

The European and Mediterranean species of *Aglaophenia* (Cnidaria: Hydrozoa)

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The eleven species of the hydroid genus *Aglaophenia* Lamouroux, 1812, recorded from European and Mediterranean waters are redescribed in detail and aspects of their biology discussed. A section on the identification of the European and Mediterranean species and a comprehensive glossary are included. Comments are given on type specimens, reproduction, ecology and distribution and, briefly, on other biological aspects. Certain of the species occur further north than previously realized. *A. acacia* Allman, 1883 and *A. parvula* Bale, 1882, are newly recorded from British waters, the latter being almost new to Europe. It differs only minutely from the widely-known *A. pluma*. *A. kirchenpaueri* (Heller, 1868) is added to the Irish faunal list, and has only recently been confirmed as present in British waters.

Re-identifications are made of some specimens about 250 years old probably collected by John Ellis and forming part of the Linnean collection in London.

Type specimens are discussed, newly identified, or designated, as follows: *Aglaophenia lophocarpa* Allman, 1877 (lectotype, p. 22); *A. parvula* Bale, 1882 (lectotype, p. 25); *A. pluma* (Linnaeus, 1758, as *Sertularia*) (neotype, p. 30); *A. tubulifera* (Hincks, 1861, as *Plumularia*) (holotype identified, p. 36).

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Introduction

In the subtidal waters of most European countries *Aglaophenia* is one of the most conspicuous of hydroid genera. Yet identifying its species is notoriously difficult and there is no adequate guide. Svoboda's (1979) account, in German, partly fills the gap but its objective was to define the species and to describe their differing ecologies rather than to highlight identification features. A recent illustrated guide to the species occurring in British waters is also available (Cornelius & Ryland, 1990) but fewer than half the total European species are covered. Continued attention by marine biologists to macrofaunal assemblages within reasonable SCUBA depths throughout European and Mediterranean waters has prompted us to provide an account which would both describe the European and Mediterranean species and assist in their identification.

We regard it necessary for the identification of *Aglaophenia* species to have detailed taxonomic descriptions alongside notes on identification in a single work.

The account is based partly on that of Svoboda (1979) but considers also work by several more recent authors who were perhaps stimulated by that publication. We have also examined much newly-collected material.

The conclusions presented are thus largely based on a study of the first author's collections of *Aglaophenia*. Most of his collections of this genus have been deposited in the Rijksmuseum van Natuurlijke Historie [RMNH], Leiden. Many of the specimens have been accessed into that institution's coelenterate collections in the normal way and are cited here as 'coll. A.S., RMNH Coel. 12345'. In some cases the 'A.S.' numbers that the specimens were given when formerly in his collection are given here as well to facilitate their future retrieval. Many of these specimens have been cited by those numbers in A.S.'s earlier publication. But a recent substantial donation to the RMNH of virtually his entire remaining personal collection of microslide preparations of this genus has been accessed as a single unit and these specimens do not carry individual RMNH numbers. In the RMNH collections these specimens are identified from their original 'A.S.' numbers. In the present paper these numbers are given in the format 'RMNH Coel., A.S. Hydrozoa subcollection, microslide preparation no. 123'.

A relatively small amount of *Aglaophenia* material collected by the first author is now preserved in the collections of the British Museum (Natural History) [BMNH], London. He has also deposited material of *Aglaophenia* in the Naturhistorisches Museum, Vienna, and the Zoologische Staatssammlung, Munich. Although all the included species, and much type material, is represented in the BMNH by far the longest series of the species are in the RMNH. This is true both of A.S. material in those institutions and of material from other collectors. However, workers in the

British Isles will find BMNH material adequate for that faunal area.

Our approach towards discriminating between the species has been traditional in that it has comprised a comparison of morphological data from populations coupled with a range of other data such as reproductive season, ecology, phenetic variation in response to local environmental factors, symbiotic associations, pigmentation, and so on. Certain recent developments in hydroid taxonomy might assist in future studies of this difficult group. Comparison of the ultramorphology of nematocysts has proved successful in some genera of Campanulariidae (Östman, 1987); the anatomy of the hydranth might differ slightly between species of *Aglaophenia* (present accounts of *Aglaophenia pluma* and *A. tubulifera*; also Cornelius, 1987); and starch-gel electrophoresis has been employed in discriminating two other *Aglaophenia* species (Thorpe, Ryland & Cornelius, unpublished data; discussed here under *A. parvula*, p. 28). Much of the new and important material from the British Isles, especially from Ireland, was collected and placed at our disposal by our friend and colleague Bernard Picton (B.E.P.), to whom we are most grateful.

Finally, Bogle (1975) studied aglaopheniinid hydroids on the eastern U.S. coast and Bryant (1985) in Queensland. Both collected a mass of relevant biological data on the group but their work has so far remained unpublished.

Glossary

Some words defined are in use throughout hydroid literature but are included for the benefit of non-specialists. The glossary applies throughout the Aglaopheniinae. A brief glossary mostly of terms used in the genus *Aglaophenia* was provided by Svoboda (1979), and an extensive one to the Plumulariidae sensu lato by von Schenck (1966), both in German.

Abortive hydrotheca or pseudonematotheca (= apophyse of Bedot, 1919) — small structure resembling a hydrotheca on a stem segment; precise homology uncertain, possibly a vestigial hydrotheca.

Annulus — ring-like constriction of stem or branch, usually with thinning of perisarc, permitting passive bending.

Apical stolon — tendril, or stolonial extension of a cormidial shoot.

Athecate — see Thecate.

Basal stolon — a stolon growing over a substrate.

Bifid — see Dichotomous.

Blastostyle — a reproductive polyp, in thecate hydroids enclosed within a gonotheca. See also Gonangium.

Caulus — monosiphonic shoot-axis of a cormoid; the 'main stem' of a plume. See also Monopodium and Rachis.

Cladium — primary branch; comprising serially repeated (iterated) cormidia. In most thecates termed hydrocladium.

Cnidostyle — see Nematophore.

Corbula — a 'basket' forming in place of a cladium (branch). The alternately inserted (not paired) sub-branches, or ribs, are reduced and surround a space open to the exterior, protecting the reduced gonangia. In *Aglaophenia* the ribs are separate at first but usually partially fuse during development. Fusion is apparently always

complete in female corbulae (except at the very base) but small gaps are left between the ribs in male ones (fig. 4e). Exceptions are noted on pp. 22, 37. See also Corbulacosta and Free rib.

Corbulacosta — rib of corbula, comprising metabasal cladium and nematocladium (fig. 4e). The corbulacostae are alternate, not paired.

Cormidium — a repeated unit of the cladium comprising an internode, one hydrotheca and usually three nematothecae; delimited by annuli (fig. 4c-f).

Cormoid — sub-unit of cormus with a single caulus; a 'single erect stem' and its cladia; comprising one plume. Cormoids are joined by a basal stolon, together comprising the whole colony or cormus. See also Primary cormoid.

Cormus — a whole colony; all parts connected by the stolon; everything resulting from a single larval settlement.

Dichotomous division, dichotomy — the division of a caulus (stem) into two identical branches. The division is interpreted as ultimately arising from the division of a single apical cell, and the two branches have identical age and origin. In certain species, such as *A. acacia*, very close successive branching can result in a pseudo-dichotomous or pseudotridentate appearance. The less precise terms bifid and trifid can be used to refer to such branch arrangements.

Fascicled — see Polysiphonic.

Free rib — small, unfused rib of corbula, usually proximal. Growing either from the rachis of the corbula or, as often in *A. tubulifera*, from the distal end of a fused rib (fig. 15d).

Frontal side (of cormoid) — the side supporting the hydrothecae, usually facing away from main water current; opposite of versal side.

Gonangium — in thecate hydroids, a blastostyle together with its gonotheca.

Gonotheca — the theca (fig. 5g, go) surrounding a blastostyle. Reduced in many aglaopheniinids, but present in most other thecaes. See also Corbula.

Hydranth — a feeding polyp (fig. 5h).

Hydrocladium — see Cladium.

Hydrotheca — the theca surrounding a hydranth.

Internode — part of stem occupied by single cormidium; minimum modular unit of stem over which pattern of modified hydrotheca plus associated nematothecae is repeated; delimited above and below by an annulus.

Intersegment — a segment of the caulus (stem) supporting one nematotheca and no hydrotheca, inserted between segments supporting cladia; short internodes bearing only mesial nematothecae, lacking hydrotheca and lateral nematothecae; in European *Aglaophenia* found only in *A. harpago*.

Intrathecal ridge — small internal perisarc extension into cavity of hydrotheca, for structural reinforcement (fig. 1f, ir).

Intrathecal septum — see Septum.

Lateral nematothecae — nematothecae arranged one each side of hydrothecal aperture (rim), to which they are lateral in position.

Marginal cusps ('teeth') — projections of the hydrothecal rim. In *Aglaophenia* usually nine, but seemingly eleven in *A. parvula*.

Mesial (median) nematotheca — a single nematotheca usually adnate to the outer wall of the hydrotheca in the mid-line (but, rarely, on the stem below, for example

- on rachial branch in *A. acacia*).
- Metabasal cladium — a reduced cladium bearing lateral paracladia, forming part of a corbula.
- Monopodium — main shoot of a colony. See also Caulus and Rachis.
- Monosiphonic — (of stem or branch) comprising a single tube. Same as unfascicled, the opposite of polysiphonic (fascicled).
- Nematocladium — The upper, fused part of a corbula rib; a cladium derived from cormidia which have reduced hydrothecae but which still bear (modified) nematothecae.
- Nematophore — a minute but very extensile polyp lacking functional mouth and tentacles but thickly armed with nematocysts and probably functioning to prevent attack or settlement on the colony. In *Aglaophenia* comprising two portions, sarcostyle and cnidostyle (= nematostyle) (figs 5f, n).
- Nematostyle — see Nematophore.
- Nematotheca — a theca surrounding a nematophore, usually minute.
- Node — imaginary junction between two internodes, often but not always having an annulus at or near the same point.
- Paracladium — a cladium arising from another cladium; a tertiary branch, or a 'branch off a branch'. See also Metabasal cladium and Nematocladium.
- Pedunculus — stalk of a corbula, comprising a single cormidium.
- Phylactocarp — modified cladium with side-branches arching over and protecting gonothecae but with wider spaces between ribs than in corbulae and with ribs not fused. Not occurring in fully-developed corbulae of *Aglaophenia* spp.; characteristic of for example *Litocarpia*.
- Polyp — the basic sessile hydroid (and cnidarian) individual; in hydroids primitively comprising body or column, hypostome (with mouth) and tentacles. In *Aglaophenia* there are three kinds of polyps, hydranths, nematophores and blastostyles, only the first having hypostome and tentacles.
- Polysiphonic — comprising more than one tube; same as fascicled. See also Monosiphonic.
- Primary cormoid — the cormoid developing first from the newly settled planula; having cauline hydrothecae, lacking in subsequent cormoids.
- Primary monopodium — shoot axis; the 'main stem'.
- Prosegment(s) — the basal segment(s) of the caulus, each having one nematotheca and lacking cladia; probably reduced cormidia. See also Primary cormoid.
- Pseudotrichotomous — see Dichotomous.
- Pseudonematotheca — see Abortive hydrotheca.
- Rachis — secondary monopodium; also the axis of a corbula. See also Caulus.
- Ramus — secondary, tertiary or higher order branch of axis, arising from a rachis.
- Rib — see Corbulacosta.
- Ridge — see Intrathecal ridge.
- Sarcostyle — see Nematophore.
- Segment — a unit of the main axis delimited by two annuli; presumed to be homologous with a cormidium. See also Internode.
- Septum — an internal transverse partition; an inward projection of the perisarc, in either cormidium or caulus. A well developed intrathecal septum in *Aglaophenia*

kirchenpaueri divides the hydrotheca, and in other European species there are less well developed intrathecal ledges (e.g. figs 4c-d).

