 133A–C


**Diagnosis.** Stem fascicled, unbranched, reaching a height of 39 mm, bearing alternate hydrocladia from the anterior surface of an axial tube. Axial tube unsegmented, bearing two, or occasionally three, nematothecae between two successive hydrocladia, one of which is seated in the axil of the hydrocladial apophysis.

Hydrocladium consisting of up to 14 thecate internodes separated by slightly oblique nodes. Internodes straight, containing four or five septa, one below hydrotheca and three or four behind it; with thick perisarc; each with three nematothecae, one median inferior and one pair laterals.

Hydrotheca tubular, with triple curvature; abcauline wall convex in basal part, concave in central part and with maximum concavity below half height, convex above this; adcauline wall with similar curvature but less pronounced; an abcauline intrathecal septum arising from indentation in abcauline wall and projecting half-way across cavity; 0.3–0.4 mm in height and 0.10–0.13 mm in marginal diameter; margin with one straight median abcauline tooth.

Median inferior nematotheca free from hydrotheca, short and not reaching thecal base, with two apertures, one terminal and one on upper surface near base. Lateral nematotheca tubular, overtopping thecal margin, with two apertures, one terminal and one mesial. Cauline nematothecae tubular to triangular.

Phylactocarps borne in a double row on front of stem, one on the first internode of each hydrocladium, unbranched, curved over towards centre, unsegmented, with 3–5 pairs of long nematothecae and a varying number of septa, bearing gonothecae on concave surface. Nematothecae with two apertures, one distal and one lateral. Gonotheca (only male known) curved-oval, with subterminal circular aperture.

**Distribution.** Endemic to South Africa.

*Distribution in South Africa.* Agulhas Bank off Mossel Bay in 155–200 m. (This species has been rediscovered as a fertile colony from practically the same position as the type locality.) 35/22 (d)

Genus *Gymnangium* Hincks, 1874

*Syn. Halicornaria* Allman, 1874.

**Diagnosis.** Stem branched or unbranched, bearing pinnately arranged hydrocladia. Hydrocladia unbranched. Hydrotheca cup- or flask-shaped, with or without an intrathecal septum, usually with a toothed margin. Nematothecae usually with more than one aperture; median inferior adnate to abcauline
the cal wall, often very long and overtopping thecal margin. Gonothecae unprotected in any way, usually borne on the hydrocladia or their apophyses, which are unmodified.

Type species: *Aglaophenia penmatula* Hincks, 1868 (nec. auct.)

(= *Halicornaria montagui* Billard, 1912)

**KEY TO SPECIES**

1. Stem fascicled and branched. Hydrocladia usually with internodal septa. Hydrotheca with untoothed and an adcauline intrathecal septum...

   - Stem unfascicled. Hydrocladia without internodal septa. Hydrotheca without adcauline intrathecal septum...

   1. Hydrotheca with adcauline intrathecal septum...

   2. Hydrotheca with no intrathecal septum...

3. Median inferior nematotheca short, seldom overtopping hydrotheca...

   - Median inferior nematotheca long, about twice length of hydrotheca...

4. Median inferior nematotheca tubular, with two openings, one just above thecal margin, one on summit...

   - Median inferior nematotheca gutter-shaped, opening along entire upper surface...

5. Median inferior nematotheca trifid, with three terminal openings...

   - Median inferior nematotheca with one terminal point or opening...

6. Median inferior nematotheca short, never reaching thecal margin...

   - Median inferior nematotheca long, overtopping thecal margin, at least in some part of hydrocladium...

7. Hydrotheca with a pronounced median adcauline marginal tooth...

   - Hydrotheca without median adcauline marginal tooth...

8. Lateral thecal teeth low and rounded. Median inferior nematotheca gently curved with free part forming an angle of 40-50° with internode...

   - Lateral thecal teeth longer than wide. Median inferior nematotheca markedly bent, with free part parallel with internode...

_Gymnothecium africanum* (Millard, 1958)

Fig. 134A–E

_Halicornaria africana* Millard, 1958: 215, fig. 15A–C. Millard, 1968: 280, fig. 6A.

_Gymnothecium africanum*: Millard, 1973: 25, fig. 2A–B.

**Diagnosis.** Stem unfascicled, unbranched, reaching a maximum height of 165 mm, bearing opposite or subopposite hydrocladia, divided into internodes by transverse nodes. Internodes without septa, bearing two hydrocladial apophyses and six nematothecae, three to each apophysis, one on anterior surface below apophysis, one axillary anterior and one axillary posterior.

Hydrocladium bearing hydrothecae on anterior surface, consisting of thecate internodes separated by slightly oblique nodes. Internodes without septa.

Hydrotheca flask-shaped, widening to margin, without intrathecal septum, 0.2–0.3 mm in height and 0.16–0.19 mm in marginal diameter. Margin forming an angle of 40–60° with internode, with seven marginal teeth, one sharp adcauline and three pairs low laterals of which the most adcauline is the smallest. Hydropore surrounded by small spines.
Median inferior nematotheca long, adnate to abcauline thecal wall and continued beyond it for about the same distance; free part curved gently distalwards and tapering to a point which may be open or closed; with a second aperture on upper surface at beginning of free part; no opening into hydrotheca. Lateral nematotheca saccular, not reaching thecal margin, with one broad terminal aperture. Cauiline nematotheca similar to lateral.

Gonothecae unknown.

*Variation.* The lower part of the stem is devoid of hydrocladia, irregularly segmented and bears scattered nematothecae.

Variation occurs in the marginal thecal teeth, which may be 'smoothed out' and indistinct, particularly towards the base of the hydrocladium.

The corner of the lateral nematotheca may be raised into a short tubular structure, thus forming two apertures, particularly towards the tip of a hydrocladium and on the stem.

An epizootic form occurs, in which solitary hydrocladia arise direct from an epizootic hydorhiza. The internodes are more slender, the marginal thecal teeth indistinct, and the median inferior nematothecae very strongly reduced so that they do not reach the margin of the hydrotheca. The latter character is always more extreme towards the base of the hydrocladium.

*Distribution.* Endemic to South Africa.

*Distribution in South Africa.* Natal in 27 to 91 m. Type locality: 28°28'S/32°25.8'E. 30/31 (s), 28/32 (s)

*Gymnangium allmani* (Marktanner-Turneretscher, 1890)

Fig. 134J–K

*Halicornaria plumosa* Allman, 1883: 52, pl. 18.

*Halicornaria allmani* Marktanner-Turneretscher, 1890: 277 (name only, for material see *G. montagui*).


*Diagnosis.* Stem unfascicled, unbranched, reaching a maximum height of 99 mm, bearing alternate hydrocladia, divided into internodes by straight nodes. Internodes without septa, bearing hydrocladial apophyses with three nematothecae, one inferior anterior, one posterior axillary and one anterior axillary. The two rows of hydrocladia more or less in one plane.

Hydrocladium bearing hydrotheca on anterior surface, consisting of thecate internodes separated by straight or slightly oblique nodes. Internodes without septa.

Hydrotheca cup-shaped, with convex abcauline wall and more or less straight abcauline wall, with an abcauline intrathecal septum reaching about half-way across, 0.16–0.20 mm in height and 0.11–0.14 mm in marginal diameter. Margin facing outwards and forming an angle of 20–30° with internode; with a
Fig. 134.

Gymnangium africanum. A and B, distal and proximal ends of hydrocladium; C, stem; D, anterior view of stem showing origins of hydrocladia (gonothecal scars shaded); E, hydrocladium of epizoic form.

Gymnangium montagui. F, hydrotheca, redrawn from Marktanner-Turneretscher (1890, as Halicornaria allmanii var.).

Gymnangium hians. G and H, hydrothecae from distal and proximal ends of hydrocladium.


Scale: C in cm, the rest in mm/10.
distinct but low triangular lateral tooth on each side and adcauline to it a bay of varying depth; no median teeth.

Median inferior nematotheca long, tubular, adnate to adcauline thecal wall and continued beyond it for about the same distance; free part curved distally; with two apertures, one terminal and one on upper surface at beginning of free part, no opening into hydrotheca. Lateral nematotheca pear-shaped, not reaching thecal margin, with one or more apertures. Cauleine nematotheca broad, with two or three terminal apertures.

Gonothece borne on hydrocladal apophyses and forming a double row on front of stem, sac-shaped and truncated distally.

Variation. The most variable feature is the hydrothecal margin. In the South African material the lateral tooth has a straight or oblique posterior edge and the bay behind it is shallow. In material from other regions, however, the bay is deeper and may be recessed below the lateral tooth. The bay is also said to be more pronounced towards the base of a hydrocladium (Billard 1912).

The lateral nematotheca is of variable structure. In addition to the terminal aperture with a tubular neck, there is a sac-like projection over the thecal wall which may have one to several apertures.

There may be two hydrocladia to an internode in the lower part of the stem and one in the upper part.

Distribution outside South Africa. Off Brazil in 59 m (type locality), Marshall Islands (Pacific).

Distribution in South Africa. Natal and Moçambique in 42 to 64 m. 29/31 (s), 25/33 (s), 28/32 (s)

Gymnangium arcuatum (Lamouroux, 1816)

Fig. 135A–F

Aglaophenia Arcuata Lamouroux, 1816: 167, pl. 4 (fig. 4).
Halicornaria cornuta Allman, 1886: 153, pl. 23 (figs 1–4).

Diagnosis. Stem unfascicled, usually unbranched, reaching a maximum height of 128 mm, bearing alternate hydrocladia, divided into short, broad internodes by oblique nodes. Each internode without septa, bearing one hydrocladal apophysis and three nematothecae adjacent to apophysis, two on anterior surface and one on posterior surface.

Hydrocladium bearing hydrothecae on anterior surface, consisting of thecate internodes separated by slightly oblique nodes. Internodes without septa.

Hydrotheca flask-shaped, widening to margin, without true intrathecal septum, 0.19–0.3 mm in adcauline height and 0.12–0.19 mm in marginal diameter, with a small adcauline projection overarching hydropore and bearing
two or three minute denticles. Margin forming an angle of approximately 50° with internode; with six or eight marginal teeth, one incurved adcauline, one incurved abcauline and two or three pairs low, rounded laterals.

Median inferior nematotheca long, adnate to abcauline thecal wall and continued beyond it usually for about the same distance; curved distally; with free part compressed laterally and tapering distally to a point, which may be open or closed; with a second aperture on upper surface at base of free part; no opening into hydrotheca. Lateral nematotheca sac-shaped, reaching approximately to thecal margin, with two terminal apertures, of which one may be prolonged into a tube or a long, closed spine. Cauline nematothecae similar to laterals, with two or three apertures.

Gonothecae borne on hydrocladial apophyses, one to each, and forming a double row on anterior surface of stem, spherical to oval and truncated distally.

*Variation.* South African material is so far all unbranched, but the type material branched several times 'dichotomously', and Billard (1907a) reports branching stems from Madagascar. Branching hydrocladia have been observed once, probably the result of injury.

In the hydrotheca the shape and number of the lateral marginal teeth vary. There may be two or three pairs. In the latter case the middle tooth may be the smallest, which is usually the case in the distal regions of the hydrocladia, or the most adcauline tooth may be poorly defined, which is usually the case in the proximal regions of the hydrocladia.

In the nematothecae the length of the free part of the median inferior is very variable, even in the same stem. The production of one of the apertures of the lateral nematotheca into a tube or spine usually occurs in the distal regions of the hydrocladia.

An epizootic form of the species occurs growing on the stems of other hydroids (*Thecocarpus formosus*) or on the stem of the normal form (var. *epizootica* Millard, 1958; subsp. *epizootica*: Millard, 1962). This consists of solitary hydrocladia arising directly from the epizootic hydorhiza, and, occasionally, stunted stems bearing hydrocladia. In the latter some of the hydrothecae may be normal, at any rate on the terminal parts of the hydrocladia, but on the proximal parts of the hydrocladia and in all solitary hydrocladia the hydrothecae and their nematothecae are stunted, this process becoming more marked towards the base of the colony. The stunting involves

(a) the hydrocladial internodes which are more slender and delicately formed,
(b) the hydrothecae, which are smaller, as little as 0.11 mm in depth and 0.11 mm in marginal diameter,
(c) the marginal thecal teeth, which tend to be 'smoothed out', with the exception of the median abcauline tooth which remains normal,
(d) the median inferior nematotheca, which no longer reaches the margin of the hydrotheca, so that the free portion with its aperture is missing,
(e) the lateral nematotheca, which is smaller and usually has only one aperture.
Rarely the solitary hydrocladia consist of only one internode each, this occurs when the hydrorhiza extends along the hydrocladia of the host.

Distribution outside South Africa. Sea of Antilles (type locality), Algiers, Madagascar.

Distribution in South Africa. South West Africa (exact locality not recorded), Agulhas Bank to Natal, littoral to 55 m. 34/21 (s), 34/22 (s), 34/23 (s), 33/25 (s), 33/27 (s), 33/28 (s), 32/28 (s), 31/29 (l, s), 30/30 (s), 29/31, 29/31 (l, s), 28/32 (s)

Gymnangium exsertum (Millard, 1962)

Fig. 135G–L

Halicornaria exserta Millard, 1962: 309, fig. 11A–H.