Stolon — the basal strand of perisarc plus coenosarc (tissues) growing across a substrate and from which one or more cormoids arise. See also Apical stolon.

Theca — a cup-like extension of the perisarc or exoskeleton surrounding a polyp. See also Gonotheca, Hydrotheca and Nematotheca.

Thecate hydroid — one fundamentally having hydrothecae, gonothecae and, in some families, nematothecae; corresponding to the suborder Thecata (=Leptomedusae), in contrast to the Athecata (=Anthomedusae) which fundamentally lack them. There are exceptions in each group.

Trifid — see Dichotomous.

Versal side of cormidium, cormoid or caulus — the side away from the hydrothecae and nematothecae; normally facing into the prevailing water current; opposite of frontal side.

Systematics

Family Plumulariidae Agassiz, 1862

Remarks.— The family has been redefined by Millard (1975). Johnston (1847) and many earlier workers referred plumulariid genera to the Sertulariidae, from which the Plumulariidae was first separated off by Agassiz (1862: 358).

Subfamily Aglaopheniinae Broch, 1910

'Statoplea' Allman, 1883: 3, 4.

Aglaopheniidae Broch, 1910: 131, 206.

'Statoplea = Aglaopheniinae' Stechow, 1911: 194.

Statopleinae Billard, 1913: 63.

Aglaopheniinae; Millard, 1975: 407.

Diagnosis (after Millard, 1975).— Thecata with: branched or unbranched upright colonies; hydrothecae uniseriate, usually completely adnate, margin usually cusped, absent from hydrocaulus except in primary cormoid; paired lateral nematothecae always present, fused with hydrotheca and situated lateral to its aperture; usually one mesial nematotheca per cormidium; (5 nematothecae per cormidium in *Pentandra* von Lendenfeld, 1885); comprising a pair of laterals and one mesial; all nematothecae one-chambered and immovable, with one to several openings of which typically one communicates with hydrotheca; gonotheca unprotected, or enclosed in phylactocarp or corbula.

Remarks.— The Aglaopheniinae was probably first recognized as a group of genera distinct from the rest of the Plumulariidae by Allman (1883) under the name Statoplea, but seems not to have been given either the name or the status of a family group till Broch (1910) introduced the name Aglaopheniidae. Billard's (1913) name Statopleinae is junior to Aglaopheniidae, and the two names are objective synonyms.

Some reviewers, most recently Bouillon (1985), have again raised the subfamily to family rank, basing the distinction on (1) the elaboration of the cormidium with fusion of the component hydrotheca plus nematothecae, (2) the aggregation of the gonothecae within modified, protective hydrocladia (or corbulacostae) to form corbulae, and (3) the nature of the hydrotheca and the nematothecae. Others, notably Millard (1975), have regarded similarities in the remaining morphological features across the Plumulariidae *sensu lato* as over-riding in importance and have consequently recognized four subfamilies (Aglaopheniinae, Halopteriinae, Kirchenpaueriinae, Plumulariinae). Relevant common features are the primitively adnate and uniseriate hydrothecae, and typically a repetitive grouping of hydrotheca plus one or more mesial and two or more paired lateral nematothecae into cormidia. These characters serve to distinguish the Plumulariidae *sensu lato* from the other thecate families.

The four divisions are widely accepted, and recent authors have differed only in the taxonomic rank to be assigned to them. Thus, although Bouillon (1984) upgraded each to family level he recognized their unity by proposing a superfamily to embrace them all, the Plumularioidea. (Under the International Code of Zoological Nomenclature the correct citation of this superfamily name is Plumularioidea Agassiz, 1862.) However, he treated other, previously more widely recognized, families similarly (Bouillon, 1984, 1985). Thus the Halopteriidae Millard, 1962, previously usually regarded a subfamily, was then again upgraded to family status and became equal in taxonomic rank to, for example, the Sertulariidae.

There is clearly value in both classifications. Millard (1962, 1975) did emphasize that the four divisions within the Plumulariidae were not always clear. Certainly they are less so than between most other recognized thecate families. It has been suggested recently (Cornelius, 1987) that a parallel case could be made for recognizing affinities within the Sertulariidae by proposing subfamilies, and the genera of the Campanulariidae have long been so grouped (summary in Cornelius, 1982). But it would seem illogical to upgrade each of these subfamilies to family rank since the recognized thecate families are themselves well circumscribed and widely accepted. We feel that, so long as the traditional and rather coarse taxonomic ranks of family and subfamily are employed, it is preferable to regard the Plumulariidae *sensu lato* as equivalent in rank to the Sertulariidae, the Haleciidae, and other hydroid families with clearly demarcated limits, and to continue to accept the four subfamily divisions of the Plumulariidae.

The Plumulariidae *sensu lato*, and indeed the polypoid stage in the Order Hydroida, reaches its greatest elaboration and complexity in the Aglaopheniinae (analysis in Naumov, 1960, 1969). Within this subfamily the genus *Aglaophenia* is considered here as among the most derived, since the corbulae show a greater condensation of the basic cladia and thecae than those of other genera. The lateral fusion of the corbulacostae in some species, and the reduction and loss of the corbulacostine nematothecae, are phenomena of condensation probably unmatched in other thecate Hydroida.

Aspects of the homologies within the Plumulariidae *sensu lato* were studied in detail by von Schenck (1966).

Genus *Aglaophenia* Lamouroux, 1812

Aglaophenia Lamouroux, 1812: 184 (part); McCrady, 1857: 200 (part); Nutting, 1900: 106; Naumov, 1960: 487; Naumov, 1969: 527; Millard, 1975: 407; Svoboda, 1979: 61.
Plumularia Lamarck, 1816: 125 (part).

Type species: *Sertularia pluma* Linnaeus, 1758, by designation by McCrady (1857; see Remarks); reiterated by Naumov (1960, 1969), Millard (1975) and Svoboda (1979).

Diagnosis (after Millard, 1975).— Main stem branched or unbranched, hydrocladia primarily alternate and unbranched. Hydrotheca sac-shaped to deep, rim usually deeply cusped; bilaterally symmetrical; wholly accommodating hydranth. Mesial (= median inferior) nematotheca partly to wholly adnate. Gonothecae surrounded by corbula formed from modified hydrocladia bearing alternately-inserted secondary ribs with nematothecae. Dispersive stage planulae in almost all species; free medusoid reported recently in one (Boero & Bouillon, 1989: 37).

Remarks.— The genus as originally defined by Lamouroux (1812) included five species: *Aglaophenia pluma* (Linnaeus, 1758), '*Sertularia pennatula*' Ellis & Solander, 1786 (the identity of which was questioned by Millard, 1975: 446), *Sertularia pennaria* Linnaeus, 1758 (still of uncertain identity; discussion in Calder, 1988), *Lytocarpia myriophyllum* (Linnaeus, 1758; previously widely referred to *Thecocarpus*, discussion in Rees & Vervoort, 1987) and '*Sertularia echinata*' Linnaeus, 1761 (= *Sertularia cupressina* Linnaeus, 1758; see Cornelius, 1975: 405). McCrady (1857) was evidently the first to restrict the genus *Aglaophenia* to include only species today referred to the *Aglaopheniinae*. He stated 'I take the *P. cristata* as the nucleus of the group'. We regard this as designation of the type species. *Plumularia cristata* Lamarck, 1816, was introduced as a nom. nov. for *Aglaophenia pluma* (Linnaeus, 1758). Hence *A. pluma* can validly be regarded type species of *Aglaophenia*.

McCrady included in *Aglaophenia* the species until recently known as *Thecocarpus myriophyllum* (see above). Kirchenpauer (1872) wrote at length on the genus, but *Aglaophenia* was first restricted to its current scope by Nutting (1900: 106) when proposing *Thecocarpus*. Totton (1930: 240) challenged the distinction of *Thecocarpus*, but the recognized limits of *Aglaophenia* seem stable. Rees & Vervoort (1987: 177) supported Stechow's (1920, 1923) view that the name *Thecocarpus* should be dropped in favour of *Lytocarpia* Kirchenpauer, 1872.

Three species of *Aglaophenia* are so far known to harbour symbiotic algae, two occurring in Europe (p. 12).

Identification

(See also table 1, p. 46)

1. Field identification from gross characters.

Certain European species can be identified from major features without optical aid, either under water using SCUBA or after collection. A variety of characters can be helpful, as follows:

A. Branched colonies.— Five species can immediately be distinguished as forming colonies in which the cormoids comprise more than one plume. *Aglaophenia aca-*

cia commonly, perhaps typically, has trifid branching (occasionally apparently bifid) and the colony is notably erect, while occasional colonies of *A. parvula*, *A. pluma* and *A. tubiformis* branch dichotomously but never 'trichotomously'. In the last three species the branches themselves branch so that there appears no single main axis to the colony, whereas in *A. acacia* growth of the side branches ceases, resulting in a pseudoracemose growth pattern in which a main axis is apparent. In addition, *A. acacia* is the only European species to bear hydrothecae at the base of the rachial ramus.

In *Aglaophenia elongata* branches develop from a normal caulus segment, not replacing the cladium which always stays below the branch. The new branch has the same direction as the cladium. The branch consists of a complete cormoid, having an unsegmented caulus basally which is followed by prosegments and then a normal cladial arrangement. The orientation of the side-branch is the same as that of the basal cormoid, as in *A. acacia* also, but in dichotomous colonies of *A. parvula*, *A. pluma* and *A. tubiformis* the orientation turns through 90° at each branching point.

The differing seasonality of occurrence of the branching forms of *A. pluma* and *A. tubiformis* is discussed below (p. 32). Apparently the first species produces such colonies in response to warm temperatures, the second to lowered ones either in winter or in sufficiently cold upwellings in summer (p. 35). The questionably 'bifid' plumes identified by Hincks (1868) as *A. tubulifera*, and a single forked stem undoubtedly of that species, are discussed below (p. 38).

B. Single-plumed erect shoots.— Many European species do not form branching cormoids and the erect portions of their colonies comprise just single plumes. In addition, young cormoids of branching species inevitably pass through a single-plumed stage. The young of (1) *Aglaophenia pluma* and *A. acacia*, of (2) *A. kirchenpaueri*, *A. octodonta*, *A. picardi*, *A. tubulifera* and *A. lophocarpa*, and (3) unbranched but mature colonies of *A. parvula* and *A. pluma*, are probably too similar morphologically to separate confidently without optical aid. In life, however, colour may be useful (see below and table 1).