Gymnangium exsertum: Millard, 1973: 25, fig. 2C–D.

Diagnosis. Stem unfascicled, unbranched, reaching a maximum height of 83 mm, bearing alternate hydrocladia, divided into short, broad internodes by slightly oblique nodes. Internodes without septa, bearing one hydrocladal apophysis and three nematothecae, one anterior inferior, one axillary anterior and one axillary posterior.

Hydrocladium bearing hydrothecae on anterior surface, consisting of thecate internodes separated by transverse nodes. Internodes without septa.

Hydrotheca flask-shaped, widening to margin, with axis curved outwards and abcauline wall concave in lower part, adnate for over \( \frac{1}{3} \) abcauline length, then free, without intrathecal septum, 0.3–0.4 mm in abcauline height and 0.2–0.3 mm in marginal diameter. Margin forming an angle of approximately 60° with internode, with eight marginal teeth, one low, rounded abcauline, one narrow abcauline and three pairs laterals.

Median inferior nematotheca short, adnate to abcauline thecal wall and reaching to about one-third of its height, with one terminal aperture; no opening into hydrotheca. Lateral nematotheca ovoid, not reaching thecal margin, with one broad terminal aperture. Caucline nematothecae similar to lateral.

Gonothece borne on hydrocladal apophyses, one to each, and forming a double row on anterior surface of stem, bowl-shaped and truncated distally.

Variation. The proximal part of the stem may be devoid of hydrocladia and nematothecae and unsegmented. Beyond this may occur a short region with irregular segmentation bearing one or two nematothecae to each segment, before the hydrocladia-bearing part starts.

An epizootic form of the species occurs growing on the stems of other hydroids (Thecocarpus flexuosus), consisting of solitary hydrocladia arising directly from the epizootic hydrorhiza and stunted stems bearing a few short hydrocladia (subsp. epizootica Millard, 1962). The hydrocladal internodes are longer and narrower than in the normal form and the hydrotheca smaller and with the axis not so strongly bent outwards. The nematothecae are all smaller,
Fig. 135.

*Gymnangiun arenatum*. A, fertile stem; B and C, hydrothecae from distal and proximal ends of hydrocladium; D, anterior view of stem showing origins of hydrocladia; E, male gonotheca; F, hydrothecae of epizootic form.

*Gymnangiun exsertum*. G, stem; H, gonotheca; J, anterior view of stem showing scars for gonothecae (shaded) and origins of hydrocladia; K, hydrocladium; L, hydrocladium of epizootic form.

Scale: A and G in cm, the rest in mm/10.
especially in the proximal regions of solitary hydrocladia where the median inferior may not reach to the base of the hydrotheca.

**Distribution.** Endemic to South Africa.

**Distribution in South Africa.** Agulhas Bank, 50 to 115 m. Type locality: 33°49'S/25°56'E, depth unknown. 33/25, 34/25 (s), 34/25 (d), 32/28 (s)

*Gymnangium ferlusii* (Billard, 1901)

Fig. 137A-C

*Halicornaria ferlusii* Billard, 1901: 121, figs 3-4. Billard, 1907a: 370, fig. 14, pl. 25 (fig. 8).

*Halicornaria ferlusii* var. *brevis* Jarvis, 1922: 354, fig. 5, pl. 26 (fig. 27).

**Diagnosis.** Stem unbranched, reaching a maximum height of 148 mm, bearing alternate hydrocladia, divided into internodes by oblique nodes which slope alternately to left and right. Internodes without septa, bearing one hydrocladal apophysis and three nematothecae, one anterior inferior, one axillary anterior and one axillary posterior. Mamelon present on upper surface of apophysis.

Hydrocladium bearing hydrothecae on anterior surface, consisting of thecate internodes separated by slightly oblique nodes. Internodes without septa.

Hydrotheca flask-shaped, widening to margin, without intrathecal septum, 0.2-0.3 mm in abcauline height and 0.15-0.19 mm in marginal diameter. Margin forming an angle of approximately 50° with internode; with five marginal teeth, one abcauline and two pairs laterals of which the more adcauline is small and sharp and the more abcauline broad and low; adcauline edge indented in centre.

Median inferior nematotheca long, adnate to abcauline thecal wall and continued beyond it for the same distance or less, free part curved distally, trifid, with three terminal apertures of which the centre one is higher than the others; with an additional aperture on upper surface at beginning of free part; no opening into hydrotheca. Lateral nematotheca kidney-shaped, not reaching thecal margin, with 3-4 apertures. Cauline nematotheca similar to lateral, with 3-5 apertures.

Gonothecae borne on hydrocladal apophyses, one to each, and forming a double row on anterior surface of stem, ovoid, truncated distally when mature.

**Variation.** Jarvis reports a variety from East Africa in which the median inferior nematothecae are much shorter, reaching to only just above the thecal margin.

**Distribution outside South Africa.** Fort Dauphin in Madagascar (type locality), Wasin in East Africa.

**Distribution in South Africa.** East coast of Cape Province and Natal in 27 to 48 m. 31/29 (s), 30/30 (s), 28/32 (s)
Gymnangium gracilicaule (Jäderholm, 1903)

Fig. 136

Lytocarpus gracilicaulis Jäderholm, 1903: 299, pl. 14 (figs 3-4).
Halicornaria gracilicaulis: Billard, 1913: 63. Jäderholm, 1920: 9, pl. 2 (fig. 9).

Diagnosis. Hydrorhiza attached to hard objects or forming a branched rootstock for penetration of the substratum. Stem fascicled, bearing alternate branches which may redivide in the same way giving up to four orders; all branching in one plane. Stem and branches bearing alternate hydrocladia from an axial tube, which is always exposed on anterior face. Axial tube of branch arising from peripheral tube of stem, in smaller branches divided into regular internodes by oblique nodes; segmentation invisible in larger branches. Internodes without septa, bearing one hydrocladal apophysis and two nematothecae, one anterior inferior and one anterior axillary. Peripheral tubes bearing one or more longitudinal rows of nematothecae.

Hydrocladium bearing hydrothecae on anterior surface, consisting of thecate internodes separated by transverse or slightly oblique nodes. Internodes usually curved, with or without septa.

Hydrotheca deep, sigmoidally curved, not obviously widening to margin; 0.2–0.5 mm in total height and 0.09–0.16 mm in marginal diameter; abcauline wall convex in lower part, concave in upper part and with a perisarcal thickening below margin; containing a short abcauline intrathecal septum immediately above hydropore. Margin facing away from internode; without definite teeth, smooth, sinuated, or with a low triangular lobe on each side.

Median inferior nematotheca adnate to abcauline thecal wall to just above level of intrathecal septum, then free and divergent; with two apertures, one terminal and one on upper surface at beginning of free part; with an additional opening into hydrotheca near top of adnate part. Lateral nematotheca tubular, overtopping thecal margin, with two apertures, one terminal and one mesial. Cauleine nematotheca pear-shaped, with two apertures, one terminal and one abcauline.

Gonothecae borne on hydrocladal apophyses, flattened. Male, when mature (not recorded from South Africa), with two distal horns of unequal size subtending a terminal aperture. Female truncated distally and containing one egg.

Variation. The basal part of a branch is unsegmented and devoid of hydrocladia though it bears a row of nematothecae. This part may or may not be separated from the distal hydrocladium-bearing part by a hinge-joint.

The length of the free part of the median inferior nematotheca is variable and on this character Billard (1913) established a var. armata for a form with very long nematothecae (0.38 mm) from the Dutch East Indies. In South African material the length of the free part varies from 0.02 to 0.22 mm.

Variation in the degree of branching and general appearance of the colony has led to the separation of two subspecies in the South African material (Millard 1968).
Fig. 136.

Gymnangium gracilicaule gracilicaule. A, stem; D, hydrocladium.
Gymnangium gracilicaule lignosum. B, stem; C, anterior view of stem showing gonothecae and origins of hydrocladia; E, hydrocladium.

Scale: A and B in cm, the rest in mm/10.
**Distribution outside South Africa.** Tropical and subtropical waters from the western Pacific through the Indian Ocean to the Red Sea, Suez and east coast of Africa. Type locality: China Sea, 27°35′N/123°35′E in 91 m.

**Distribution in South Africa.** Natal and Moçambique in 42 to 350 m, with one record from off Cape Town. There is no essential difference in the distribution of the two subspecies, except that *G. g. gracilicaule* seems to penetrate to greater depths (to 350 m) than *G. g. lignosum* (to 100 m). 33/18, 30/30 (s), 29/31 (d), 28/32 (s, d), 26/32, 25/33 (s), 24/35 (s), 21/35

**KEY TO SUBSPEcies**

1. Stem flexuous. Internodal septa of hydrocladium poorly developed, not more than two ... ... ... ... 
   - Stem stiff. Internodal septa of hydrocladium well developed, more than two *G. g. lignosum*

*Gymnangium gracilicaule gracilicaule* (Jäderholm, 1903)

Fig. 136A, D


**Diagnosis.** Stem lightly fascicled, flexible, reaching 171 mm, with two orders of branching only (i.e. stem bearing alternate branches which bear hydrocladia). Branches unfascicled, flexible. Hydrocladal internodes slender and long, with internodal septa poorly developed or absent. Hydrotheca deep and slender (0,3–0,5 mm in total height), sigmoidal curvature not pronounced and margin usually forming an angle of 45° or more with internode, with an interval of at least 0,1 mm between abcauline margin and point of separation of median inferior nematotheca from hydrotheca.

*Gymnangium gracilicaule lignosum* (Millard, 1968)

Fig. 136B–C, E

*Halicornia gracilicaulis* Billard, 1907a (pp): 364, fig. 12, pl. 25 (fig. 7). Millard, 1958: 219, fig. 151–J.

**Diagnosis.** Stem strongly fascicled and woody, rigid, reaching 205 mm in height, with up to four orders of branching. Branches fascicled or unfascicled, rigid. Hydrocladal internodes short and well-marked, with up to six well-developed internodal septa. Hydrotheca comparatively short (0,2–0,3 mm in total height), sigmoidal curvature pronounced and margin forming an angle of less than 45° with internode, with a distance of about 0,05 mm between abcauline margin and point of separation of median inferior nematotheca from hydrotheca. Perisarc strongly developed and thickening in abcauline thecal wall very conspicuous.
Gymnangium hians (Busk, 1852)

Fig. 134G–H

Plumularia hians Busk, 1852: 396.
Halocornaria hians var. profunda: Ritchie, 1910a: 24, pl. 4 (figs 13–14).

Diagnosis. Stem unifascicled, unbranched, reaching a maximum height of 9 mm, bearing alternate hydrocladia, divided into internodes by straight nodes. Internodes without septa, bearing one or two hydrocladial apophyses and three nematothecae to each apophysis, one anterior inferior, one axillary anterior and one axillary posterior.

Hydrocladium bearing hydrothecae on anterior surface, consisting of thecate internodes separated by straight or slightly oblique nodes. Internodes without septa.

Hydrotheca cup-shaped, with convex adcauline wall and indented adcauline wall; with an adcauline intrathecal septum reaching about half-way across, the edge of which is thickened, upturned and denticulate, 0.13–0.3 mm in height and 0.16–0.2 mm in marginal diameter. Margin facing outwards and forming an angle of 20–40° with internode, with three pairs of broad lateral teeth; no median teeth; adcauline edge indented.

Median inferior nematotheca of variable length, adnate to adcauline thecal wall to approximately the level of the intrathecal septum, then free, with tip reaching approximately to thecal margin; with one aperture extending along upper surface of free part; with a perisarcal thickening in adcauline wall; no opening into hydrotheca. Lateral nematotheca sac-shaped, not reaching thecal margin, with one wide terminal aperture. Cauline nematothecae similar to lateral.

Gonothecae (not yet found in South Africa) borne on hydrocladial apophyses, one to each, and forming a double row on anterior surface of stem, vase- or cup-shaped and truncated distally.

Variation. The only record from South Africa is an epizootic colony growing on Gymnangium gracilecaule and as is so often the case in epizootic forms the hydrothecae and nematothecae are probably somewhat stunted. The free-living form could be expected to have better-developed marginal thecal teeth and a longer median inferior nematotheca, with possibly two apertures, one terminal and one on upper surface.

In this material the stem internodes usually bear one hydrocladium, and only rarely two. In material from elsewhere two hydrocladia to an internode is the rule and many more have been reported.

The marginal hydrothecal teeth are known to be very variable, either sharp and pointing towards the adcauline side, or low and bluntly rounded. In var. balei the most adcauline tooth is reduced.

The length of the median inferior nematotheca is variable in the single colony from South Africa. In the proximal parts of the hydrocladia the adnate
part terminates below the level of the intrathecal septum and the tip does not reach the thecal margin. In the distal parts of the hydrocladia the adnate part terminates above the intrathecal septum and the tip overreaches the thecal margin.

**Distribution outside South Africa.** Centre of distribution in East Indies from where it extends into the Pacific Ocean to Japan, Hawaii and the Kermadec Islands and into the Indian Ocean to the Red Sea and the east coast of Africa. Also from the Caribbean Sea. Type locality: Torres Strait in 16 m.