Single, young and unbranched plumes of *A. tubiformis* and *A. elongata*, together with the usually single-plumed shoots of *A. harpago*, can be distinguished from the group just listed by their generally having widely-spaced hydrocladia; though all but the very youngest colonies of *A. elongata* are branched. However, in *A. tubiformis* and *A. parvula*, and maybe some other species, cladial spacing increases with depth. Hydrocladia of *A. elongata* are long but those of *A. harpago*, also widely spaced, are characteristically short. The terminal hooks of *A. harpago*, by which it attaches to and colonizes new seagrass leaf blades, are visible underwater in ideal conditions, as might be the long nematothecae of *A. tubulifera*. With a good hand lens these characters are certainly recognizable to an observer already familiar with them.

C. Substrate association.— *A. harpago* is confined to the leaf blades of seagrasses. *A. pluma* and *A. tubiformis* are most often associated with the brown alga *Halidryx siliquosa* (Linnaeus) Lyngbe, 1819, but also occur on species of *Cystoseira* and *Sargassum*. *A. octodonta* and, rarely, *A. kirchenpaueri* also occur on these algae; and some *Aglaophenia* spp., such as *A. kirchenpaueri* and *A. picardi*, occur sometimes on the rhizomes at the bases of the seagrass *Posidonia oceanica* (Linnaeus) Delile, 1813. Thus substrate association alone can be misleading. For example, the alga *H. siliquosa*

occurs south to Portugal but has not been recorded from the Mediterranean (I. Tittley, pers. comm.), so that the western Mediterranean records of the two species normally associated with it in more northerly areas are presumably based on material from other substrata.

D. Colour.— This might be used to separate certain species while still living (table 1). All have brownish stems (grading to yellow in *A. kirchenpaueri* in the Adriatic Sea). Stem colour is due to pigmentation of the perisarc in most species but in *A. harpago* and *A. tubiformis* it is due to symbiotic zooxanthellae. The stem of *A. lophocarpa* is noticeably darker, and of *A. tubulifera* slightly paler, than in other European species; and in *A. elongata* the growing tips of the stems are often bright yellow.

In many species the hydrocladia are white (*A. pluma*, *A. acacia*, *A. lophocarpa*, *A. octodonta*, *A. elongata*), in others yellow (*A. tubulifera*) or light brown (*A. tubiformis*) to brown (*A. kirchenpaueri*, but yellow in specimens from the Adriatic; *A. harpago*), or translucent (*A. picardi*).

The corbulae of most species are white (*A. pluma*, *A. acacia*, *A. lophocarpa*, the male of *A. octodonta*), but those of others are translucent white (*A. picardi*), white to yellowish (*A. elongata*), yellow (female of *A. octodonta* and both sexes of *A. tubulifera*), or brown (*A. tubiformis*, *A. harpago*).

Specimens of *A. kirchenpaueri*, in which the brown to yellowish-brown colour is due to pigment in the perisarc, retain the colour when stored in alcohol. But those of *A. tubiformis* and *A. harpago* fade since in them the brown coloration is due to the alcohol-soluble pigments of their symbiotic zooxanthellae.

E. Hydranths.— Finally, although hydranths in this genus are rather uniform those of some species may prove distinctive in their dimensions and proportions. Thus the hydranth of *A. elongata* is unusually large (p. 17) and preliminary results suggest that there are slight differences between those of *A. pluma* and *A. tubulifera* (pp. 31, 37); Cornelius, 1987, in prep. 1).

2. Laboratory identification.

The following key uses both gross characters and microscopic ones, and avoids characters visible only in life.

There is much variation between colonies, and overlap in character states between species is common. In addition, some of the characters on which species limits are based are those of living populations (Svoboda, 1979), often not apparent in preserved material. Thus *A. octodonta*, *A. pluma* and *A. tubiformis* can appear identical, especially if badly preserved. Hence the key allows some species to key out at more than one place.

In many species the basalmost hydrotheca on a hydrocladium differs morphologically from subsequent ones, so characters should be taken from those more distal.

Aglaophenia acacia might prove to be conspecific with *A. lophocarpa* (p. 15) but is taken as distinct here.

Only two European species are known to have symbiotic zooxanthellae (*A. harpago*, *A. tubiformis*). Staining for starch with iodine is a convenient way of demonstrating the zooxanthellae in these species (fig. 25), but in badly preserved specimens this may not be possible. However, in specimens of non-zooxanthellate species which have undergone bacterial decay the bacteria themselves sometimes give a

dark staining reaction. If the zooxanthellae are visible in preserved specimens this can be helpful in identification (Svoboda, 1979) but their apparent absence should not be taken as firm evidence since in specimens lacking tissues the zooxanthellae will be absent too. Lastly, in acid-treated specimens the starch may disappear and iodine will hence not demonstrate the zooxanthellae.

Key to the European and Mediterranean species of *Aglaophenia*

1. Length of mesial nematotheca usually about equal to breadth of hydrothecal aperture; end of mesial nematotheca tubular (fig. 16) *A. tubulifera* (p. 36)
 - Mesial nematotheca much shorter; end of mesial nematotheca gutter-shaped 2
2. Internal hydrothecal septum greatly developed, recurved (fig. 4c-d)
 - *A. kirchenpaueri* (p. 20)
 - Septum absent or much less developed, comprising an internal ridge, straight . 3
3. Hydrotheca with length approximately equal to breadth at rim, or only slightly longer 4
 - Hydrotheca elongate, length usually greater than 1.8 times breadth at rim 9
4. Mature cormoid comprising more than one plume. (Three species in which single plumes are particularly difficult to separate) 5
 - Mature cormoid a single plume 7
5. Hydrotheca usually noticeably longer than breadth at rim ... *A. tubiformis* (p. 34)
 - Hydrotheca usually only just longer than breadth at rim 6
6. Frontal (outermost, unpaired) cusp on hydrothecal rim directed towards lumen of hydrotheca; first pair of cusps (counting towards rachis) directed outward, in lateral view crossing over frontal cusp; with secondary cusp between first and second pairs of cusps; rear cusp conspicuous, long and acute in side view (figs 8-9)
 - *A. parvula* (p. 25)
 - Frontal cusp directed upwards; first pair of cusps not crossing over outermost cusp; no secondary cusp; rear cusp inconspicuous and usually covered by lateral nematotheca (fig. 13) *A. pluma* (p. 30)
7. (*A. tubulifera* with unusually short mesial nematothecae may also key out here.)
 - Caulus without prosegment *A. picardi* (p. 29)
 - Caulus with prosegment 8
8. Intrathecal septum usually straight and strongly thickened, extending across lumen of hydrotheca *A. octodonta* (p. 23)
 - Intrathecal septum thin or absent, usually not extending across hydrotheca
 - *A. pluma* (p. 30)
9. Mature cormoid branched, comprising many plumes (young colonies may comprise single plumes) 10
 - Mature cormoid a single plume 13
10. Ramus always arising from a normal caulus segment (or ramus segment) which has one normally developed cladium *A. elongata* (p. 16)
 - Ramus arising from apical end of a segment with prosegment(s), comprising several roughly normally-arranged cormidia 11
11. Corbula often apparently growing in place of a plume to make a bifid junction in place of a trifid one, with bent peduncle, corbula not parallel with cladia or

- rachis *A. acacia* (p. 14)
- Corbula clearly growing in place of a cladium 12
 - 12. Hydrocladia generally widely spaced, light brown in life; corbulae brown; stem brown, colour due almost entirely to symbiotic algae *A. tubiformis* (p. 34)
 - Hydrocladia more closely spaced, white in life; corbulae white; brown colour of stem due to pigment in perisarc *A. pluma* (p. 30)
 - 13. Without basal prosegment *A. picardi* (p.29)
 - With basal prosegment(s) 14
 - 14. Only on seagrass (*Posidonia* and *Cymodocea*); in summer, having hooked terminal stolon; with intersegments *A. harpago* (p. 17)
 - Never recorded on seagrass; never with a hooked terminal stolon; lacking intersegments 15
 - 15. Mesial nematotheca arising roughly from middle of hydrotheca *A. lophocarpa* (p. 22)
 - Mesial nematotheca arising from upper half of hydrotheca *A. parvula* and *A. pluma*; return to 6

***Aglaophenia acacia* Allman, 1883**

(figs 1, 17a-b, 20a-b, 21a-b)

Aglaophenia acacia Allman, 1883: 38, pl. 12 figs 1-4; Marktanner-Turneretscher, 1890: 270, pl. 7 fig. 7; Pictet & Bedot, 1900: 44, pl. 10 figs 4-7; Kühn, 1909: 254, figs Ub, V; Svoboda, 1979: 79-82, figs 12d, 13d, 14b, 15d(1-5), 16d.

Aglaophenia elongata; van Gernerden-Hoogeveen, 1965: 79-80, fig. 44.

Material.— Type: near Azores, 822 m (450 fm), 38°37'N, 28°30'W, 2.vii.1873, coll. HMS Challenger, sta. 75; holotype, BMNH 1888.11.13.85; subsample in RMNH Coel. 25296. c. 150 mm colony in spirit plus two microslide preparations, hydrocladia from colony on microslide in RMNH Coel. 25296.

Non-Type: NE ATLANTIC: **British Isles:** Ireland 3 fertile colonies up to c. 50 mm, 20 m, on rock in exposed situation, S Brandie Rocks, Saltee I, Co. Wexford, 52°5.6'N, 6°35.3'W, 28.v.1981, coll. B.E.P., BMNH 1985.8.1.1, 1a; Northern Ireland: 35 m, Kearney Point, Co. Down, 54°20'12"N, 5°24'26"W, 16.vi.1982, coll. B.E.P., BMNH 1985.8.1.2, 2a; W Scotland: 52 mm fertile colony, Sligneath Mor, entrance of Loch Sunart, NGR 47/562602, 9.viii.1984, coll. R. Earll, BMNH 1985.11.6.40 (first Scottish record); N Wales: single infertile plume, LWST, Church I (West), Llanfairpwllgwyngyllgogerch-wyrdrobwlltysiliogogoch, Anglesey, 'under stones', 22.v.1963, coll. W. J. Rees, det. S. J. Moore, BMNH 1987.6.17.50 (first Welsh record); SW England: 14 m, Gannets Rock, Lundy I, 30.vii.1971, coll. K. Hiscock, RMNH Coel. 13349 (this and next comprise the first English records); c. 12 m, on artificial reef of concrete blocks, tidal current on spring tides up to c. 1.5 knots (2.8 km/h), Poole Bay, Dorset, 3.vii.1990, coll. J. Mallinson, BMNH 1991.1.1.1; NW France: Brittany: 35 m, Leonyne Haer, Glénan Is, 7.vii.1965, coll. A. Castric-Fey (A.C.-F.), RMNH Coel. 13532; 28 m, Pietro, Glénan Is, 3.ix.1964, coll. A.C.-F., RMNH Coel. 13536, BMNH 1988.4.1.41; 80 m, Roscoff, coll. A.C.-F., RMNH Coel. 13544; N of I de Batz, Roscoff, 12.vi.1963, coll. A.C.-F., BMNH 1988.4.1.42; Glénan Is, 1964, coll. A.C.-F., RMNH Coel., A.S. Hydrozoa subcollection, microslide preparations nos 424, 448, 452, 492, 512; S Spain: 125 m, Tarragona, coll. J.-M. Gili (ACUDE), vii.1981, RMNH Coel. 25040; MEDITERRANEAN: Tunisia: Cap Bon, subsample from NHM Vienna no. 5970, RMNH Coel. 13535, ex A.S. Hydrozoa slide subcollection 283, 284; Italy: 50 m, Pta Massullo, Villa Malaparte, Capri, 19.viii.1984, ex coll. A.S., RMNH Coel. 25262; 30-40 m, Scilla, Str Messina, 10.vii.1977, ex coll. A.S., BMNH 1988.4.6.2-3; 40 m, Ganzirri, Str Messina, 7.vii.1977, ex coll. A.S., BMNH 1988.4.6.4; Israel: 71 m, Haifa Bay, 32°53'30"N, 34°54'E, 28.iv.1975, coll. M. Tom, sta. no. 74, ex coll. Univ. Tel Aviv 20232, subsample in RMNH Coel. 25211, slide 598; 70 m, Haifa Bay, 32°53'30"N, 34°54'30"E, 11.vi.1975, coll. M. Tom, sta. no. 84, ex coll. Univ. Tel Aviv 20234, subsample in RMNH Coel. 25212, slide 616; W ATLANTIC: U.S.A.: 9 m, Tortugas, Florida, 10.vi.1925, RMNH Coel. 1701 (mentioned, van Gernerden-Hoogeveen, 1965, as *A. elongata*).