**Distribution in South Africa.** Natal in 73 m. 30/30 (s)

*Gymnangium longirostre* (Kirchenpauer, 1872)

*Aglaophenia longirostris* Kirchenpauer, 1872: 28, 42, pl. 1 (fig. 19), pl. 5 (fig. 20).

*Halicornaria longirostris*: Bale, 1884: 181, pl. 13 (fig. 7), pl. 16 (fig. 3), pl. 19 (fig. 30). Mark-tanner-Turneretscher, 1890: 279. Ralph, 1961b: 54, fig. 7 h-i. Millard, 1961: 207.

**Diagnosis.** Stem unfascicled, branched or unbranched, bearing alternate or subalternate hydrocladia, divided into internodes by oblique nodes. Internodes without septa, bearing one or two hydrocladial apophyses and three nematothecae to each apophysis, two anterior and one posterior.

Hydrocladium consisting of thecate internodes separated by slightly oblique nodes. Internodes without septa.

Hydrotheca cup-shaped, widening to margin, without intrathecal septum. Margin forming an angle of about 60° with internode, with seven teeth, one median abcauline incurved and three pairs of well-formed laterals of which the two most adcauline pairs are the longest. Hydropore surrounded by minute denticles.

Median inferior nematotheca long, adnate to abcauline thecal wall and continued beyond it for about the same distance; free part bent distally and its end approximately parallel to internode; with two apertures, one terminal and one on upper surface at beginning of free part; no opening into hydrotheca. Lateral nematotheca sac-shaped, not reaching thecal margin, with terminal and lateral openings which may be confluent. Cauline nematotheca similar to lateral.

Gonothecae borne on hydrocladial apophyses, small and truncated distally.

**Remarks.** This species was reported by Millard from Busk's collection of South African hydroids in the British Museum collected in 1899. It has not been found since and its occurrence in South Africa needs verification. The above diagnosis has been taken from the literature.

**Distribution outside South Africa.** Australia (type locality), New Zealand.

**Distribution in South Africa.** Algoa Bay. 33/25
Gymnangium montagui (Billard, 1912)

Fig. 134F

Aglaophenia pennatula: Hincks, 1868: 292, fig. 33, pl. 63 (fig. 3).
Halicornaria allmanii var. Marktanner-Turneretscher, 1890: 277, pl. 6 (fig. 23).
non Sertularia pennatula Ellis & Solander, 1786: 56, pl. 7 (figs 1–2).
?Plumataria pennatula: Busk, 1851: 118.

Diagnosis. Stem unfascicled, unbranched, about 140 mm in height, bearing subalternate hydrocladia, divided into internodes by oblique nodes. Internodes bearing two closely approximate subalternate hydrocladial apophyses and three nematothecae to each apophysis, one inferior anterior, one posterior axillary and one anterior axillary.

Hydrocladium consisting of thecate internodes separated by oblique nodes. Internodes without septa.

Hydrotheca cup-shaped, with convex adcauline wall and more or less straight adcauline wall, with an adcauline intrathecal septum reaching about half-way across, about 0,26 mm in height and 0,21 mm in marginal diameter. Margin facing outwards, with a distinct but low triangular lateral tooth on each side and adcauline to it a bay of varying depth, the bay never recessed below the lateral tooth; no median teeth.

Median inferior nematotheca long, adnate to adcauline thecal wall and continued beyond it for about the same distance, free part curved distally, gutter-shaped and open along entire upper edge, no opening into hydrotheca. Lateral nematotheca sac-shaped, not reaching thecal margin, with one broad terminal aperture. Cauline nematotheca with one terminal aperture.

Gonothecae (not yet found in South Africa) borne on stem, pear-shaped, truncated distally, smooth (Hincks).

Variation. As in the closely related G. allmanii, the margin of the hydrotheca is variable. The lateral tooth and the bay behind it tends to be more distinct towards the distal end of a hydrocladium (Billard 1912).

Distribution outside South Africa. Europe, Atlantic coast of Morocco. Type locality doubtful.

Distribution in South Africa. One certain record, that of Marktanner-Turneretscher from the Cape of Good Hope and a doubtful record from Mossel Bay (Krauss).

Genus Lytocarpus Allman, 1883

Syn. Lytocarpia Stechow, 1919.
Macrorhynchia Stechow, 1919.

Diagnosis. Stem bearing alternate hydrocladia and usually branched and fascicled. Hydrocladia unbranched. Hydrotheca cup-shaped, usually with an adcauline intrathecal septum and a toothed margin. Median inferior nemato-
theca partly adnate to abcauline thecal wall and partly free, usually long and reaching at least to level of thecal margin, usually with two openings to the exterior and one into the hydrotheca.

Gonothecae borne on unbranched phylactocarps which are modified hydrocladia and may be aggregated into a pseudocorbula.

**Type species:** *Lytocarpus spectabilis* Allman, 1883

(= *Plumularia phoenicea* Busk, 1852).

**KEY TO SPECIES**

1. Hydrotheca without abcauline marginal tooth, but with two or more pairs lateral teeth
   - Hydrotheca with an abcauline marginal tooth and one pair of low lateral teeth
     - Segments of hydrocladium sharply demarcated on posterior surface and often produced as a spine. Abcauline thecal tooth equal to or longer than lateral teeth. Abcauline intrathecal septum reaching about ¼ distance across hydrotheca
     - Segments of hydrocladium not sharply demarcated on posterior surface. Abcauline thecal tooth shorter than lateral teeth. Abcauline intrathecal septum reaching halfway across hydrotheca or nearly so

2. Segments of hydrocladium sharply demarcated on posterior surface and often produced as a spine. Abcauline thecal tooth equal to or longer than lateral teeth. Abcauline intrathecal septum reaching about ¼ distance across hydrotheca

**Lytocarpus filamentosus** (Lamarck, 1816)

Fig. 137E–G

*Plumularia filamentosus* Lamarck, 1816: 128.

*Agaophenia ligulata* Kirchenpauer, 1872: 42, pl. 1 (figs 21–22), pl. 2 (fig. 21), pl. 5 (fig. 21).

*Agaophenia fusca* Kirchenpauer, 1872: 43, pl. 1 (figs 21–22), pl. 2 (fig. 22), pl. 6 (fig. 22).

Marktanner-Turneretscher, 1890: 266, pl. 6 (fig. 17).

*Agaophenia patula* Kirchenpauer, 1872: 44, pl. 1 (fig. 23), pl. 2 (fig. 23), pl. 6 (fig. 23).

*Halicornaria segmentata* Warren, 1908: 328, pl. 48 (figs 33–36).

*Aglaophenia plumosa* Stechow, 1925a: 514 (nec. auct.)

**Diagnosis.** Stem fascicled, branching irregularly, reaching a maximum height of 150 mm, bearing alternate hydrocladia from an axial tube. Branches arising from peripheral tubes of stem, un fas c iced or lightly fascicled, bearing alternate hydrocladia. Axial tube of stem and branch with a hinge-joint separating a short basal part bearing median nematothecae only, from a distal part bearing hydrocladia; basal part segmented, often indistinctly, distal part divided into regular internodes by oblique nodes. Each internode bearing one hydrocladial apophysis and two nematothecae, one inferior anterior and one axillary anterior. Mamelons present on anterior surface of apophysis. The two rows of hydrocladia not in one plane but displaced on to anterior surface.

Hydrocladium bearing hydrothecae on anterior surface, consisting of thecate internodes separated by oblique nodes. Internodes sharply demarcated, with distal end of posterior surface often produced as a spine, with two internodal septa.

Hydrotheca cup-shaped and curved away from internode; with a thick abcauline intrathecal septum reaching about one third of the distance across
Fig. 137.

*Gymnangium ferlusi*. A, hydrocladium; B, anterior view of stem showing gonotheceae and origins of hydrocladia; C, fertile stem.
*Lytocarpus phoeniceus*. D, hydrocladium.
*Lytocarpus filamentosus*. E, stem; F, hydrocladium; G, anterior view of stem showing phylactocarps bearing gonotheceae, and origins of hydrocladia.

Scale: C and E in cm, the rest in mm/10.
and an adcauline intrathecal septum at a lower level reaching about half-way across; 0.2–0.3 mm in adcauline height and 0.11–0.2 mm in marginal diameter. Margin forming an angle of about 40° with internode; with three marginal teeth, one pair broad triangular laterals and one median adcauline in the form of a solid keel continuous basally with the adcauline intrathecal septum and projecting distally as a sharp spine reaching to just above the level of the lateral teeth.

Median inferior nematotheca adnate to adcauline thecal wall as far as the adcauline intrathecal septum, then free; free part tapering, straight or curved, usually overtopping median tooth; with three openings, one transversely elongated distal, one on upper surface at base of free part and one into hydrotheca. Lateral nematotheca tubular, overtopping thecal margin, with two apertures, one distal and one mesial. Cauilne nematothecae conical, with two apertures, one distal and one lateral. Nematothecae on basal part of branch broad, with two distal apertures directed sideways.

Phylactocarp replacing every third hydrocladium, displaced towards anterior surface of branch, curved, twisted through 180° after first internode, consisting of one normal thecate internode, one internode in which the hydrotheca is replaced by a gonotheca, and a distal region of variable length with indistinct segmentation bearing pairs of nematothecae only. Gonotheca lens-shaped, more flattened on adcauline side.

Variation. Young colonies have unbranched stems which may be unfascicled. Nodes may be indistinct or absent on the stem or on the basal parts of older branches. Occasionally two subopposite hydrocladia arise from one branch internode; these have between them three cauline nematothecae, one inferior to each and one shared anterior axillary. Only the lower apophysis bears a mamelon. On the first internode of a hydrocladium the median inferior nematotheca is shorter than usual and does not reach the margin of the hydrotheca.

Remarks. Stechow's material from the Agulhas Bank, which he assigned to Aglaophiphnia plumosa Bale in 1925, is none other than a young colony of L. filamentosus. This was ascertained by examination of a slide prepared by Stechow kindly loaned by the Munich Museum.

Distribution outside South Africa. Australia (type locality), Madagascar, Vema Seamount (South Atlantic).

Distribution in South Africa. South West Africa to Natal, littoral to 80 m. 34/18 (l, s), 35/19 (s), 34/20 (s), 34/21 (s), 34/22 (s), 34/23 (s), 33/25 (s), 34/25 (s), 33/27 (s), 31/29 (l, s), 30/30 (l), 29/31 (s), 28/32 (s)

Lytocarpus philippinus (Kirchenpauer, 1872)

Fig. 138A–C

Aglaophiphnia Philippina Kirchenpauer, 1872: 29, 45, pl. 1 (fig. 25), pl. 2 (fig. 26), pl. 7 (fig. 26).
Lytocarpus philippinus: Nutting, 1900: 122, pl. 31 (figs 4–7). Vervoort, 1968: 88, fig. 41.
Macrorhyncha philippina: Gravier 1970b: 253, fig. 1.
Diagnosis. Stem fascicled, branching irregularly, reaching a maximum height of 155 mm, bearing alternate hydrocladia from an axial tube. Branches arising from peripheral tubes of stem, unesculated or lightly fascicled, divided by a hinge-joint into a short unsegmented basal part bearing median nematothecae only, and a distal part bearing alternate hydrocladia. Axial tube of stem and distal part of branch divided into internodes by oblique nodes, each internode bearing one hydrocladal apophysis and two nematothecae, one inferior anterior and one axillary anterior. Mamelon present on anterior surface of apophysis. The two rows of hydrocladia not in one plane but displaced on to anterior surface.

Hydrocladium bearing hydrothecae on anterior surface, consisting of thecate internodes separated by transverse or slightly oblique nodes. Internodes with two internodal septa.

Hydrotheca cup-shaped and curved away from internode; with a thick abcauline intrathecal septum reaching about half-way across and an abcauline intrathecal septum at a lower level overarching the hydropore; 0.15–0.2 mm in abcauline height and 0.14–0.20 mm in marginal diameter. Margin forming an angle of 30–40° with internode; with three marginal teeth, one pair broad triangular laterals and one median abcauline in the form of a solid keel continuous basally with the abcauline intrathecal septum and projecting distally as a short spine which does not quite reach the level of the lateral teeth.

Median inferior nematotheca adnate to abcauline thecal wall as far as the abcauline intrathecal septum, then free; free part more or less straight, usually overtopping thecal margin; with three openings, one rounded distal, one on upper surface at base of free part and one into hydrotheca. Lateral nematotheca tubular, overtopping thecal margin, with two apertures, one distal and one mesial. Cauline nematothecae conical, with two apertures, one distal and one lateral. Nematothecae on basal part of branch broad, with two distal apertures directed sideways.

Phylactocarp replacing every third hydrocladium, displaced towards anterior surface of branch, consisting of one normal thecate internode, then one or (usually) two internodes in which the hydrotheca is replaced by a gonotheca, then a distal region twisted through 180° and consisting of up to four internodes bearing nematothecae only. Gonotheca lens-shaped.

Colour: stem black or brown, hydrocladia cream.

Variation. Young colonies have unbranched and unfascicled stems.

The arrangement of branches on the stem is very irregular; usually there are two rows, in one plane or displaced anteriorly, with variable intervals between them, and they may be opposite, alternate or quite irregular.

On the first internode of the hydrocladium the median inferior nematotheca is shorter than usual and barely reaches the level of the lateral marginal teeth. On the phylactocarp the number of nematothecae on the internodes of the distal part varies, there are usually two, sometimes three and sometimes one.
Gravely (1927) says the species 'stings like a nettle when touched'.

Gravier (1970b) describes the release of degenerate medusae from the gonothecae. These are without tentacles, mouth and canals, but have a hypostome and velum and a circle of refringent corpuscles round the margin.

**Distribution.** Circumglobal in tropical and subtropical waters. Type locality: Manilla, Philippine Islands.

**Distribution in South Africa.** Natal and Moçambique, littoral to 44 m. 29/31 (s), 26/32 (l, s), 25/32, 24/35 (s), 23/35 (l, s), 21/35

*Lytocarpus phoeniceus* (Busk, 1852)

Fig. 137D

*Plumularia phoenicea* Busk, 1852: 398.
*Lytocarpus spectabilis* Allman, 1883: 43, fig. 2, pl. 15.
*Aglaoephina phoenicea*: Bale, 1884: 159, pl. 15 (figs 1–5), pl. 17 (figs 1–4), pl. 19 (fig. 31).

**Diagnosis.** Stem fascicled, branching pinnately and in one plane, reaching a maximum height of 39 mm, bearing alternate hydrocladia from an axial tube. Branches arising from peripheral tubes of stem, unfascicled or lightly fascicled, consisting of a short, unsegmented basal part bearing median nematothecae only and a distal part bearing alternate hydrocladia, but no hinge-joint. Axial tube of stem and distal part of branches indistinctly segmented, the segmentation more obvious in unfascicled parts, where each internode bears one surface of apophysis. The two rows of hydrocladia arising from anterior hydrocladial apophysis. Two nematothecae associated with each apophysis, one inferior anterior and one axillary anterior. Mamelon present on anterior surface of stem and curved outwards to lie in one plane.

Hydrocladium bearing hydrothecae on anterior surface, consisting of thecate internodes separated by transverse or slightly oblique nodes. Internodes with two septa.

Hydrotheca cup-shaped and curved away from internode; with an abcauline intrathecal septum stretching over half-way across and a short abcauline intrathecal septum at a lower level overarching the hydropore; 0,12–0,17 mm in abcauline height and 0,13–0,16 mm in marginal diameter. Margin forming an angle of about 30° with internode; with one or two pairs of broad and low triangular lateral teeth and a small rounded lobe on abcauline edge, no abcauline tooth.

Median inferior nematotheca adnate to abcauline thecal wall to approximately the level of the abcauline intrathecal septum, then free; free part bent distally at an angle to adnate part, straight, usually overtopping thecal margin; with three openings, one distal, one on upper surface at base of free part and one small one into hydrotheca. Lateral nematotheca tubular, overtopping thecal margin, with two apertures, one distal and one mesial. Cauline nematothecae saccular, with two distal openings.
Lytocarpus philippinus. A, hydrocladium; B, anterior view of stem showing one phylactocarp bearing gonotheceae, and origins of hydrocladia; C, stem.

Theocarpus formosus. D, stem; E and F, hydrothecae with short and long spines; G, female corbula.

Scale: C and D in cm, the rest in mm/10.
Phylactocarps (not yet reported from South Africa) replacing every third hydrocladium, strongly curved, consisting of one normal thecate internode, then one internode in which the hydrotheca is replaced by a gonotheca, then a distal region consisting of six or more segments each bearing two or three nematothecae only. Gonotheca lens-shaped.

Variation. Although only small colonies are known from South Africa, this species is known to form magnificent fan-shaped colonies up to 200 mm in height and with a thick, branching stem. The branches in turn bear secondary branches with a pinnate arrangement.

According to the literature there is much variation in the character of the marginal thecal teeth. There may be as many as four pairs of small lateral teeth and the abcauline rounded lobe may be produced into a tooth which is either straight or curved over the hydrotheca. So far these variations have not been observed in South Africa.

Distribution outside South Africa. Tropical Indo-Pacific, from the Pacific Ocean to the east coast of Africa. Type locality: Torres Strait in 16 m.

Distribution in South Africa. Natal, 49–64 m. 29/31 (s)

Genus *Thecocarpus* Nutting, 1900


Diagnosis. Stem branched or unbranched, bearing alternate hydrocladia. Hydrocladia unbranched. Hydrotheca sac-shaped to deep, usually with toothed margin and often with a median keel-like spine outside the abcauline tooth. Median inferior nematotheca fairly short, usually not reaching thecal margin. Gonothecae in corbulae formed by modified hydrocladia bearing secondary ribs. Ribs bearing nematothecae and at least some of them in at least one sex, bearing one hydrotheca.

Type species: *Sertularia myriophyllum* Linnaeus, 1758.

KEY TO SPECIES

1. Stem branched, each branch forming a spirally twisted symposium. Hydrotheca usually with a second point outside abcauline marginal tooth of approximately the same length and which may be solid or hollow ............... *T. flexuosus*
   - Stem unbranched, or if branched, not as a symposium .............. 2

2. Hydrotheca with long, hollow, curved spine arising from abcauline surface outside abcauline marginal tooth ............... *T. formosus*
   - Hydrotheca with no spine or second point outside abcauline marginal tooth .............. 3

3. Hydrotheca sigmoidally curved, margin with seven teeth, of which four may be bifid ............... *T. brevirostris*
   - Hydrotheca sac-shaped, margin with five distinct teeth and sometimes two rounded lobes ............... *T. delicatulus*
Theocarpus brevirostris (Busk, 1852)

Fig. 139A–C

Plumularia brevirostris Busk, 1852: 397.
Plumularia vitiana Kirchenpauer, 1872: 34, pl. 1 (fig. 9), pl. 3 (fig. 9).
Agaophenia vitiana: Billard, 1907a: 388, figs 22–23.

Diagnosis. Stem unfascicled and unbranched in young colonies, fascicled and branched in old ones, reaching a maximum height of 90 mm. Branching roughly alternate and strictly in one plane; branches arising from superficial tubes of stem, themselves often fascicled and rebranched. Stem and branches bearing alternate hydrocladia, divided into internodes by transverse nodes in the younger parts only. Two nematothecae to each hydrocladal apophysis, one inferior anterior and one axillary anterior. Mamelon present on anterior surface of apophysis. The two rows of hydrocladia arising from anterior surface of stem and directed outwards to lie in the same plane as the branches.

Hydrocladium bearing hydrotheca on anterior surface, consisting of thecate internodes separated by slightly oblique nodes. Internodes with a variable number of septa.

Hydrotheca deep, with that part of abcauline wall above the level of the median nematotheca at least slightly concave and thickened, with a short adcauline intrathecal septum about one-fifth of height from base, 0,2–0,3 mm in abcauline height and 0,10–0,16 mm in marginal diameter. Margin forming an angle of 50–60° with internode; with seven marginal teeth, one median abcauline and three pairs laterals, of which the two most abcauline may be bifid.

Median inferior nematotheca adnate to thecal wall for about half height of latter, then free and bent away from it, usually not reaching to thecal margin, with three apertures, one terminal, one on upper surface at base of free part (these two often confluent) and one into hydrotheca. Lateral nematotheca tubular and bent backwards, reaching thecal margin, with two apertures, one terminal and one mesial (these two sometimes confluent).

Corbula with a pedicel of two hydrotheca-bearing segments, bearing 6–8 pairs of ribs and terminating in one or two hydrotheca-bearing segments. Each rib bearing proximally a perisarcal crest supporting one hydrotheca and two lateral nematothecae, and continued as a broad blade with nematothecae on the outer edge and fused to the rib behind by the inner edge. Outer edge of rib often with a leaf-like outgrowth bearing one or more nematothecae.

Colour: rich brown.

Variation. Several authors have noted a tendency to reverse the faces of the stem, so that in the lower part the hydrocladia face one way and in the upper part the opposite way. This has not been observed in South Africa.

Considerable variation occurs in the hydrocladal internodes. Internodal septa may be poorly developed and limited to one opposite the intrathecal sep-
tum, or there may be two fairly distinct ones, the second situated behind the centre of the hydrotheca. The intrathecal septum may be very short or may extend halfway across the hydrotheca. The depth of the hydrotheca varies and this influences the curvature of the abcauline wall above the level of the median nematotheca, which may be short, strongly concave and distinctly thickened, or long, weakly concave and only slightly thickened. Variation also occurs along the length of the hydrocladium, the first hydrotheca commonly being shorter and with a more distinctly curved abcauline wall than the last one. The first and second pairs of marginal teeth may be simple and triangular, or subdivided. The length of the median inferior nematotheca is also variable but it does not reach beyond the level of the thecal margin.

It is to be noted that in the only two corbulae seen in South Africa, there are two hydrothecate internodes on the pedicel, whereas only one is reported from other areas.

Distribution outside South Africa. South Pacific islands, northern Australia, tropical Indian Ocean from the East Indies to Africa. Type locality: off Cumberland Island, Queensland, in 49 m.

Distribution in South Africa. Natal and Moçambique, in 2–70 m. 29/31 (s), 29/32 (s), 28/32 (s), 25/33 (s), 24/35 (s)

Thecocarpus delicatus (Busk, 1852)

Fig. 139D–E

Plumularia delicatula Busk, 1852: 396.
Aglaophenia delicatula: Bale, 1884: 167, pl. 14 (fig. 4), pl. 17 (fig. 11). Billard, 1913: 106, fig. 95.
Theocarpus delicatus: Millard & Bouillon, 1973: 94, fig. 11J–K.

Diagnosis. Stem unfascicled, unbranched, reaching a maximum height of 30 mm, bearing alternate hydrocladia, with one or two hinge-joints separating a short basal part from a distal hydrocladia-bearing part. Distal part divided into internodes by slightly oblique nodes, each internode bearing one hydrocladal apophysis and three nematothecae, one inferior anterior, one axillary anterior and one axillary posterior. Mamelon present on anterior surface of apophysis. The two rows of hydrocladia arising from the anterior surface of the stem and curving backwards.

Hydrocladium bearing close-set hydrothecae on anterior surface, consisting of thecate internodes separated by transverse nodes; each internode usually with two internodal septa, one opposite the intrathecal septum and one opposite the base of the lateral nematotheca.

Hydrotheca sac-shaped, with a complete intrathecal septum at about \( \frac{1}{4} \) of height, 0.18–0.2 mm in abcauline height and 0.13–0.16 mm in marginal diameter. Margin forming an angle of 55–60° with internode; with five distinct marginal teeth, one median inturned abcauline and two triangular laterals on each side of it, abcauline half of margin straight or sinuated.
Fig. 139.

*Thecocarpus brevirostris*. A, stems; B, corbula (openings into interior shaded); C, distal and proximal regions of hydrocladium.

*Thecocarpus delicatus*. D, stem; E, hydrocladium.

Scale: A and D in cm, the rest in mm/10.
Median inferior nematotheca adnate to abcauline thecal wall to just below origin of marginal teeth, then free; reaching approximately to tips of marginal teeth; with an aperture extending all the way along upper surface of free part and another into hydrotheca. Lateral nematotheca tubular, curved, reaching just beyond level of thecal margin, with one distal aperture extending also along mesial surface.

Corbula (not reported from South Africa) replacing hydrocladium, consisting of a pedicel of one thecate segment followed by about ten segments bearing alternate ribs. Corbula open and ribs quite free. Each rib with one hydrotheca near base subtended by a pair of lateral nematothecae and followed by a double series of alternate nematothecae.

*Variation.* In the younger (distal) parts of the hydrocladia the more proximal of the two internodal septa tends to disappear. The adcauline half of the thecal margin may be quite straight or a distinct rounded lobe may be present.

*Distribution outside South Africa.* Tropical Indo-Pacific, from the east coast of Africa to Queensland. Type locality: Torres Strait in 16 m.

*Distribution in South Africa.* Santa Carolina in Moçambique, only. 21/35

_Thecocarpus flexuosus_ (Lamouroux, 1816)

Figs. 140–141

_Aглаопения flexuosa_ Lamouroux, 1816: 167.
_Thecocarpus flexuosus_: Millard, 1962: 312, fig. 12.

*Diagnosis.* Stem fasciuled and branching irregularly, generally thick and woody at base. Branches unfasciuled or lightly fasciuled, in the form of a scorpionid symposium, the whole twisted in a spiral manner and with each successive podium arising from the anterior surface of the one before and facing towards it. Each podium typically divisible into a basal part divided into internodes bearing one large median nematotheca each, and a distal part, continued to end of branch and divided into internodes bearing one hydrocladium and three nematothecae each. Nodes transverse or slightly oblique. Nematothecae of hydrocladium-bearing segment including one axillary anterior, one axillary posterior and one inferior anterior. A mamelon present on anterior surface of hydrocladiad apophysis. Hydrocladia alternate, the two rows not in one plane but shifted onto anterior surface.