Description.— Stolon short, little branched. Stems erect, thick, monosiphonic, grouped closely; up to c. 150 mm recorded; basal 30-60 mm without annuli, followed by 1 prosegment and several internodes; often lacking cladia below first pair of branches 30-100 mm above prosegment, due to frequent mechanical loss of cladia from this region. Major branches widely spaced on stem, typically paired; or one of a pair may replace a corbula which, by a bend in the peduncle, grows towards and overlies the branch with which it is paired; at point of branching, caulus bending back versally resulting in a trifold arrangement.

Hydrotheca narrow and deep, length/breadth ratio 1.0-2.0, rim with 9 cusps, outermost longest grading to shortest on stem side; intrathecal ridge short, distinct.

Mesial nematotheca arising from middle of hydrotheca, free part c. 80 μ m long with gutter-shaped opening along upper side; connection with hydrotheca secondarily closed by membrane in older parts of colony; mesial nematotheca in rachial cladia sometimes not borne on hydrotheca but on free part of cormidium below. Lateral nematothecae arising slightly above hydrothecal rim; gutter shaped.

Colonies dioecious; up to c. 10 corbulae per erect stem; female corbula with ribs completely fused (male not seen), long, typically with 9-12 ribs on each side; sometimes first/last (proximal/distal) rib on each side free.

Young colonies, and perhaps all growing under certain conditions, are unbranched. Rachial ramification is not invariably 'trifold' since sometimes a corbula grows in place of a branch, or the corbula might be additional. Unbranched colonies cannot be distinguished from those referred to *A. lophocarpa* Allman, 1877 (see Remarks).

Reproductive season.— Little information. Fertile material noted late May in Ireland, August in W Scotland (present material). Svoboda (1979) recorded ripe corbulae in July in the Mediterranean, the same month in which the fertile holotype was collected in the Azores.

Habitat and ecology.— In Mediterranean, on hard substrates, 40 m and deeper, in slight currents; off N Spain recorded at 12-27 m (Svoboda, 1979). The Saltee I material came from 20 m depth on rock (B.E.P.), and the Scottish material from a moderately sheltered situation. The holotype came from 822 m. [Proof note: Azores, 100 m and deeper (P.F.S.C.)].

Symbiotic algae.— Absent (Svoboda, 1979: 82).

Distribution.— Newly recorded from all four component countries of the United Kingdom and also from the Irish Republic, as follows: Saltee I (Co Wexford) and Kearney Pt (Co Down), Irish Republic; Loch Sunart, W Scotland; Lundy I (Bristol Channel) and Poole Bay (Dorset), SW England; and Church I, Menai Strait, N Wales (see Non-Type material). In NE Atlantic region recorded from Mediterranean (Tunisia, Italy), Canaries, Azores (holotype), N Spain (Svoboda, 1979; see Remarks); Glénan Is, Brittany, NW France (unpublished observation; material coll. A. Castric-Fey, det. A.S.); S Spain and Israel (present material). In W Atlantic recorded off N Carolina (Fraser, 1944), Tortugas, Florida (van Gemerden-Hoogeveen, 1965, as *A. elongata*) and 'Caribbean' (Svoboda, 1979).

Remarks.— This species is similar to *A. lophocarpa* Allman, 1877. It may prove that *A. acacia* was based simply on older, branching specimens of *A. lophocarpa*, and that the original description of the latter was based on young, unbranched material; but this seems unlikely. In both nominal species the opening between hydrotheca

and mesial nematotheca may close secondarily, a character state unusual in the genus and indicating close affinity between the two (fig. 17a), but this is nevertheless rare in *A. lophocarpa*. The two taxa as thus distinguished have been recorded growing side by side and both fertile in the Strait of Messina and off Monte Argentario, Grosseto, Italy (Svoboda, 1979; also new observations) and may after all prove distinct.

The branching pattern of *A. acacia* was well illustrated by Bedot (1919) and is distinctive. It comprises a long central stem with the branches paired, opposite, and rather widely spaced. The branches combined with the main stem are trifid in arrangement. In places one branch of a pair develops as a corbula and - unique within *Aglaophenia* - turns back owing to a bend in the pedicel and overlies the base of its partner plume. The corbula and plume then superficially appear to arise from the same side of the stem.

The corbulae of this species and of *A. lophocarpa* are longer than in other nominal species of the genus recorded from Europe.

An association with a Mediterranean shrimp is mentioned under *A. elongata* (p. 17).

Aglaophenia elongata Meneghini, 1845 (fig. 2)

Aglaophenia elongata Meneghini, 1845: 192, pl. 13; Marktanner-Turneretscher, 1890: 262, pl. 7 figs 8, 12; Broch, 1933: 56, fig. 18f (part from Stobrec only); Picard, 1955: 190 (?part only); Svoboda, 1979: 74, figs 12c, 13c, 15c, 16c.

Plumularia elongata; Heller, 1868: 39, pl. 32 fig. 2.

Aglaophenia microdonta Pieper, 1884: 217.

Material.— Type: The type material described by Meneghini is considered lost. A neotype specimen was designated by Svoboda (1979: 74) comprising one cormoid with 8 rami and 18 corbulae (in spirit) and one microslide preparation bearing a cladium from this specimen. The collecting details of the material are as follows: SW of Banjole I, Rovinj, Yugoslavia, 25.vii.1971, 35 m, coll. A. Svoboda, Nat. Mus. Vienna cat. no. 13.219 plus slide 772; subsample in RMNH Coel. 25294. Additional material collected from the same place on the same date has the cat. no. 13.220. Samples of hydrocladia from neotype on slide in RMNH Coel. 25294. Measurements: Cormoid length 80 mm, hydrotheca breadth $150 \pm 8 \mu\text{m}$, depth $312 \pm 19 \mu\text{m}$; length of cladium segment $435 \pm 33 \mu\text{m}$ ($\bar{x} \pm \sigma$).

Non-Type: **MEDITERRANEAN:** Italy: Capo d'Enfola, Elba, 32-42 m, 29.vii.1988, coll. A.S., RMNH Coel. 25034; Scoglio Corbella, Capo Stella, Elba, 25-30 m, coll. A.S., RMNH Coel. 25249; Israel: Numerous spirit-preserved samples, mainly from Haifa region, RMNH Coel. 25214-236, plus microslide preparations of each specimen (ex Univ. Tel Aviv samples NS 20.181, 202, 210, 212, 228, 230-1, 233, 235-6, 238-40, 244-5, 248, 250-6, 261-2). [Added in proof: E Spain: Vandellos, 74 m, 06.viii.1977 coll., r.v. Calypso 1977, stat. 1., RMNH Coel. 16599; Cale San Francesc, Banes, 22-23 m., 18.ix.1991, coll. A.S., RMNH Coel. 17990].

Description.— Basal stolon short, branching only occasionally; *cormoids closely set giving colonies bushy appearance*. Basal undifferentiated part of caulus c. 10 mm, above which 1-4 prosegments with frontal nematotheca and shallow, oblique annuli; following caulus segments not clearly separated, each bearing the usual 3 nematothecae and 1 abortive hydrotheca. When rami arise they do so between mesial, proximal nematotheca and cladium (or corbula), and have 1-3 prosegments basally as has main caulus. *Rami and cladium of same segment aligned parallel with each other*; ramifications of 4th order occurring. Overall length of cauli and rami c. 300 mm; widely-spaced cladia comprising 7-12 cormidia with *narrow, deep hydrothecae, length/breadth ratio* c. 1.7-2.5. In Adriatic and Israeli specimens mesial nematotheca arising in lower

third of hydrotheca, in Tyrrhenian and Ligurian populations from about middle of it; free end short, gutter shaped; lateral nematothecae slightly overtopping hydrothecal rim; 9 delicate cusps uniform in length. Colonies dioecious; *corbulae short, egg-shaped*, without free ribs; 4-6 pairs of ribs, fully fused in female, with tiny slits between nematothecae in male.

Reproductive season.— June–November in Adriatic. In other localities only summer-collected material is known, mostly mature.

Habitat and ecology.— Commonly collected on shells, dead bryozoans and calcareous red algae, occasionally on gravelly, slightly muddy sand; in moderate currents; so far usually reported 30–50 m, once 10 m (E of Prvic I, Gulf of Rijeka, on *Cystoseira*, coll. A.S.) and 74 m SE Spain (present material).

Symbiotic algae.— None (Svoboda, 1979: 77).

Distribution.— So far validly recorded only from Tyrrhenian, Ligurian and Adriatic Seas and Israel (Svoboda, 1979; present material). Although the species has been widely reported around the world, records outside the limited area just mentioned all seem erroneous (for example Brittany, Fey, 1969, also Castric & Michel, 1982; S Spain, Gili, 1987; Algeria, Picard, 1955; Tortugas, U.S.A., van Gemerden-Hoogeveen, 1965; see also Svoboda, 1979). [Proof note: also E Spain (see Material)].

Remarks.— The species seems unique in its special mode of branching. The rami are identical in structure with complete cormoids in that they have basal segments without hydrothecae. In a sense, therefore, their relation to the caulus segment from which they arise is the same as that between main caulus and stolon in other species.

Slightly different arrangements are not uncommon in several species following structural damage. For example, *Aglaophenia tubiformis* has been recorded having such irregular branching in addition to the normal dichotomous branching. An example is a cormoid from Naples (Munich Mus., 'Bedot material' 237); *A. kirchenpaueri* (see Svoboda, 1979: 76, figs c1, c2) has been recorded with a similar modification to the basic pattern; but in *A. parvula* such a form is quite common. But in *A. elongata* there can arise from a single rachial segment both a hydrocladium and, subsequently, the basal segment of a new ramus which supports an entire new cormoid.