Hydrocladium bearing hydrotheca on anterior surface, consisting of thecate internodes separated by slightly oblique nodes. Internodes typically with two septa.

Hydrotheca sac-shaped, expanding to margin, with an adcauline intrathecal septum near base, 0,2–0,4 mm in abcauline height and 0,14–0,2 mm in marginal diameter. Margin forming an angle of 50–70° with internode; with nine marginal teeth, one median abcauline and four pairs laterals, some of which may be
bifid; median abcauline tooth sometimes double with an internal and an external point.

Median inferior nematotheca short, adnate to abcauline thecal wall to approximately level of intrathecal septum, then free; never reaching level of thecal margin; with one aperture extending along upper surface of free part; no opening into hydrotheca. Lateral nematotheca tubular, reaching to thecal margin, with one aperture. Cauline nematotheca sac-shaped, with three to six apertures.

Corbula with a pedicel of one to seven hydrotheca-bearing segments followed by segments bearing alternate paired ribs. Each rib bearing a series of nematothecae along outer edge, a hydrotheca near the base and a crested process of variable length proximal to the hydrotheca. Corbula closed, with inner edge of each rib fused to the rib behind. Proximal side of first rib with a rounded projection facing towards pedicel.

**KEY TO SUBSPECIES**

[Subspecies not represented in South Africa are bracketed]

1. Sympodial branches with umbel-like appearance: first podium long, subsequent ones short and forming a close spiral  
   - Symposidal branches not umbel-like: all podiums of approximately the same length and forming a loose or tight, but regular, spiral  
   - T. f. umbellatus
   - T. f. plumiferus

2. Abcauline thecal tooth simple, with no outer point  
   - Abcauline thecal tooth double, with an inner and an outer point  
   - T. f. solidus

3. Outer point of abcauline thecal tooth normally solid  
   - Outer point of abcauline thecal tooth normally hollow  
   - T. f. flexuosus

4. Median nematotheca often bifurcated, lateral nematotheca with two openings  
   - Median nematotheca not bifurcated, lateral nematotheca with one opening  
   - T. f. percarinatus

*Theocarbus flexuosus flexuosus* (Lamouroux, 1816)

Fig. 140A–C

*Aphoephia flexuosa* Lamouroux, 1816: 167.


*?Aphoephia bifida* Stechow, 1923b: 117. Stechow, 1925a: 515, fig. 53.


**Diagnosis.** Colony reaching 238 mm. Sympodium geniculate and twisted in a spiral which may be tight or loose. Podia of approximately equal length, with no regular hinge-joints. Hydrocladia usually short and about 6 mm in length.

Hydrothecal margin with the two most abcauline lateral teeth typically bifid; median abcauline tooth double, with the outer point hollow and longer than the inner.

Corbula reaching 7 mm and bearing up to 13 pairs ribs. Crested processes of ribs sometimes produced and bearing nematothecae.
Fig. 140.

*Theocarpus flexuosus flexuosus*. A, part of stem including one spirally twisted sympodial branch; B, hydrothecae; C, corbula.

*Theocarpus flexuosus solidus*. D, hydrothecae.

Scale: A in cm, the rest in mm/10.
Distribution outside South Africa. Madagascar. Type locality: East Indies.

Distribution in South Africa. False Bay to Moçambique in 5 to 100 m. 34/18 (s), 35/20 (d), 34/21 (s), 34/23 (s), 33/28 (s), 30/30 (s), 29/31 (s), 28/32 (d), 24/34 (s)

*Thecocarpus flexuosus plumiferus* (Kirchenpauer, 1872)

Fig. 141B, D

*Aglaophenia plumifera* Kirchenpauer, 1872: 31, pl. 1 (fig. 6), pl. 3 (fig. 6). Stechow, 1923c: 255, fig. K'.

*Thecocarpus flexuosus plumiferus*: Millard, 1962: 313, fig. 12C–D.

Diagnosis. Colony reaching 460 mm. Sympodium of branch not obviously geniculate, twisted in a spiral which may be tight or loose. Podia of approximately equal length, usually with hinge-joints separating basal and distal parts and situated distal to origin of next podium. Hydrocladia short, 3–6 mm in length.

Marginal teeth of hydrotheca not bifid; median abcauline tooth simple, with no outer point, though abcauline wall somewhat thickened near margin.

Corbula sometimes very long, reaching 20 mm and bearing up to 39 pairs ribs.

Variation. Occasional hydrothecae show the beginnings of an outer point on the abcauline thecal tooth, thus tending towards subsp. *solidus*, but this secondary point never equals the abcauline tooth in length.

Distribution. Endemic to South Africa. Type locality: Algoa Bay.

Distribution in South Africa. Agulhas Bank from off Still Bay to off East London in 50 to 104 m. 34/21 (s), 33/35, 33/26 (d), 33/27 (s), 32/28 (s)

*Thecocarpus flexuosus solidus* (Millard, 1958)

Fig. 140D

*Thecocarpus giardi* var. *solidus* Millard 1958: 222, fig. 16B–C.

*Thecocarpus flexuosus solidus*: Millard, 1962: 316, fig. 12E–H.

Diagnosis. Colony reaching 550 mm, very similar in appearance to subsp. *flexuosus*. Sympodium of branch more or less geniculate, twisted in a spiral which may be tight or loose. Podia of approximately equal length, usually with one or two hinge-joints separating basal and distal parts and situated proximal or distal to origin of next podium. Hydrocladium short, about 6 mm in length.

Marginal teeth of hydrotheca not bifid; median abcauline tooth double, with outer point forming a solid spine and longer than the inner.

Corbula reaching 5 mm in length and bearing up to 16 pairs ribs.

Variation. Rarely the outer point of an abcauline thecal tooth may be hollow, resembling subsp. *flexuosus*, and rarely the outer point may be poorly developed, resembling subsp. *plumiferus*.

Examples have been seen of a double corbula, in which the pedicel bifurcates in the fifth segment, and also of branching hydrocladia.
Distribution. Endemic to South Africa. Type locality: off Natal, 28°28'S/32°25.8'E, 27 m.

Distribution in South Africa. Agulhas Bank off Still Bay to Moçambique in 18 to 110 m. 35/21 (d), 33/26 (s), 33/27 (s), 33/28 (s), 32/28 (s), 30/30 (s), 30/31 (s), 29/31 (s), 29/32 (s), 28/32 (s), 25/33 (s), 24/35 (d)

Thecocarpus flexuosus umbellatus Millard, 1962

Fig. 141A, C

Thecocarpus flexuosus: Millard, 1961: 208 (specimen 1899.7.1.6093 only, others too fragmentary to establish subspecies).
Thecocarpus flexuosus umbellatus Millard, 1962: 316, fig. 12B, M.

Diagnosis. Colony reaching 138 mm. Branches like an umbel in appearance, sympodium formed from one long podium followed by several very short ones (usually five in all), the whole spirally twisted. Two hinge-joints present in first podium, separating basal and distal parts. ‘Umbels’ breaking easily at hinge-joints and commonly occurring separately in dredges. Podia other than the first with no hinge-joints and no basal part. Hydrocladia long, reaching 15 mm.

Marginal teeth of hydrotheca not bifid; median abcauline tooth double, with outer point hollow and longer than inner.

Corbula reaching 12 mm and bearing up to 20 pairs ribs. Terminal parts of ribs and their crested processes sometimes produced to give a spidery appearance.

Variation. Although the first podium is always the longest, subsequent ones are occasionally longer than normal, so tending towards subspecies flexuosus.

Distribution. Endemic to South Africa. Type locality: Agulhas Bank, 32°15.2'S/28°57.7'E, 49.5 m.

Distribution in South Africa. Agulhas Bank, from off Still Bay to off East London in 18 to 120 m. 34/21 (s), 33/25 (s), 34/25 (s, d), 33/26 (d), 34/26 (d), 33/27 (s), 32/28 (s)

Thecocarpus formosus (Busk, 1851)

Fig. 138D–G

Plumularia formosa Busk, 1851: 118.
Aglaoephina formosa: Marktanner-Turneretscher, 1890: 264, pl. 6 (fig. 11).
Aglaoephina parasitica Warren, 1908: 332, fig. 17, pl. 48 (figs 28–32).

Diagnosis. Stem unfascicled, unbranched, reaching a maximum height of 240 mm, with one to three hinge-joints separating a short basal part from a distal part bearing alternate hydrocladia. Distal part divided into short, broad internodes by transverse or oblique nodes sloping in alternate directions. Each internode bearing one hydrocladiad apophysis and three nematothecae, one inferior anterior, one axillary anterior and one axillary posterior. Mamelon present on
Fig. 141.

*Theocarpus flexuosus umbellatus*. A, a sympodial branch; C, hydrothecae.

*Theocarpus flexuosus plumiferus*. B, hydrothecae; D, a sympodial branch bearing corbulae.

Scale: A and D in cm, the rest in mm/10.
anterior surface of apophysis. The two rows of hydrocladia not in one plane, but displaced onto the anterior surface.

Hydrocladium bearing close-set hydrothecae on anterior surface, consisting of thecate internodes separated by transverse or slightly oblique nodes. Internodes with or without an internodal septum across central region, last internode with an extra median nematotheca and terminating in a blunt spine.

Hydrotheca sac-shaped, with an adcauline intrathecal septum, 0.2–0.3 mm in adcauline height and 0.13–0.19 mm in marginal diameter. Margin forming an angle of about 60° with internode; with seven marginal teeth, one median inturned adcauline and three pairs double laterals, each with an internally and an externally directed point, the external point of the most adcauline tooth the largest; with a long, hollow spine arising from the adcauline surface below the median adcauline tooth and curving distally.

Median inferior nematotheca adnate to adcauline thecal wall as far as the median spine, then free; not quite reaching thecal margin; with an aperture extending all the way along upper surface of free part and sometimes a second opening into hydrotheca. Lateral nematotheca tubular, reaching approximately to level of thecal margin, with one distal aperture extending also along mesial surface. Caueline nematothecae gutter-shaped.

Corbula with a pedicel of two to five hydrotheca-bearing segments followed by segments bearing alternate paired ribs. Each rib bearing a series of long tubular nematothecae along outer edge, and with inner edge fused to the rib behind. Each rib with a free lateral branch close to proximal end bearing nematothecae on both edges. A hydrotheca seated in axil of lateral branch. Corbula reaching 3–11 mm in length. Female corbula with ribs very firmly attached; each rib with proximal branch well developed and sometimes equal to it in length, often with one or two extra lateral branches distal to hydrotheca. Male corbula usually longer and thinner than female and with distal parts of ribs only partly attached; each rib with a proximal lateral branch only, which is poorly developed and bears at most two or three pairs nematothecae.

Colour: reddish brown.

Variation. The hydrorhiza of this species has the ability to produce suckers which act as holdfasts. Since the suckers can penetrate into pebbles, barnacle-shells and coralline algae (a common host), they must produce some calcium-dissolving substance. It has been shown by Warren (1908) that they can also penetrate into the cells of the host algae where they possibly obtain nourishment.

The size of the hydrotheca varies along the length of a hydrocladium, tending to be smaller near the proximal end and with a shorter median inferior nematotheca. The change in length in the median spine is most marked; its length being approximately 0.03 mm at the proximal end, increasing gradually to as much as 0.3 mm at about five internodes from the distal end, then becoming shorter again.

Distribution outside South Africa. Ceylon, Torres Strait (Australia) and
Mediterranean, with doubtful records from Labrador and New Zealand.

**Distribution in South Africa.** Common all round the south and east coasts from off Still Bay to Richard’s Bay, littoral to 90 m. One record from South West Africa. Type locality: Algoa Bay. 34/21 (s), 34/22 (s), 34/23 (s), 33/25 (s), 34/25 (s), 33/26 (s), 33/27 (1, s), 32/28 (l, s), 32/29 (s), 31/29 (1, l, s), 31/30 (l), 30/30 (s), 29/31 (l, s), 28/32 (s)

**SUBORDER: LIMNOMEDUSAE**

**Diagnosis.** Hydranth usually small, sessile and solitary, but with powers of asexual reproduction; with no definite hydrotheca or gonotheca; with or without a few tentacles; producing medusae. Medusa with gonads either on stomach or on radial canals; with hollow marginal tentacles usually without marginal bulbs; with or without endodermal statocysts.

**KEY TO FAMILIES**

[Families not treated in this monograph are bracketed]

1. Medusa with gonads on radial canals only; with statocysts but without ocelli [OLINDIIDAE]
   - Medusa with gonads on stomach, but often extending along radial canals as well . . . . 2
2. Medusa generally with branched radial canals; without statocysts and without ocelli. Hydranth with not more than 2 tentacles . . . . PROBOSCIDACTYLIIDAE p. 467
   - Medusa with unbranched radial canals . . . . . . . . . . 3
3. Medusa without statocysts but with ocelli. Hydranth with more than 2 tentacles
   - Medusa with statocysts but without ocelli. Hydranth without tentacles [LIMNOCNIIDAE]

**Family Moerisiidae**

**Diagnosis.** Hydranths small and athecate, normally solitary, with more than two capitate or moniliform tentacles, with conical hypostome. Perisarc poorly developed, never reaching to tentacular region. Asexual reproduction possible by budding, transverse fission or stolonization. Producing medusa-buds on hydranth body.

Medusa with four unbranched radial canals, at least four hollow marginal tentacles, usually no statocysts, abaxial ocelli on marginal bulbs, quadrangular stomach. Gonads on stomach wall and on radial lobes of stomach extending outwards along radial canals.

Nematocysts of three kinds, always including stenoteles and desmonemes. Mostly brack-water forms.

**Introduction.** The family Moerisiidae contains a number of relatively rare forms known from brackish waters in various parts of the world. One or two forms can also exist in the sea. There are in total only five genera and nine species. The species are known best by their medusae, which are of moderate size. The hydranth generation is relatively inconspicuous and is known in six species. It lives attached to water-weeds, grass, sand-grains, etc., and though essentially solitary, possesses the power of asexual reproduction.

The hydranth is athecate; the tentacles are scattered on the distal part of the
body or arranged in one or two rough whorls and are moniliform or capitate. Medusa-buds are borne on the hydranth body, either amongst or below the tentacles. A poorly developed perisarc occurs, which surrounds the stolons when present (see below), may continue for a short distance over the hydranth body and in some species forms thickened pedal discs for attachment.

Asexual reproduction may occur in several ways.

(i) By transverse fission (‘decapitation’), described for *Moerisia lyoni*.
(ii) By production of lateral buds, usually immediately below the tentacles. The buds separate off, produce tentacles and develop into new hydranths. Occasionally a bud may fail to separate and develops a hydranth in situ.
(iii) By stolonization. The base of the hydranth produces slender, branching stolons which give rise to new hydranths which sooner or later separate off from the parent body.
(iv) In some species the basal discs, which contain an extension of the body wall, act as resting stages (podocysts) and can survive the death of the hydranth to regenerate later. They can also divide, each daughter podocyst producing a hydranth.

Unlike most hydroids both hydranth and medusa possess hollow tentacles, their cavities communicating directly with the coelenteron.

The medusa is peculiar in the cruciform shape of its stomach, of which four lobes spread outwards along the radial canals. The gonads develop on the stomach wall and on its radial lobes, sometimes almost reaching the margin of the bell. The reddish ocelli on the marginal bulbs are a prominent feature.

Kramp, in various papers, includes the Moerisiidae, together with the Olindiidae, Limnocnididae and Proboscidactylidae, in the order Limnomedusae, mainly on the basis of the hollow tentacles and the quadrate nature of the stomach in the medusa. The Olindiidae and Limnocnididae have internal statocysts but there is some doubt as to their presence in the Moerisiidae. Kramp claims to have found microscopic statocysts in *Ostromouvia*, a claim which, however, is rejected by Valkanov (1954).

Rees (1958) on the other hand, places the Moerisiidae among the capitate Athecata, where he creates a superfamily, Moerisioidae, for their reception. He claims that they have many features in common with the lower Corymorphines, including the nematocyst types. All Moerisiidae have three types of nematocysts: stenoteles, desmonemes and a third type which is variable: isorhizas in *Ostromouvia inkermanica*, atrichous isorhizas in *Moerisia lyoni*, basitrirchous isorhizas in *Ostromouvia horii*, anisorhizas in *Ostromouvia gemmata* and microbasic euryteles in *Odessia maeotica*.

KEY TO GENERA

[Genera not represented in South Africa are bracketed]

1. Hydranth tentacles capitate and with adaxial batteries of nematocysts. Fixation by pedal disc. Medusa tentacles with irregular transverse batteries of nematocysts
   [Odessia]
   - Hydranth and medusa tentacles moniliform, with complete rings of nematocysts along the whole length 2
2. Fixation of hydranth by pedal discs. Medusa tentacles with basal part adnate to exumbrella Ostroumovia, p. 466
   - Hydranth without pedal discs, loosely attached by thin perisarcal covering of hydro-
   rhiza. Medusa tentacles with globular bulbs, not clasping over exumbrella [MOERISIA]

**Genus Ostroumovia Hadži, 1928**

**Diagnosis.** Hydranth with moniliform tentacles armed with rings of nematocysts along whole length; tentacles irregularly arranged or in one more or less distinct whorl. Fixation by one or more perisarcal pedal discs. Asexual reproduction by podocysts, by budding from hydranth body, or by stolonization. Perisarc continued as a thin, gelatinous layer over stolons and to a varying extent over basal part of hydranth. Medusa-buds borne on body of hydranth amongst the tentacles.

Adult medusa without peduncle, with cruciform mouth without distinct lips, smooth gonads. Tentacles armed with annular rings of nematocysts throughout length, with basal part adnate to exumbrella.

Type species: *Moerisia inkermanica* Paltschkowa-Ostroumowa, 1925.

One species from South Africa.

**Ostroumovia inkermanica** (Paltschkowa-Ostroumowa, 1925)

Fig. 142A–G

*M. inkermanica* Paltschkowa-Ostroumowa, 1925: 273, figs 1–3.


**Diagnosis.** Hydranth attached to substratum by one or more perisarcal pedal discs, slender at base and widening to tentacular region, reaching about 3 mm in height, with 4–12 tentacles in one whorl or in two roughly alternating whorls. Asexual reproduction possible by lateral buds arising from the hydranth just below the tentacles or by stolonization from the base. A delicate, gelatinous perisarcal sheath with adhering silt covering stolons and basal part of hydranth body.

Newly liberated medusa with four tentacles. Adult medusa hemispherical, reaching 8 mm in diameter and 6 mm in height, with very thick jelly, very small stomach, 32 marginal tentacles. Gonads extending along radial lobes of stomach nearly to bell margin, with distal parts sac-like, pendent (from Kramp).

Nematocysts of three types:

(i) Stenoteles, $9.0 \times 6.3 - 13.1 \times 10.8 \mu$.
(ii) Desmonemes, $5.9 \times 2.7 - 8.1 \times 4.1 \mu$.
(iii) A third type, probably isorhizas, present only on the hypostome of the hydranth, with elongated capsules, $8.1 \times 2.7 - 9.9 \times 2.7 \mu$. 
**Variation.** Variation in appearance of the polyp generation occurs as a result of asexual reproduction. The hydranth may be solitary with a single pedal disc at the base, or stolonization at or near the base may result in a branching hydrorhiza with four or more pedal discs. Some of the stolons may taper off into very fine filaments. In at least one case a new hydranth has remained attached to the same hydrorhiza as the parent. Lateral buds occur on the hydranth body. These are said to separate from the parent and give rise to new hydranths though this has not been observed in this material. The pedal discs (podocysts) have the power to divide and to regenerate after the death of the hydranth. Again this has not been observed in South Africa.

The development of the perisarcal sheath varies among individuals and may be hardly visible on the body of the hydranth or may reach about half-way up its length.

Half-grown medusae (1.7 × 1.7 mm) have been found together with the hydranths in Kosi Bay, and mature medusae (4.4 × 3.4 mm) with 16–28 tentacles in Lake St. Lucia. The known salinity range in South Africa to date is 3–10.8‰.

**Remarks.** Rees & Thursfield (1965) have included *Annulella gemmata* Ritchie, 1915, from India and eastern Spain, as a synonym of *O. inkermanica*. However, there appears to be a difference in nematocysts; Ritchie reports anisorhizas in *gemma* and Valkanov ‘glutinants’, or isorhizas, in *inkermanica*. It was not possible to classify exactly the third nematocyst type in the present material.

Calder & Burrell (1969) suggest that moerisiid hydroids are distributed by shipping, but it is hardly possible that *O. inkermanica* could have been introduced in this way into South African lakes which are not navigable by ocean-going vessels.

**Distribution outside South Africa.** Black Sea (type locality), India, France, Netherlands.

**Distribution in South Africa.** Brack-water lakes: Nhlanje Lake (Kosi Bay), Lake St. Lucia and Lagoa Poelola on the east coast. Hydranths in 2–16 m, medusae in plankton. 27/32 (s)

**Family Proboscidactylidae**

**Diagnosis.** Small atrate hydroids forming stonorial colonies commensal on the tubes of sabellid polychaets. Perisarc totally absent. Hydranths of two types: gastrozooids and gonozooids. Gastrozooids with two filiform tentacles and a prominent hypostome bearing a pad of large nematocysts. Gonozooids without mouth or tentacles, bearing gonophores which develop into free medusae.

Medusa with 4–6 or more radial canals which are generally branched, usually with tentacles, without statocysts or ocelli, stomach with 4–6 or more lobes extending along the proximal parts of the radial canals. Gonads on stomach wall.
Ostrooumovia inkermanica. A-C, medusae, mature (B) and young stages (A and C); D-G, hydromes. Proboscisactyla sp. H, gastrozooid; J, sterile gonozooid; K, fertile gonozooid with medusa-buds; L, older medusa-bud.

Scale: A-C in mm, the rest in mm/10.
Nematocysts of three kinds: macrobasic euryteles, microbasic euryteles and desmonemes.

Introduction. This family includes only two genera, Proboscidactyla and Pochella, of which the polyp generation is known only in the former. The diagnosis is thus based on this genus and may require modification to include Pochella when its life-history has been traced.

The hydramths of Proboscidactyla are, in those species where they are known, very similar to one another and cannot with any certainty be distinguished without knowledge of the medusa. Radiation has occurred in the medusa phase and any keys must be based on medusa characters. In this genus the medusa is distinguished by special sacs or cnidophores on the umbrella margin between the tentacles, containing about five large nematocysts. These are easily visible in medusa-buds still attached to the hydranth.

The life-history has been worked out for five species:

P. circumsabella Hand, 1954, by Hand;
P. flavicirrata Brandt, 1835, by Uchida & Okuda (1941) and by Hand (1954);
P. occidentalis (Fiewkes, 1889), by Hand (1954);
P. ornata (McCready, 1857), by Brinckmann & Vannucci (1965) and by Calder (1970b);
P. stellata (Forbes, 1846) by Hincks (1872) and by Browne (1896). The hydranth of this species was originally described as Lar sabellarum by Gosse (1857)—the posturing polyp of the British coasts.

In all of these the two-tentacled gastrozooids are arranged in a rank around the rim of the tube of the polychaet host with their tentacles towards the cavity and the asymmetrically placed pad of nematocysts on the hypostome away from it. In life they are very active and perform bowing and waving movements, they have also been seen to stroke the crown of the polychaet with their tentacles as though salvaging food particles. When the worms spawn the eggs are consumed in quantities by the hydranths.

Gonozooids are situated below the gastrozooids and often arise from their bases by small ‘tails’. They may form a distinct ring or be scattered for some distance down the tube. The lowest gonozooids are usually smaller and sterile. The upper ones produce up to 12 medusa-buds at about \( \frac{2}{3} \) the height of the body.

Experimental work (Strickland 1971) has shown that the hydroids cannot survive without their host polychaets and nor can the planulae develop. They are thus true obligatory commensals.

In at least some species (e.g. P. ornata) the medusa can reproduce asexually by budding either medusae or polyps from stolons which arise from the stomach or radial canals. The medusae do not occur in mid-ocean but frequent coastal areas and bays, habitats where the host polychaets commonly occur. In one species, P. abyssicola (hydranth unknown) the medusa has no marginal tentacles.

Nematocysts are very similar from species to species, differing only in small details of size and shape. In all, the same three types occur, macrobasic eury-
teles, microbasic euryteles and desmonemes, though the microbasic euryteles are absent from the medusae. The hydranth tentacles are remarkably poor in nematocysts, possessing only microbasic euryteles, but all three types are present in the nematocyst pads on the hypostome of the gastrozooid and on the gonozooid. The largest type, the macrobasic eurytele, is very striking and abundant.

KEY TO GENERA
[Genera not represented in South Africa are bracketed]

1. Medusa without cnidophores. Gonads on interradial walls of stomach only [Pochella]
   = Medusa with cnidophores between the tentacles. Gonads extending on to radial lobes of stomach . . . . . . . . . . Proboscidactyla p. 470

Genus Proboscidactyla Brandt, 1835

Fig. 142H–L

Syn. Lar Gosse, 1857.
Willia Forbes, 1846.

Diagnosis. Hydranth as for family.

Adult medusa with 4–6 or more branched radial canals, usually with many marginal tentacles corresponding in number to the radial canals, rarely without; usually without an open circular canal; with cnidophores on the exumbrella margin between the tentacles. Gonads surrounding stomach and extending onto its radial lobes.

Type species: Proboscidactyla flavicirrata Brandt, 1835.

Remarks. Hydranths of Proboscidactyla have been found at Inhaca, Moçambique, commensal on tubes of the polychaet Laonome (Millard & Bouillon 1974), but since the medusae have not been reared it is not possible to identify the species.