The long cauli and rami bend down in currents and since the rami themselves are curved their tips thus become orientated perpendicular to the current.

The hydranths of this species are exceptionally big and have unusually long tentacles. It is the only *Aglaophenia* species described herein which in the laboratory accepts *Artemia* nauplii.

Meadows of *A. elongata* (at Elba) and of *A. acacia* (at Almeria) are inhabited by the shrimp *Periclimenes scriptus* (Risso, 1822), which normally associates symbiotically with the sea anemone *Condylactis aurantiaca* (Delle Chiaje, 1825) (Svoboda & Svoboda, 1975). Possibly the unusual stinging powers of these species offer a similar protection from predation by squid and fish.

Aglaophenia harpago von Schenck, 1965 (figs 3, 25b)

Aglaophenia sp. Nutting, 1895: 969; von Schenck, 1962: 117, figs 1-4.

Aglaophenia helleri; Müller-Calé & Krüger, 1913: 42; Müller, 1913: 111, figs 7-8; Müller, 1914: 346; Neppi, 1917: 55; Neppi, 1920: 24.

Aglaophenia adriatica; Stechow, 1919: 143.

Aglaophenia pluma f. *gracillima*; Broch, 1933: 52, fig. 18d-e (part).

Aglaophenia pluma; Picard, 1955: 223, ?191.

Aglaophenia nanella; Parenzan, 1956: 628, fig. 2 (non Stechow, 1919 = *A. tubiformis* q.v.).

Aglaophenia sp. von Schenck, 1962: 117, figs 1-4.

Aglaophenia harpago von Schenck, 1965: 211; von Schenck, 1966: 951, figs 20, 34e; Svoboda, 1979: 95, figs 12i, 13i, 15i, 16i, 17, pl. 3b-c, also fig. 9b(1-4).

Material.— Type: 'Holotype' in Stazione Zoologica di Napoli, in spirit; coll. by D. A. von Schenck at Capo Posilippo, Naples, 14.iv.1965, 15 m; habitat a mixed meadow of *Posidonia oceanica* (Linnaeus) Delile, 1813 and *Cymodocea nodosa* (Ucria) Aschers, 1869. Collecting data shows that the species was not in fact described from the specimens designated as type since the manuscript of von Schenck's paper reached the journal concerned on 11.xii.1963; but the identity of the species is not in question and we have not attempted to resolve this inconsistency. Subsample on 2 slides, RMNH Coel., A.S. Hydrozoa subcollection, microslide preparations 196, 196A.

Non-Type: MEDITERRANEAN: S Spain: Cabo de Gata, Almeria, 6-10 m, 10.viii.1975, coll. A.S., RMNH Coel. 13519; La Parra, Almeria, 1-8 m, 14.vi.1975, coll. A.S., RMNH Coel. 13520; Italy: Diano Marina, Imperia, on drifting *Posidonia*, iv.1987, coll. A.S., RMNH Coel. 25253, BMNH 1988.4.6.5; Ogliaastro, Gulf of Salerno, 10 m, ix.1987, coll. A.S., RMNH Coel. 25250; Pta Massullo, nr Villa Malaparte, Capri, 13 m, 19.viii.1974, coll. A.S., RMNH Coel. 25254; Pta M. Vico, Ischia, 29.iv.1974, coll. A.S., RMNH Coel. 25252, also same locality and date, 25 m, RMNH Coel. 25254; Formiche di Vivara, Ischia, 10-12 m, 11.v.1975, coll. A.S., RMNH Coel. 25251; Secca di Meloria, 10 km off Livorno, 12-13 m, iv.1971, coll. A.S., RMNH Coel. 13527; Filicudi, Lipari I, Sicily, 10-12 m, viii.1969, coll. Velimirov, RMNH Coel. 13523; Malta: Off Cominio Hotel, 12 m, 17.ix.1973, coll. H.-E. Schmidt, RMNH Coel. 13522. ADRIATIC: Yugoslavia: Near Dubrovnik, 'summer 1973', coll. H.-E. Schmidt, RMNH Coel. 13521; Lido at Albaroni, Venice, on drifting *Cymodocea*, 24.iv.1975, coll. A.S., RMNH Coel. 13525.

The material described by Broch (1933) as *Aglaophenia pluma* f. *gracillima* (Ciovo, Split, 5-10 m, Oslo Mus. cat. no. B 78, microslide preparation in RMNH Coel. 13526), collected from dead *Posidonia* leaves, is identical with *A. harpago*. Previously unrecorded specimens were collected also by A.S. from Almeria, Spain, 14.vi.1975, at 8 m depth.

Description.— *Stolons* long, growing along seagrass blade parallel with edges; seldom crossing to other side of leaf. Cormoids arising at intervals of 10-15 mm, erect when small but bending backwards with increasing size. Prosegment separated from stolonial shoot by extremely deep oblique furrows, permitting bending in response to current surge. Caulus monosiphonic, comprising 20-50 cladia or corbulae, segments having nematothecal arrangement typical of the genus; cladia comprising 3-6 cormidia; in some large cormoids 1-5 intersegments with frontal nematothecae sometimes inserted between the more distal cladia-bearing segments, but cladia still alternate. Due to presence of intersegments, the nearly rectangular insertion of cladia and their short length, cladia are notably more widely spaced than in other *Aglaophenia* spp; in large cormoids, occurring mainly in spring and summer, caulus terminated by thick, narrow hook, bent backwards in same direction as caulus. Hydrothecae in Adriatic specimens long and narrow (length/breadth ratio c. 1.8-2.0), in specimens from Sicily north to Tyrrhenian and Ligurian Sea, and also off S Spain, broader and shorter (l/b ratio 1.5 and less), giving rise to much confusion with *A. elongata* and *A. octodonta*. In addition, cormidial segments in Adriatic populations are longer than in W Mediterranean Sea. Colonies dioecious, corbulae short, with 4-6 pairs of ribs laterally fused in female corbulae, partly open in male.

Reproductive season.— Reportedly March-July around Rovinj (Svoboda, 1979: 21), but data throughout year not available.

Habitat and ecology.— The species occurs at 3-40 m depth, but at the deeper part

of this range only in clear water. It has been recorded only on the leaf blades of the seagrasses *Posidonia oceanica* and *Cymodocea nodosa*. *Aglaophenia picardi*, *A. octodonta* and *A. kirchenpaueri* also settle on *Posidonia oceanica* but whereas they settle on the remains of the leaf bases (also sometimes referred to as the 'stipes' or 'rhizomes') only *A. harpago* occurs on the living, elongating leaf blades, and in fact is apparently restricted to them (Svoboda, 1979; see also Boero, 1987, and Garcia Rubies, 1987).

Cymodocea nodosa is found along the W African coast westwards to the Canaries but in its extra-Mediterranean distribution has yet to be recorded as bearing *A. harpago* or any other *Aglaophenia* species.

Symbiotic algae.— Like *Aglaophenia tubiformis* this species always harbours the symbiotic zooxanthella *Symbiodinium microadriaticum* Freudenthal, 1962. It is found in all endodermal tissues in densities similar to those reported in *A. tubiformis* (p. 36). As in that hydroid species, decreasing algal productivity with increasing depth is compensated by a greater density of the symbiont (Svoboda, 1979: 36). Although the description of the species by Nutting (1895, as *Aglaophenia* sp.?) cited above mentioned zooxanthellae they were not noted by von Schenck (1965).

Distribution.— Endemic to Mediterranean Sea, as is one of its favoured substrate hosts, the seagrass *Posidonia oceanica*. Well known from N and Mid-Adriatic (Svoboda, 1979; RMNH colln.; Broch, 1933, Oslo Mus. cat. no. B78, subsample in RMNH colln.), and also Castiglione, Algeria (Picard, 1955, as *Aglaophenia pluma*). Known from present material also from Sicily, Ogliaastro, Ischia, Capri, Diano Marina (Ligurian Sea) and Almeria. There are no records from the E Mediterranean. See also the sections Habitat and ecology, and Material.

Remarks.— The hydrotheca of Adriatic populations of this species are slender whereas those in the W Mediterranean are relatively broad (see above). Possibly Adriatic surface currents tend to keep the Adriatic population, perhaps along with those of the E Mediterranean, genetically separated from those further west.

The species has a method of vegetative propagation unique among known species of the genus (von Schenck, 1962). Hooked terminal regions of cormoids become fastened around the leaves of neighbouring substrate plants. Often the cormoid then breaks away from the basal part of the colony and from it grows a new one on the new host plant. Breakage takes place at the deep furrows of the prosegment, and is thought to occur during periods of strong water movement. The process represents a remarkable evolutionary convergence with certain other European hydroids more or less restricted to seagrasses [*Laomedea angulata* Hincks, 1861 (see Cornelius, 1982), *Sertularia perpusilla* Stechow, 1919, and others (Boero, 1987)].

Most seagrass leaf blades are slightly buoyant, changing in orientation in passive response to both constant currents and wave surge. Such leaves are settled by *Aglaophenia harpago*, plumes of which become oriented backwards with their cormoids directed towards the plant base. If the seagrass blades become entangled their freedom of movement is restricted. In this situation the cormoids of *A. harpago* specially reduce the rigidity of the deep oblique furrows near the base of the rachial prosegment so that the fan can orientate passively in response even to slight currents, functioning somewhat like a hinge with a rotation of up to 180° (Svoboda, 1970, 1979). The 'hingejoints' were studied in further detail by Hughes & Henderson (1988).

Aglaophenia kirchenpaueri (Heller, 1868)

(figs 4, 17c-d, 20d, 21c-d)

Sertularia pluma Linnaeus, 1758: 811 (part; discussion in Svoboda, 1979: 100).*Plumularia kirchenpaueri* Heller, 1868: 40, 82, pl. 2 fig. 4 (syn. '*P. algirensis*' Kirchenpauer, in litt. to Heller).*Aglaophenia kirchenpaueri*; Marktanner-Turneretscher, 1890: 263, pl. 7 figs 9, 22; Picard, 1955: 189; Svoboda, 1979: 87-90, figs 12g, 13g, 14c, 15g(1-2), 16g, pl. 5 fig. f.*Aglaophenia septifera* Broch, 1912: 6, fig. 8; Stechow, 1919: 148; Riedl, 1959: 665.

Material.— Type: Piran, Yugoslavia, N Adriatic Sea. Material probably lost (Svoboda, 1979: 65, 88). There is currently no necessity to designate neotype material. See Remarks.

Non-Type: (See also notes on the Linnean material, p. 38.) Since the species has only been recently recognized as occurring so far north as the British Isles, all known material from that region is listed. NE ATLANTIC: British Isles: Ireland: Skerd Rocks, S Skerdmere, Galway, 30 m, 23.vii.1982, coll. B.E.P., BMNH 1985.8.2.2 (first Irish record); England: 'Cornwall', three colonies on herbarium sheet (plus one of *A. pluma*), ex coll. G. Johnston (originally labelled *Aglaophenia cristata*, redet. *A. kirchenpaueri* by A. K. Totton, confirmed by P.F.S.C.; see Distribution), herbarium plus one microslide prep., BMNH 1847.9.24.12; 100 m SE of Eddystone Lighthouse, SE Cornwall, 16.x.1974, coll. & det. A.S., BMNH 1974.10.25.2 (mentioned, Svoboda, 1979); 20 m, Gannets' Rock Pinnacle, Lundy I, 51°11'N, 4°39'W, Bristol Channel, SW England, 23.viii.1982, coll. B.E.P., BMNH 1985.8.2.1; NW France: Glénan Is, 1964, coll. A. Castric-Fey, RMNH Coel., A.S. Hydrozoa subcollection, microslide preparations nos 408, 411, 415, 417, 419, 420, 425, 427, 429, 431, 437, 442, 446, 451, 454, 464-5, 467, 490-1, 493-5, 497-8, 500-2, 507-8, 510; duplicates in BMNH 1988.4.1.12-27, spirit-preserved; N Spain: Ciervana, Bilbao, 11 m, 15.vii.1984, coll. I. Isasi, RMNH Coel. 25286; Portugal: Near Cape Espichel, 8 m, viii.1971, coll. H. Zibrowius, RMNH Coel. 13493; MEDITERRANEAN: S Spain: Calahonda, 20 m, summer 1975, coll. A.S., RMNH Coel. 13538; Cabo de Gata, Almeria, 6-10 m, 10.viii.1975, coll. A.S., RMNH Coel. 13543; Ciervana, Bilbao, 11 m, 15.vii.1984, coll. I. Isasi, RMNH Coel. 25286; Pta Carnera, Algeciras (nr Gibraltar), 10-17 m, 25.viii.1975, coll. A.S., RMNH Coel. 13522; Italy: Messina, Sicily, 1852 or 1853, fragments of colonies, coll. & det. M. Sars (as *Aglaophenia pluma* var. *dichotoma* sensu Sars, 1857), Zool. Mus., Oslo, F1171, subsample RMNH Coel. 13472 (see Remarks).

Description.— (After Svoboda, 1979.) Colony up to 200 mm in calm, deep water in Mediterranean but perhaps more often to 20-50 mm in the cooler waters of the British Isles in the north of the geographical range; perisarc yellow to brownish in both living and preserved specimens. Stolon much branched. Unsegmented base of hydrocaulus up to c. 15 mm high, followed by 1-3 prosegments each with 1 frontal nematotheca, separated by oblique annuli. Above this region hydrocladia are inserted, from here upward arrangement of nematothecae being typical of genus (1 mesial, 2 lateral). Small hole at base of branch which may represent remains of a hydrotheca (= apophyse of Bedot, 1919, = abortive hydrotheca of von Schenck, 1966). Hydrocladia alternate. Hydrotheca length/breadth ratio c. 1.1-1.25; with 9 marginal cusps, mesial longest (60-80 µm); cusps grading shorter on each side towards hydrocladium; *hydrotheca divided by thick transverse septum projecting across 0.5-0.65 of hydrothecal lumen*; hydranth contracting below septum; mesial nematotheca commonly long, sometimes projecting nearly to level of hydrothecal rim but often shorter; it and lateral nematothecae gutter-shaped.

Colonies dioecious; up to 10 corbulae per erect shoot (cormoid); nematocladia (ribs) of male corbula not completely fused, with oval openings between nematothecae of the ribs; these openings absent in female, which is otherwise identical; basalmost rib frequently free and not fused with next; 8-10 ribs on each side of corbula rachis; nematothecae of corbula with gutter-shaped openings.

In the Mediterranean, at a single locality, colonies from near the surface may be

just 50 mm high while those from some tens of metres depth, exposed to much lower current velocities, may attain heights of up to 200 mm. Colonies in deep water growing in rapid currents remain short (A.S., Strait of Messina).

Reproductive season.— Gonophores present summer to autumn in Adriatic and Tyrrhenian Seas, corbulae being apparent June–November.

Habitat and ecology.— 1–15 m on exposed Mediterranean coasts, down to 90 m in Strait of Messina; in both strong and weak tidal currents. Typically on hard substrates such as rock, coralline algae and gorgonians but recorded rarely also on *Cystoseira*. On W coast of Ireland in shallow water to 30 m, in exposed sites, on rock; scarce (B.E.P.).

Symbiotic algae.— None.

Distribution.— Special interest attaches to the recent and new British Isles records of the species since they are at the north of its known geographical range. They will therefore be considered separately.

British Isles: So far known only from Lundy I, Bristol Channel (Hiscock, 1974, det. A.S.; also present material); 'Cornwall' (present material); off Plymouth, Devon/Cornwall border (coll. E. T. Browne, material in both BMNH and Marine Biological Association, Plymouth, collections; also Svoboda, 1979); Galway, W Ireland (present material, first Irish record); and, more generally, noted as scarce, W coast of Ireland (B.E.P.). Some 18th century material now in the Linnean collection in London was also probably collected from British waters (p. 39).

The Cornish material, once in George Johnston's collection and collected in or before 1847, was first identified as *Aglaophenia kirchenpaueri* by A. K. Totton, curator of the Recent Cnidarian collections of the BMNH 1914–1953, on 20 August 1926 (note with specimen). Totton's identification, confirmed here (P.F.S.C., 1986), has apparently not been published before but probably represents the earliest recognition of the species from the British Isles. The first published records of *A. kirchenpaueri* from British waters were by Svoboda (1979) based on his own specimens taken from off the Eddystone Rock, near Plymouth, and on material in the collections of the BMNH and the Marine Biological Association, Plymouth.

Material in the Linnean Collection in London may well have been collected from the British Isles by John Ellis (?1710–1776). Although the provenance of the material has yet to be conclusively demonstrated the collection of which it forms part was largely collected by the London-based Ellis. It was he who virtually alone supplied Linnaeus with hydroids at least before 1760 when the bulk of the Linnean '*Sertularia*' specimens reached Linnaeus (Cornelius & Wells, 1988, and other reference cited therein). The material would thus almost certainly have been collected before 1760, and if the locality were confirmed as British it would demonstrate that the species was present in British waters in the 18th century (p. 39).

The evidence from the Johnston and Linnean Herbaria material might imply that there has been no recent northward range extension of the species into British waters and that it was present during both 18th and 19th centuries, but the possibility of successive northerly advances and withdrawals is nevertheless open. Material collected on a greater number of dates would seem necessary to resolve the question.

Elsewhere: Recorded from English Channel S to Morocco (Patrii, 1970) and the Cape Verdes (Svoboda, 1979); in Mediterranean Sea reported from as far east as Adriatic but not beyond.

Remarks.— Heller (1868) based *Aglaophenia kirchenpaueri* on the bell-shaped

hydrotheca and long mesial nematotheca of Adriatic material, features absent in other Adriatic species. Heller's hydroid collection is apparently lost. The characteristic intra-hydrothecal septum was described by Marktanner-Turneretscher (1890) who was first to realize its taxonomic importance. Marktanner-Turneretscher's collection, deposited in the Naturhistorisches Museum, Vienna, includes several specimens.

The remaining fragments of the type series of *Aglaophenia pluma* var. *dichotoma* sensu Sars, 1857, were found to be of the present species.

Growth of the intra-hydrothecal septum was studied at Naples by Kühn (1909).

The Linnean Collection, London, material of the present species is discussed further below (p. 38).

Aglaophenia lophocarpa Allman, 1877

(fig. 5)

Aglaophenia lophocarpa Allman, 1877: 41, pl. 24 figs 1-4; Stechow, 1923: 250; Svoboda, 1979: 82, figs 12b,e, 13e, 15e(1-3); Gili, Vervoort & Pagès, 1989: 92-94, fig. 20A.

Aglaophenia apocarpa Allman, 1877: 41, pl. 24 figs 5-9; Bedot, 1921: 43, pl. 6 figs 45-47.

Aglaophenia elongata; Picard, 1955: 190; Gili, 1987: 146, figs 4.34 E-G (in part).

Material.— Type: Type series collected W of Tortugas, Florida, 16.i.1869, dredge haul no. 1, c. 130 m ('65 fm'), by Pourtales' Gulf Stream Expedition (Allman, 1877); preserved in Museum of Comparative Zoology, Harvard [MCZ]. The series comprises 7 fragments of cauli from 2-3 cormoids 7-50 mm in length. Two of the fragments each have two stolon roots and unsegmented caulus lengths of 25 and 38 mm respectively; the shorter fragment delimited by two prosegments and having inconspicuous annulation, the longer one having one prosegment with deep, oblique septa; both bearing cladia having segments without conspicuous annulation. The material includes two female corbulae, the larger (4.5 mm) with 14 pairs of completely fused ribs, the other with about 8 pairs of ribs and still infertile with several distal ribs unfused. There are also about a dozen cladial fragments. One having 13 cormidia was mounted in balsam and designated lectotype (MCZ colln), another deposited in the RMNH (Coel. 25248). Dimensions of lectotype: length of hydrotheca $410 \pm 9 \mu\text{m}$, breadth $160 \pm 9 \mu\text{m}$, internodal length $506 \pm 9 \mu\text{m}$ ($\bar{x} \pm \sigma$).

Previously unreported type specimens of *Aglaophenia apocarpa* Allman, 1877, today referred to the present species (e.g. Svoboda, 1979), were located by M. A. Bogle (in litt. to A.S., 10.vi.1974). They 'were found mixed in with the type material of *Cladocarpus ventricosus* Allman, 1877. Station data present in the jar corresponded with that of the type material of *A. apocarpa* - off Sand Key, May 9th, 1868, cast no. 14, 100 fm., Pourtales Gulf Stream Exploration.' There were 13 cormoids, some with cladia, and two corbulae with numerous fragments of cladia. Several were mounted as two microslide preparations (MCZ; RMNH Coel. 25244). The material resembles *A. lophocarpa* in all details, excepting certain trivial deformities. The corbulae are unusual in that the elongated, unfused ribs form a small basket as in *Thecocarpus myriophyllum*, but they lack the basal hydrothecae characteristic of that species. We know of no other similar material but the male corbulae of *A. tubulifera* and a cormoid of dichotomously branched *A. pluma* was found in Bilbao showing a similar growth pattern (see under *A. pluma*, p. 31, Material Examined, RMNH Coel. 25287). The corbulae lack tissues, so cannot be sexed with certainty. The measurements of the type material of *A. apocarpa* are as follows: length of hydrotheca $423 \pm 20 \mu\text{m}$, breadth $176 \pm 8 \mu\text{m}$, internodal length $511 \pm 19 \mu\text{m}$ ($\bar{x} \pm \sigma$).

Non-Type: MEDITERRANEAN: S France: NE point of La Gehiniere, 45 m, 24.vii.1970, coll. N. Gravier-Bonnet, RMNH Coel. 13546 (ex A.S. slide coll. 366); Italy: Numerous specimens, off Capo Caccia, NW Sardinia, 5-10 m, coll. J. Schmitting, duplicate material used experimentally (Schmitting, 1984), RMNH Coel. 25246-7 (=BMNH 1988.4.6.18); Numerous colonies, N & S Elba, 40-50 m, vii.1988, coll. A.S., RMNH Coel. 25042; S Spain: Several cormoids, Cape Creus, Costa Brava, 35 m, 1986, coll. J.-M. Gili, det. A.S., RMNH Coel. 25245.