Medusae of P. ornata (McCrady, 1857), a circumglobal species, have been found at Mombasa on the tropical east coast of Africa (Kramp 1965) and of P. mutabilis (Browne, 1902) from Saldanha Bay on the west coast of the Cape (University of Cape Town unpublished records, W. J. Rees det.).
LIST OF SPECIES AND AUTHORITIES FOR PREVIOUS SOUTH AFRICAN RECORDS

* new species
† new record from South Africa

ATHECATA

Family Corymorphidae

Branchiocerianthus imperator. Vervoort 1966b
Corymorpha sp. Millard 1959a

Family Tubulariidae

Ectopleura bethae. Millard & Bouillon 1974
   As Tubularia betheris. Warren 1908
† Hybocodon unicus
Tubularia crocea. Broch 1914, (Doubtful species)
Tubularia larynx. Stechow 1925a. Millard 1959b
   ? As Tubularia sertularella. Stechow 1923b
Zyzyzus solitarius. Millard & Bouillon 1974
   As Tubularia solitaria. Warren 1906b. Millard 1957, 1966a

Family Halocordylidae

Halocordyle disticha. Millard & Bouillon 1974
   As Halocordyle cooperi. Warren 1906a, 1907b
   As Pennaria australis var. cooperi. Warren 1908
   As Halocordyle disticha var. australis. Vervoort 1946b
   As Pennaria disticha var. australis. Millard 1959a

Family Myriothetaidae

Monocoryne minor. Millard 1966a
Myriotheta capensis. Manton 1940. Millard 1957, 1966a
Myriotheta tentaculata. Millard 1966a

Family Corynidae

Bicorona elegans. Millard 1966a
Sarsia eximia. Millard 1959b, 1966a
   As Coryne sp. Millard 1957.
   As Clavatella multitentaculata. Warren 1908.

Family Cladonemiidae

Staurocladia vallentini. Millard 1966a
   As Cnidonema capensis. Gilchrist 1919

Family Solanderiidae

Solanderia atrorubens. (Doubtful species)
   As Dehitella atrorubens. Brazier 1887
Solanderia labyrinthica. (Doubtful species)
   As Ceratella labyrinthica. Hyatt 1877
Solanderia minima. Millard & Bouillon 1974
Solanderia procumbens. Millard 1966a
   As Ceratella procumbens. Carter 1873
   As Ceratella spinosa. Carter 1873
   As Solanderia atrorubens. Marshall 1892
Solanderia rugosa. Marshall 1892. (Doubtful species)

Family Asyncorynidae

Asyncoryne ryniensis. Warren 1908
Family Cladocorynidae


Family Zanclidae

Zanclia sp. Millard & Bouillon 1974

Family Clavidae

Clava sp. Millard 1966a
Merona cornucopae. Millard 1966a
Rhizogeton nudum. Millard & Bouillon 1974
Turritopsis nutricula. Millard & Bouillon 1974

Family Eudendriidae

Eudendrium angustum. Warren 1908
Eudendrium capillare. Millard & Bouillon 1974
As Eudendrium parvum. Warren 1908
As Eudendrium ?parvum. Millard 1959a
Eudendrium carneum. Millard 1959a
Eudendrium deciduum. Millard 1957, 1966a
Eudendrium mozskosowskai. Millard & Bouillon 1974
As Eudendrium ?capillare. Millard 1966a
*Eudendrium ritchiei sp. nov.
As Eudendrium annulatum (?). Ritchie 1909
As Eudendrium ?carneum. Millard 1966a

Family Bougainvillidae

Bimeria fluminalis. Millard 1959a
Bimeria rigida. Warren 1919a
As Leuckartiaria vestita f. nana. Vervoort 1946b
Bougainvillia meinerttai. Jäderholm 1923a
As Bougainvillia sp. Millard 1966a, 1968
Clavopsella navis
As Rhizorhagium navis. Millard 1959b
Dicoryne conferta. Millard 1966a
Rhizorhagium robustum. Millard 1966a
As Parawrightlia robusta. Warren 1907a

Family Hydractiniidae

*Clavactinia multitentaculata sp. nov.
As Hydractinia sp. Millard 1968
Hydractinia atispsina. Millard 1955, 1957, 1966a
As Hydractinia sp. Broch 1914
Hydractinia canalifera. Millard 1957
Hydractinia kaffiriana. Millard 1955, 1959a, 1966a
*Hydractinia marsupialis sp. nov.
As Podocoryne carnea. Ritchie 1907b. Millard 1966a
As Hydractinia parvispsina. Vanhöffen 1910
As Hydractinia carnea. Millard 1957
Hydractinia pacifica. Stechow 1925a. (Doubtful record)
?Stylactis siphonis. (Doubtful species)
As Stylactella siphonis. Stechow 1921b
As Halereella siphonis. Stechow 1925a
Family Cytaeidae

Cytaeis nassa. Millard & Bouillon 1974
   As Podocoryne nassa. Millard 1959a

Family Pandeidae

Hydrichtythus boyei. Warren 1916. Millard 1959a
Leuckartiara octona. Millard 1957, Millard 1966a
   As Perigonimus vestitus f. radicans. Vanhöffen 1910.

THECATA

Family Campanulinidae

Calicella oligista. Stechow 1925a
Egmundella amirantensis. Millard & Bouillon 1974
   *Lineolaria gravierea sp. nov.
      As Lineolaria sp. Millard & Bouillon 1974
Modeeria rotunda
   As Stegopoma fastigiata. Millard 1958
   As Stegopoma fastigiatum. Millard 1967, 1968
Opecularella sp. Vervoort 1966b
Phialella turrita
   As Campanulina turrita. Vanhöffen 1910

Family Haleciidae

   As Halecium parvulum, including var. magnum. Millard 1957
   †Halecium dyssymetrum
Halecium ′muricatum. Millard 1966a, 1968
Halecium sessile. Vervoort 1966b
Hydrodendron caciformis. Millard 1957
Hydrodendron cornucopia. Millard 1973
Hydrodendron gardineri. Millard & Bouillon 1974
Hydrodendron gracilis. Millard 1973
   As Zygophyllax enigmatica. Millard 1964
Hydrodendron sympodiiformis. Millard & Bouillon 1974

Family Lafoneidae

Acryptolaria conferta. Millard 1968
   As Acryptolaria conferta conferta. Millard 1964
   As Acryptolaria conferta australis. Millard 1964, 1967
   As Acryptolaria angulata. Vervoort 1966b
   †Cryptolarella abyssicola
   †Cryptolaria pectinata
Filellum antarcticum. ?Stechow 1925b. Millard 1964 (pp)
Filellum ′serpens. Stechow 1925a
   As Reticularia serpens. Millard 1957.
   As Filellum ′antarcticum. Millard 1958, 1964 (pp)
*Hebella displani*
   As *Lafoea displani*. Warren 1909.


*Hebella parvula*. Stechow 1923b.

   As *Lafoea scandens*. Warren 1908.
   As *Hebelopsis scandens*. Stechow 1925a
   As *Hebella urceolata*. Millard 1964

*Lafoea benthofila*. Vervoort 1966b

*Lafoea dumosa*. Stechow 1925a

   As *Lafoea gracillima*. Vervoort 1966b

   As *Lafoea magna*. Warren 1908

   +*Zygophy lux ?antipathes*


*Zygophy lux sibogae*. Millard 1964

**Family Campanulariidae**

*Campanularia africana*
   As *Campanularia tincta*. Warren 1908.

*Campanularia crenata*. Millard & Bouillon 1974

   As *Campanularia ?crenata*. Millard 1958

*Campanularia hincksii*. Millard 1966a

   As *Campanularia caliculata*. Warren 1908
   As *Clytia compressa*. Vanhöffen 1910
   ?As *Campanularia gracilis*. Stechow 1925a

   ?As *Campanularia tincta*. Jäderholm 1923a
   ?As *Campanularia africana*. Stechow 1925a


*Campanularia robertii*. Gow & Millard 1975

*Clytia graeveti*. Millard & Bouillon 1974
   As *Laomedea striata*. Kramp 1921
   As *Clytia serrata*. Millard 1958

   As *Clytia rari dentata*. Vanhöffen 1910
   As *Thaumantias rari dentata*. Stechow 1925a
   As *Clytia johnstoni*. Millard 1958

*Clytia hummelincki*. Millard 1966a

*Clytia latiflora*. Millard & Bouillon 1974

*Clytia paradoxa*
   As *Eucalips paradoxes*. Stechow 1923b, 1925a

   ?As *Clytia (?) utrae*. Stechow 1925a

*Clytia warreni*
   As *Clytia elongata*. Warren 1908
Eulaomedea calceolifera
   As Laomedea calceolifera. Stechow 1925a
   As Laomedea angulata. Millard 1959b
Gonothyraea loveni
   As Laomedea loveni. Millard 1959b
   As Obelia dubia. Vanhöffen 1910. Stechow 1925a

Family Syntheciidae

Hincksella cylindrica pusilla. Millard 1964
Hincksella echinocarpa. Millard 1967
Synthiaecium dentigerum. Millard 1964
   As Syntheciaceum subventricosum. Stechow 1925a

Family Sertulariidae

Abietinaria abietina
   As Sertularia abietina. Busk 1851. (Doubtful species)
Abietinaria laevimarginata. Millard & Bouillon 1974
   As Sertularia linealis. Warren 1908. Millard 1958
Amphisbetta maplestonei
   As Sertularia bidens. Warren 1908. Stechow 1912
   As Odontotheca bidens. Stechow 1919b
   As Amphisbetta bidens. Millard 1957, 1958, 1964
   As Sertularia minima. Allman 1886
   As Sertularia crinoidea. Allman 1886
   As Dynamena operculata. Krauss 1837
   As Sertularia aperta. Allman 1886
   As Odontotheca operculata. Broch 1914. Stechow 1919b
Calamphora campanulata
   As Sertularella campanulata. Warren 1908
Crateritheca acanthostoma. Millard 1964
   As Dynamena pluridentata. Kirchenpauer 1864
   As Sertularia acanthostoma. Warren 1908
   As Stereotheca acanthostoma. Millard 1958
Diphasia attenuata
   As Sertularia rosacea. Busk 1851. (Doubtful species)
Diphasia bipinnata. Allman 1886. (Doubtful species)
Diphasia digitalis. Millard & Bouillon 1974
†Diphasia heurtelli
Diphasia nigra
   As Sertularia nigra. Busk 1851. (Doubtful species)
   As Thaliaria tubuliformis. Warren 1908
   As Dynamena tubuliformis. Stechow 1919a
Dynamena pumila. Krauss 1837. (Doubtful species)
As Pasythea quadridentata. Warren 1908

Hydralmania falcata
As Plumularia falcata. Busk 1851. (Doubtful species)


Parascyphus simplex. Millard 1968

As Thuiaria ellisi. Busk 1851
As Thuiaria persocialis. Allman 1876
As Thuiaria personalis. Kirchenpauer 1884
Broch 1914
As Thuiaria pectinata. Allman 1888. Ritchie 1907b
As Dymella articulata. Vervoort 1946b. Stechow 1923c

†Salacia desmoide

Salacia distincta. Millard 1964

As Sertularella fusiiformis. Warren 1908

Sertularella agathensis. Millard 1964

†Sertularella annulaventricosa
As Sertularella tenella. Hartlaub 1901a (pp)
As Sertularella capensis delicata. Millard 1964

As Sertularia arbuscula. Busk 1851
As Sertularia polyzonias. Busk 1851 (pp.)
As Sertularella crassipes. Allman 1886
As Sertularella cuneata. Allman 1886
As Sertularella tumida. Warren 1908

Sertularella capensis. Millard 1957, 1964

Sertularella congestata. Millard 1964


As Thecocladium flabellum. Allman 1888

Sertularella fusiiformis. Millard 1957, 1964
As Sertularella lineata. Stechow 1923b

Sertularella gayi. Jäderholm 1923a
As Sertularia polyzonias, var. β. Johnston 1838
As Sertularia polyzonias. Busk 1851 (pp.). (Doubtful species)

Sertularella gilchristi. Millard 1964


As Sertularella polyzonias. Warren 1908. Stechow 1912


As Sertularella polyzonias, f. robusta. Kirchenpauer 1884
As Sertularella sp. Millard 1958

Sertularella natalensis. Millard 1968

As Sertularella polyzonias f. gracilis. Kirchenpauer 1884

Sertularella polyzonias falsa
As Sertularella falsa. Millard 1957, 1964

Sertularella polyzonias gigantea. Stechow 1925a

Sertularella polyzonias xantha
As Sertularella longa. Stechow 1923b
Sertularella pulchra. Stechow 1923b. Millard 1964
Sertularella striata. Stechow 1923a, 1925a. Millard 1964
Sertularia argentea. Busk 1851. (Doubtful species)
Sertularia distans. Millard & Bouillon 1974
  As Sertularia distans var. gracilis. Millard 1957, 1958
  As Sertularia distans gracilis. Millard 1964, 1968
Sertularia longa. Millard & Bouillon 1974
  As Sertularia linealis var. longa. Millard 1958
  As Sertularia linealis. Millard 1968
  As Sertularia loculosa. Warren 1908
  As Sertularia acuta. Millard 1958
Stereotea elongata. Millard 1968
  As Sertularia elongata. Jäderholm 1917
Symplectoscyphus arboriformis. Millard 1964, 1968
  As Sertularia polyzonia. Busk 1851 (pp.)
  As Sertularella arboriformis. Stechow 1912
Symplectoscyphus filiformis
  As Sertularella filiformis var. reticulata. Ritchie 1907b. (Doubtful species)
Symplectoscyphus indivisus. Millard 1961. (Doubtful species)
Symplectoscyphus johnstoni
  ?As Sertularia gaudiochaud. Busk 1851. (Doubtful species)
Symplectoscyphus macrogonius. Millard 1957, 1964
Symplectoscyphus paulensis. Millard 1967
Symplectoscyphus secundus
  As Sertularella secunda. Kirchenpauer 1884
  As Sertularella limbata. Allman 1886
Symplectoscyphus unilateralis
  ?As Sertularia unilateralis. Busk 1851. (Doubtful species)
Thiaria doliolus. Kirchenpauer 1884. (Doubtful species)