Description.— Stolon short, little branched, in deep-water specimens often completely overgrown by calcareous algae or other encrusting organisms. Cauli mono-

siphonic, dark, erect, rigidly stiff, always unbranched, c. 1 mm thick at base; unsegmented base in strong currents short, just a few mm high, up to c. 50 mm in deeper, stiller waters; followed above by 1-3 prosegments with frontal nematothecae; cladia-bearing segments often indistinctly separated by annuli, in larger cormoids basal cladia commonly broken off; cauli attaining c. 50 mm in some current-exposed places, up to c. 150 mm on sheltered grounds when bearing 80-200 cladia. Each cladium c. 10 mm, comprising 20-30 cormidia. *Hydrothecae* narrow, deep, length/breadth ratio (in type material) 1.6-2.0; rim with 9 equal cusps; with short intrathecal ridge in lower third of hydrotheca; mesial nematotheca arising from middle of outer edge, gutter shaped, free part 50-80 μ m, foramen into hydrotheca open in most specimens, closed less commonly than in *Aglaophenia acacia* (though present in type material); nematothecae lateral to hydrothecal aperture reaching same level as rim or slightly above. Colonies dioecious, up to c. 15 corbulae per stem; female corbulae brown, with ribs completely fused; male corbulae white, typically with nematothecae of ribs separated by narrow slits, but in Mediterranean material so far examined the ribs were invariably fused. Colonies growing in agitated water short with cladia closely packed, but with similar hydrothecal dimensions as in more sheltered areas.

Reproductive season.— Fertile material recorded April-September in Mediterranean Sea (Svoboda, 1979; Schmitting, 1984).

Habitat and ecology.— In Mediterranean on primary and secondary hard-bottom substrates such as rock and coralline algae; to c. 50 m depth, especially to this depth in sheltered areas; usually in weak currents but locally in strong currents and even wave-swept situations at depths of 5-10 m.

Symbiotic algae.— Absent (Svoboda, 1979).

Distribution (largely after Svoboda, 1979).— Range unclear owing to likely past confusion with *Aglaophenia acacia*. Material referable to *A. lophocarpa* definitely recorded from the Caribbean (60-200 m), Azores (200-500 m) and the Mediterranean Sea; and recently from Guinea Bissau by Gili, Vervoort & Pagès (1989). Most, perhaps all, Mediterranean records are given, with depths where known: Str Messina (30 m, in strong current); Eolian Is, Sicily; Monte Argentario Grosseto (40-45 m), Portofino (Genova) and Elba, Italy (40-50 m); Marseille, France; Cape Creus (35 m) and Catalanian coast, Spain; Cape Caccia, NW Sardinia (in shade, 5-10 m, with light wave action); probably Castiglione, Algeria (Picard, 1955: 190), but perhaps confused with *A. picardi* and/or *A. acacia*. Apparently absent N Adriatic, and not recorded E Mediterranean.

Remarks.— See under *Aglaophenia acacia*.

***Aglaophenia octodonta* (Heller, 1868) (fig. 6)**

Plumularia octodonta Heller, 1868: 40, pl. 2 fig. 3.

Aglaophenia helleri plus var. Marktanner-Turneretscher, 1890: 271, pl. 7 figs 3, 13-16; Stechow, 1919: 144.

Aglaophenia filicula; Kühn, 1909: 452, fig. Ua, pl. 21 figs 64-69, pl. 22 figs 40-74.

Aglaophenia adriatica Babic, 1911: 541, figs 1-2.

Aglaophenia pluma var. *helleri*; Bedot, 1919: 265.

'*Aglaophenia octodonta* = *A. pluma* var. *octodonta*'; Stechow, 1923: 247.

Aglaophenia pluma f. *helleri*; Broch, 1933: 50, fig. 18c.

Aglaophenia octodonta; Picard, 1951: 344; Rossi, 1961: 78; Svoboda, 1979: 65, figs 12a, 13a, 15a, 16a, pl.

5c; Ramil Blanco, 1988: various entries.

Aglaophenia pluma f. *octodonta*; Riedl, 1959: 662.

Material.— Type: N Adriatic; original type material lost (Svoboda, 1979). Neotype material was collected from Rovinj, N Yugoslavian coast, 1 m, as follows (designated by Svoboda, 1979: 65): 1 cormoid with 28 cladia and 1 corbula, in spirit, plus 1 microslide preparation with 1 cladium; below steep drop from town centre, 20 m W of hydrographic station, 6.viii.1971, 1 m; dep. NHM Vienna 13.217, RMNH Coel. 25293. Additional specimens from the same sample are preserved as NHM Vienna 13.218, RMNH Coel. 25293, same site and date, off rock and shell substrate; and same, behind hydrographic building, 2 m, also RMNH Coel. 25293.

Measurements of neotype.— Cormoid 12.5 mm high; microslide prep. of cladium (NHM Vienna 800): hydrothecal breadth $206 \pm 8 \mu\text{m}$, length $238 \pm 7 \mu\text{m}$; internode length $281 \pm 7 \mu\text{m}$ ($\bar{x} \pm \sigma$).

Non-Type: NE ATLANTIC: Portugal: Near Cape Espichel, 8 m, viii.1971, coll. H. Zibrowius, RMNH Coel. 13504; Morocco: Off Cape Spartel, Tangier, $35^\circ 46'N$, $55^\circ 6'W$, 3 m, 27.vi.1969, coll. J. Stirn, RMNH Coel. 13506 (ex. slide coll. A.S. 317); MEDITERRANEAN: Spain: La Parra, Almeria, 30.vii.1975, coll. A.S., RMNH Coel. 13507; France: Ile de Pome, Marseille, 7 m, coll. H. Zibrowius, RMNH Coel. 13500; Italy: Naples, 1852-3, coll. M. Sars, ex Mus. Oslo F1170, subsample in RMNH Coel. 13531; Sorrento, v.1974, 1-4 m, coll. A.S., RMNH Coel. 13501 (ex A.S. slide coll. 502); St Pancrazio, Ischia, 3.v.1974, coll. A.S., RMNH Coel. 25263; Formiche de Vivara, Ischia, 22.viii.1974, 5 m, coll. A.S., RMNH Coel. 25264; E of Capo Caccia, Sardinia, 2 m, 16.iv.1982, coll. J. Schmitting, RMNH Coel. 25266; Cala Dragunàra, E of Capo Caccia, Sardinia, 0.4 m, coll. J. Schmitting, RMNH Coel. 25267; Malta: Sliema Tower, 1-8 m, viii.1971, coll. H.-E. Schmidt, RMNH Coel. 13515; Yugoslavia: Malinska, Krk, 1 m, ix.1987, coll. A.S., RMNH Coel. 25265; Dubrovnik, viii.1971, coll. H.-E. Schmidt, RMNH Coel. 13504. Turkey: On *Cystoseira*, Kazkinitskii Bay, Cape Kamenyi, 6 m, RMNH Coel. 25691.

Description.— Stolon densely fusing and anastomosing, with up to 10 cormoids per cm^2 . Caulus monosiphonic, arising from 2-4 stolonous roots; with 1-4 annuli in basal few mm followed by 1 prosegment with oblique constrictions, with 1 frontal nematotheca; remaining caulus segments with usual pattern of alternating cladia or corbulae arising from caulus segments with 3 nematothecae and 1 pseudonematotheca. Fully grown cormoids up to c. 40 mm, with 7 cladia to several hundred; caulus never branched, lacking apical stolons and intersegments; cladia with up to 15 cormidia. Hydrotheca broad, shallow, length/breadth ratio c. 1.1-1.4; rim with 9 uniform cusps; hydrothecal wall reinforced by well developed intrathecal ledge. Mesial nematotheca arising above middle of hydrotheca, occasionally even so high up as to be contiguous with hydrothecal rim; length c. 100 μm ; lateral nematothecae flanking hydrothecal aperture; all nematothecae gutter-shaped. Colonies dioecious; large cormoids producing 4 or more corbulae; first rib of corbula frequently free, following 4-8 pairs fully fused in female but in male with small openings between nematothecae. In Adriatic populations gonophores of male corbula white, of female yellow.

Reproductive season.— In N Adriatic Sea mature colonies occur throughout year, peaking February-March when water temperatures are actually lowest of the year (7-8° C). No winter records of fertile material from other parts of Mediterranean area can be confidently distinguished from those of *Aglaophenia pluma*, *A. picardi* and *A. tubiformis*.

Habitat and ecology.— *Aglaophenia octodonta* is found predominantly in wave-washed areas and settles there on *Cystoseira*, rock, shells of *Balanus* and *Mytilus*, sponges and, locally, on *Posidonia* stipes.

Colonies growing along the Istrian coast (N Adriatic) at 0.5-1 m depth on *Cystoseira* often have a dwarf growth-habit, even having tiny corbulae. These specimens grow between the more rigid branches of *Cystoseira*, which protect them from being smashed against the surrounding rock substrate and from drying out during the

yearly extreme low tides. Such specimens were described previously by Marktanner-Turneretscher (1890: 271). See also Remarks.

Symbiotic algae.— Absent (Svoboda, 1979: 66), although the species sometimes grows alongside *Aglaophenia tubiformis* which has them.

Distribution.— Recorded throughout Mediterranean Sea and adjacent Atlantic Ocean north to Brittany.

In the Atlantic the species is not easy to distinguish from *Aglaophenia pluma*. Published records of specimens taken from the Plymouth area probably refer to *A. pluma* (Marine Biological Association, 1957: 51, as *A. helleri*, specimen assigned to 'E.T.B.'; BMNH cat. no. 1948.9.8.15, coll. E. T. Browne, Eddystone Rock, 24.i.1898, plus one fragment on slide in RMNH; also BMNH 1941.3.20.322, other data same, plus subsample of same in RMNH Coel., A.S. Hydrozoa subcollection, microslide preparation no. 200). Several recent collecting excursions to the Plymouth area have failed to locate material resembling *A. octodonta* (A.S.). The material from there assigned to *A. helleri* by Nutting (1896), also mentioned in Marine Biological Association (1957: 51, as *A. helleri*, specimen assigned to 'C.C.N.'), seems likely also to have been *A. pluma*. Although the species may yet be found in the British Isles, at the time of writing its occurrence has not been reliably demonstrated.

Remarks.— In the E and central Mediterranean Sea *Aglaophenia octodonta* is easy to distinguish from other species occurring in shallow water (see Identification section, p. 11). Difficulties arise where it grows alongside *A. pluma*, especially when the latter is not branched. Several techniques might be employed in discriminating the two. Often biometric analysis of the population may be helpful (Svoboda, 1979), but additional data such as differences in seasonal fertility, coloration in life, and perhaps substrate choice, might be useful.

Specimens from the Istrian coast (described under Habitat and ecology) which have a dwarfed growth-habit tend not to retract their tentacles when emersed and hence can easily be preserved with the tentacles extended.