Family Plumularioideae
Subfamily Halopterinae

  As Antennella quadriaurita forma africana. Broch 1914
  As Antennella africana. Stechow 1923a, 1925a
  As Antennella natalensis. Warren 1908
  As Antennella secundaria. Stechow 1925a
Corhiza helicosa. Millard 1962
Corhiza mortensenii. Millard 1968
  As Antennopsis scotiae. Ritchie 1907b, 1909. Millard 1957
Corhiza valdiviae
  As Heteroplon valdiviae. Stechow 1923a
  As Theococculus(?) valdiviae. Stechow 1925a
  As Halopteris valdiviae. Millard 1957, 1962
†Gattyia conspicua
Gattyia heurtelii. Millard 1968
  As Paragattyia heurtelii. Millard 1958
  As Paragattyia intermedi. Millard 1958
(non Millard 1958)
†Gattyia mehitecata

Haloperis gemelli para. Millard 1962

As Plumularia (Heteroplo) glutinosa. Stechow 1925a

*Haloperis pseudoconstricta sp. nov.
As Haloperis constricta. Millard 1957, 1962

*Haloperis rostrate sp. nov.

As Plumularia tuba. Kirchenpauer 1876
As Acladia africana. Marktanner-Turneretscher 1890
As Heteroplo jaederholmi. Stechow 1912
As Plumularia Jaederholmi. Jaederholm 1917
As Plumularia (Heteroplo) africana. Stechow 1925a
As Thecocaulus tuba. Leloup 1939


Monostaechas quadridentis. Millard & Bouillon 1974

Schizotrichia frutescens
As Aglaophenia frutescens. Krauss 1837


Family Plumulariidae

Subfamily Kirchenpaueriinae

Kirchenpaueria irregularis. Millard & Bouillon 1974
As Plumularia irregularis. Millard 1958

?As Plumularia gymnardi. Kirchenpauer 1876
As Plumularia unilateralis. Ritchie 1907b
As Plumularia pinnata. Ritchie 1907b
As Plumularia echinulata. Ritchie 1907b, 1909
As Plumularia pinnata, f. typica. Broch 1914


As Kirchenpaueria adhaerens. Millard 1958

As Kirchenpaueria mirabilis. Warren 1908

Family Plumulariidae

Subfamily Plumulariinae

Deutitheca bidentata. Millard & Bouillon 1974

Nemertesia antennisina. Stechow 1912
As Nemertesia antennisina irregularis. Vervoort 1966b


As Antennularia cymodoceae. Busk 1851
As Nemertesia johnstoni. ?Kirchenpauer 1876
As Nemertesia decussata. Kirchenpauer 1876
As Antennularia decussata. Marktanner-Turneretscher 1890
As Antennularia hartlaubi. Ritchie 1907b

As Antennularia ramosa. Busk 1851

Plumularia antoniobriani. Millard 1967

As Aглаophenia gainardi. Lamouroux 1824
As Plumularia lagenifera, var. septifera. Ritchie 1909
*Plumularia massambicae sp. nov.
Plumularia obliqua. Millard & Bouillon 1974
Plumularia pennuculae. Millard & Bouillon 1974
As Plumularia (Monotheca) flexuosa. Stechow 1925a
Vervoort 1966b. Millard & Bouillon 1974
As Plumularia spinulosa, var. obtusa. Millard 1957
As Plumularia spinulosa, var. typica. Millard 1958
Plumularia strictocarpa. Millard & Bouillon 1974
As Plumularia tenus. Warren 1908

Family Plumulariidae
Subfamily Aглаopheniinae

(Doubtful species)
Aглаophenia attenuata. Allman 1883. (Doubtful species)
Aглаophenia cupressina. Millard & Bouillon 1974
Aглаophenia holubi. Leloup 1934. (Doubtful species)
As Aглаophenia dichotoma. Kirchenpauer 1872. Ritchie 1907b. Stechow 1925a
As Aглаophenia pluma, var. dichotoma. Millard 1957
As Aглаophenia conferta. ?Kirchenpauer 1872
As Aглаophenia heterodonta. Jäderholm 1903. Ritchie 1909 (pp.)
As Aглаophenia parvula. Stechow 1925a. Vervoort 1946b
As Aглаophenia pluma, var. parvula. Millard 1957, 1958
Aглаophenia pluma pluma. Millard 1968
As Aглаophenia chalarocarpa. Allman 1886. Warren 1908
As Aглаophenia pluma, var. typica. Millard 1957, 1958
Aглаophenia pusilla. Kirchenpauer 1872. (Doubtful species)
Aглаophenia tubulifera. Kirchenpauer 1872
As Plumularia sp. Busk 1851. (Doubtful species)
*Cladocarpus crepidatus sp. nov.
Cladocarpus dofelini. Vervoort 1966b
Cladocarpus inflatus. Vervoort 1966b
Cladocarpus leloup. Millard 1962
As Cladocarpus flexilis. Leloup 1939
As Plumularia sp. Busk 1851
Cladocarpus millardae. Vervoort 1966b
Cladocarpus sinusus. Vervoort 1966b
Cladocarpus tenus. Vervoort 1966b
*Cladocarpus unicorns sp. nov.
Cladocarpus valdiviae. Stechow 1923b
Gymnangium africanum
As Halicornaria africana. Millard 1958, 1968
Gymnangium allmani
As Halicornaria allmani. Millard 1968
Gymnangium arcuatum. Rees & Thursfield 1965
  As Aglaophenia arcuata. Krauss 1837
  As Aglaophenia arcuata. Kirchenpauer 1872. Broch 1914
  As Halicornaria arcuata. Stechow 1912. Millard 1958 (including var. epizoootica), 1962 (including subsp. epizoootica)

Gymnangium exertum
  As Halicornaria exerta. Millard 1962 (including subsp. epizoootica)

Gymnangium ferox
  As Halicornaria ferox. Millard 1962

Gymnangium gracilecaule gracilecaule. Millard & Bouillon 1974
  As Halicornaria gracilecaulis. Millard 1967
  As Halicornaria gracilecaulis gracilecaulis. Millard 1968

Gymnangium gracilecaule lignosum. Millard & Bouillon 1974
  As Halicornaria gracilecaulis. Millard 1958

Gymnangium hians
  As Halicornaria hians. Millard 1958

Gymnangium longirostre
  As Halicornaria longirostris. Millard 1961

Gymnangium montagui
  As Aglaophenia pennatula. ?Krauss 1837
  As Plumularia pennatula. ?Busk 1851
  As Halicornaria allmani var. Marktanner-Turneretscher 1890

  As Aglaophenia fisca. Kirchenpauer 1872. Marktanner-Turneretscher 1890
  As Aglaophenia patula. Kirchenpauer 1872
  As Aglaophenia ligulata. Kirchenpauer 1872
  As Lytocarpus patulus. Marktanner-Turneretscher 1890
  As Halicornaria segmentata. Warren 1908
  As Nematophorus plumosus. Stechow 1923a
  As Aglaophenia plumosa. Stechow 1925a


Lytocarpus phoeniceus. Millard 1968

Thecocarpus brevirostris. Millard 1968
  As Aglaophenia brevirostris. ?Kirchenpauer 1872
  As Aglaophenia vitiana. Billard 1907a

Thecocarpus delicatulus. Millard & Bouillon 1974

Thecocarpus flexuosus flexuosus. Millard 1962
  As Aglaophenia (? ) bifida. Stechow 1923b

  As Aglaophenia plumifera. Kirchenpauer 1872

  As Thecocarpus giardi, var. solidus. Millard 1958

Thecocarpus flexuosus umbellatus. Millard 1962

  As Plumularia formosa. Busk 1851
  As Aglaophenia formosa. Kirchenpauer 1872. Marktanner-Turneretscher 1890
  As Aglaophenia parasitica. Warren 1908.

LIMNOMEDUSAE

Family Moerisiidae

Ostroumovia inkermanica. Millard 1970

Family Proboscidactylidae

Proboscidactyla sp. Millard & Bouillon 1974
MONOGRAPH ON THE HYDROIDA OF SOUTHERN AFRICA

RECORDS OF HYDROID MEDUSAE FROM THE SOUTH AFRICAN REGION
(between 20°-40°S and 10°-40°E)

(TUBULARIDAE)
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(BOUGAINVILIIDAE)
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*A. pensile (Eschscholtz, 1829) 35/20, 36/21, 29/31, 29/32
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Proboscidactyla mutabilis (Browne, 1902) UCT record: 33/18

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*Vanhöffen (1911, 1912) apparently included both A. macrodactyla and A. pensile under the name of Mesonema coelum pensile. These records have been omitted.
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ADDENDUM

Family Plumulariidae
Subfamily Aglaopheniinae

*Cladocarpus paries* * sp. nov.

Fig. 143


*Description*. One branching stem 75 mm high. Hydrorhiza a thickened mat 5 mm wide, flattened on under side and detached from some hard surface. Stem thick and strongly fascicled, 1,5 mm thick at base, branching and rebranching in one plane; bearing alternate hydrocladia from an axial tube. Larger branches fascicled almost to end. Axial tube, where exposed, divided into regular internodes by straight nodes, each internode bearing one hydrocladal apophysis and two nematothecae, one anterior axillary and one proximal and anterior. Peripheral tubes bearing longitudinal rows of nematothecae. The two rows of hydrocladia in one plane.

Hydrocladium 2–3 mm in length and bearing up to eight hydrothecae. First internode short and athecate, with one median nematotheca. Remaining internodes thecate, each bearing one hydrotheca and three nematothecae, one median inferior and two laterals. All nodes oblique. Two internodal septa in

*paries*: the wall of a house.
Cladocarpus puries sp. nov. A, stem; B, anterior view of stem showing origins of hydrocladia; C-D, parts of hydrocladia with hydrothecae; E, t.s. perisarc of hydrocladium showing partition in hydrotheca (internode above, hydrotheca below).

Scale: A in cm, the rest in mm/10.
first internode; four or five in thecate internodes, three or four behind hydrotheca and one proximal.

Hydrotheca deep and tubular, curved slightly outwards. Abcauline wall with slight sigmoidal curvature, margin forming an angle of 40–50° with internode. No transverse intrathecal septa, but a longitudinal septum attached to centre of abcauline wall and stretching up to halfway across cavity. Margin sinuated, with no distinct teeth, but sometimes with a low, rounded lobe on each side. Abcauline edge thickened.

Median inferior nematotheca free from hydrotheca, short, reaching to just above base of hydrotheca, bifurcated and with two terminal apertures, with a third aperture on upper surface of undivided part; no opening into hydrotheca. Lateral nematotheca bifurcated, with one terminal aperture on a long neck and reaching well above thecal margin, a second opening on a shorter neck reaching approximately to thecal margin and a third opening on mesial surface. Cauleine nematotheca sac-shaped, with one or two openings.

Gonotheceae absent.

Measurements (mm)

<table>
<thead>
<tr>
<th>Description</th>
<th>Length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydrocladium, first internode, length</td>
<td>0.10–0.13</td>
</tr>
<tr>
<td>other internodes, length</td>
<td>0.25–0.35</td>
</tr>
<tr>
<td>Hydrotheca, length</td>
<td>0.18–0.24</td>
</tr>
<tr>
<td>width at mouth</td>
<td>0.10–0.11</td>
</tr>
<tr>
<td>width/length</td>
<td>0.42–0.56</td>
</tr>
<tr>
<td>Lateral nematotheca, length</td>
<td>0.13–0.19</td>
</tr>
<tr>
<td>Median nematotheca, length of free part</td>
<td>0.03–0.05</td>
</tr>
</tbody>
</table>

Remarks. This species closely resembles Cladocarpus lignosus in general appearance and form of the colony. It differs in the narrower, outwardly-curved hydrotheca, in the absence of marginal teeth, and in the longer lateral nematotheca. The median partition in the hydrotheca is a unique feature distinguishing it from all other species of Cladocarpus; it is widest at about the centre of the hydrotheca, where it may reach halfway across the cavity, and narrows rapidly above this to peter out below the thecal margin. The hydranth bulges onto both sides of the partition.

Distribution. Endemic to South Africa.

Distribution in South Africa. The only record is the holotype recorded above.

33/27 (s)

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* References containing South African records.
† References which have not been examined by the author.


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