***Aglaophenia parvula* Bale, 1882**
(figs 7-9, 10a-e, 13h, 18, 22-23)

Aglaophenia parvula Bale, 1882: 35-36, pl. 14 fig. 3; Bale, 1884: 165-166, pl. 14 fig. 3 (sic), pl. 17 fig. 10; Bedot, 1925: 82 (syn. *A. heterodonta* Jäderholm); Vervoort, 1946b: 339, fig. 9b; Patrìti, 1970: 49, fig. 67; Gili, Vervoort & Pagès, 1989: 94-95, fig. 21A.

Aglaophenia heterodonta Jäderholm, 1904: 296-297, pl. 13 fig. 10, pl. 14 fig. 1; Ritchie, 1909: 96-98.

Aglaophenia pluma var. *parvula*; Millard, 1957: 239-240, fig. 1, d-f.

Aglaophenia dichotoma var. *heterodonta*; Patrìti, 1970: 48, fig. 66.

Aglaophenia pluma pluma; Millard, 1975: 412, fig. 129D (part).

Aglaophenia pluma dichotoma; Millard, 1975: 413, fig. 129A, C, E (part).

Aglaophenia pluma parvula; Millard, 1975: 413-415, fig. 129B, F; Isasi, 1985: (not seen); Isasi & Saiz, 1986: 67-74.

non *Aglaophenia pluma* var. *parvula*; Vervoort, 1959: 307-308, figs 52a, 53b.

Material.— Type: Bale based his description on material from Queenscliff, Port Phillip Bay, Victoria, Australia, which he obtained from 'Mr Goldstein'. Two microslide preparations from this material survive (Mus. Victoria F53313, F53249). The first slide bears two unbranched specimens, the longer fragment being 9 mm long and the other, which alone has some stolon attached, 8 mm. The latter is here designated lectotype (fig. 9a). Slide F53249 also bears a sterile fragment 7 mm long, broken from

the stolon. The hydrothecae on both slide preparations show signs of shrinkage typical of specimens which have been dried. It is not clear whether Bale based his original illustration of the species on one of these specimens but the folds along the rim of the mesial cup that he illustrated (Bale, 1882: pl. 14 fig. 3a, b) seem to indicate that he used a specimen that had become dry at some time. Newly collected, spirit-preserved specimens from a neighbouring locality (Gippsland coast, Victoria, coll. J. Watson) show rather smoothly rounded cusps without any folds (figs 9c, 10b, 23b). The hydrothecae in Bale's specimens are smaller than this modern material, possibly also due to shrinkage. Non-type material from the same collection (slide F53332, Port Phillip) is labelled '*A. parvula* var. *ramosa* Bale, 1889'. It bears a dichotomously branched, fertile tip of a cormoid c. 15 mm long. Signs of shrinkage (fig. 10a) indicate that this specimen, too, had dried out before mounting. The existence of the specimen shows that Bale could have known that the species sometimes branches dichotomously, but he seems not to have published such an observation.

Non-Type: E ATLANTIC: British Isles: Ireland (first records): Stained fragments of fertile cormoids, Dingle Peninsula, Co Kerry, two slide preparations, ex coll. R. Bassindale, BMNH 1958.11.9.1; Two fertile, dichotomous cormi, Saltee I, Co Wexford, 10 m, coll. B.E.P., BMNH 1985.8.3.2; One similar specimen, Sherkin I, Co Cork, 15 m, coll. B.E.P., BMNH 1985.8.3.5; **Wales** (first records): One dichotomously and partly irregularly branched fertile cormus, Stack Rocks, off Littlehaven, St Bride's Bay, Pembrokeshire, SW Wales, 18.viii.1987, coll. J. S. Ryland; One cormoid, unbranched and fertile, LWST, Lydstep, Pembrokeshire, 7.ix.1987, coll. P.F.S.C. & J. S. Ryland; Plume from the only colony observed, 200 m E of Garland Stack, off N coast of Skomer, Pembrokeshire, 51°44.65'N, 5°17.60'W, on mixed bottom comprising rocky outcrops, cobbles and boulders, 20 m, situation subject to intermittent 2 knot (3.7 km/h) tidal current, coll. B.E.P., det. P.F.S.C./A.S., Ulster Museum, Belfast, cat. no. BELUM: Md 794. **England** (first records): Budleigh Salterton, S Devon, two microslide preparations, Royal Museum of Scotland [RMS] 1959.33.782-783; Plymouth, Devon, one microslide preparation, ex coll. A. M. Norman, BMNH 1912.12.21.426; One unbranched cormoid, collected amongst branched *A. pluma*, 2-6 m, on Eddystone Rock, near Plymouth, SW England, 16.x.1974, coll. & det. A.S., RMNH Coel., A.S. Hydrozoa subcollection, microslide preparation no. 350. **EUROPE EXCEPTING BRITISH ISLES: NW France** (first records): Brittany: Glénan Is, 12 samples, 6-12 m, especially around cave entrances and growing on sponges, 1964, duplicates in RMNH and BMNH, coll. A. Castric, det. A. Svoboda, includes subsamples from BMNH 1988.4.1.1-11; Glénan Is, 19.viii.1964, coll. Castric-Fey, RMNH Coel. 25048; **N Spain**: Several cormi, La Galea, Bay of Bilbao, 23.vii.1984, coll. & det. I. Isasi, mentioned, Isasi, 1985, Isasi & Saiz, 1986 (first European record); Same locality and collector, 6 cormi, fertile, unbranched, 7.viii.1987, RMNH Coel. 25047; Corrubedo, Galicia, 7.vi.1976, ex Mus. Luis Iglesias, subsample in RMNH Coel. 25279. **NORTH AND WEST AFRICAN COAST** (first records): **Morocco**: W of Cape Spartel, Tangier, 35°41'40"N, 6°16'00"W, 27-32 m, 25.vii.1969, coll. J. Stirn, RMNH Coel. 13533; **Mauritania**: Numerous large but infertile colonies, 18° 50'N, 16° 18'W, 14 m, 8-9.vi.1988, coll. 'TYRO' Mauritania II expedition, sta. MAU.024, RMNH Coel. 16591. Several infertile colonies, 16 m, 9.vi.1988, other details as previous but sta. MAU.027, RMNH Coel. 16592. Other RMNH material from this expedition from 50 m depth, E of Cap Blanc, 20°49'N, 17°01'W, 7.vi.1988, and other nearby localities; Unbranched, partially fertile cormoids, lacking 'double dentition' and inverted mesial hydrothecal cusp, 'Atlantide' Stns 45, 145, off W Africa, RMNH Coel. 1261, 1275, mentioned by Vervoort, 1959 (cf. *A. parvula*); **Namibia**: Rocky Point, 'low tide level', ii.1985, coll. J.-M. Gili, samples in RMNH Coel. 25038 and BMNH 1988.4.6.25 (Gili, Vervoort & Pagès, 1989). **SOUTHERN AFRICA: Republic of South Africa**: Fertile unbranched cormoids of a small cormus, with anastomosing stolons on an algal thread, Saldanha Bay, 50 m, BMNH 1956.9.25.6; Same locality, two microslide preparations, RMS 1959.33.780-781; Same locality, two branched colonies in spirit, Scottish National Antarctic Expedition, det. J. S. Ritchie, RMS 1921.143.1378, 1378B; Several unbranched, partially-fertile cormoids with stolons, two dichotomous fragments of cormoid, and several with irregular branching (with cormoids replacing cladia), in spirit; identical with lectotype; Port Natal, coll. 'Mr Vahlberg', Stockholm Mus. cat. no. 3909; Unbranched cormoids 6-8 mm long, infertile, 'Cape', dried out, RMNH Coel. 33; 10 mm fertile cormoids, on alga *Gelidium versicolor* (S. G. Gmelin) Lamouroux, 1813, dried out, Kamp Bay, Cape Province; RMNH Coel. 507, also RMNH Coel. 751, Cansado Bay. All this RMNH material mentioned by Vervoort, 1946b (RMNH Coel. 751 as *A. dichotoma*). **INDO-PACIFIC: Australia**: Gippsland coast, Victoria, from reef 2 km offshore, 12 m, coll. J. Watson, RMNH Coel. 25036, subsample BMNH 1988.4.6.26 (ex J.W. colln no. 1762).

Description.— Colony comprising branched and/or unbranched cormoids. Stolon branching; on sponge substrates forming loose net, on filamentous algae dense

net with numerous anastomoses. Basal part of erect portion comprising short unsegmented region followed by 1-3 prosegments each with one frontal nematotheca, delimited by oblique annuli. Rest of erect stem comprising 30-50 internodes if a single plume, but up to several hundreds in dichotomous specimens which may attain 60-70 mm. In older cormoids, from which many basal cladia have broken off, irregular branching occurs. From the sites of breakage young cormoids arise which basally comprise a typical basal prosegment - each being in effect a 'young colony'. Such side branches orientate with their cauli parallel with the remaining cladia and the versal sides of their fans are directed towards the side of the caulis from which they arise. In unbranched cormoids cladia comprising up to 9 cormidia, in branched colonies up to 12. As in other *Aglaophenia* species basalmost cormidium is shortest and has least deep hydrotheca, and mesial nematotheca generally shorter than in more distal cormidia. *Hydrothecal rim apparently with 11 cusps, one pair smaller than rest; in side view mesial cusps inclined towards lumen and covered by first (outer) pair of cusps which might themselves bend in opposite direction, that is outwards. Between normal first and second pairs of cusps a small pair of cusps (sometimes merely a slight rise from contour of edge of hydrotheca) usually merged with second cusps; best seen in frontal view or under SEM (figs 8a, 10d, 18c-d).* In side view these small, additional cusps apparently varied in prominence from being distinct from second cusp to merging with it, even within length of hydrocladium, but this largely a product of viewing angle. Third pair of cusps largest. Rear pair of cusps quite acute, in present Australian specimens bending towards hydrothecal lumen. *Between rear cusps a deep gap*, in contrast to a shallow gap in *A. pluma* (compare figs 9e, 13e). Developing cormidia indicate that additional cusps develop late in growth, and after other 'normal' cusps. Mesial nematotheca branching off from hydrotheca between middle and upper third, foramen to hydrothecal lumen clearly visible; lateral nematotheca 20-30 μm below tips of rear cusps which therefore remain visible in side view. Colonies dioecious; mature male corbulae with small slits between nematophores of ribs; in mature female corbulae ribs fully fused except at rachial end; corbulae of both sexes with 5-13 ribs on each side of rachis, usually 9-11; occasionally with basalmost rib unfused.

About half the colonies so far recognized from southern British Isles, Brittany, Galicia and Morocco were branched dichotomously as were colonies from South Africa and Australia. From the Bay of Biscay coast (Bilbao) only unbranched colonies have so far been reported. Dichotomous Australian colonies look less densely branched than African and European ones due to their longer caulis segments.

In the Australian specimens the rear pair of hydrothecal cusps bends slightly towards the hydrothecal lumen.

The characteristic 'extra cusp' seems not to vary geographically, but is everywhere varied in expression from colony to colony.

Both branched and unbranched specimens may bear corbulae.

Reproductive season.— Fertile specimens so far taken May-September in North Atlantic. Since some of the September- collected corbulae were young it is likely that planula release continues into October. A colony from the Eddystone Rock, off Plymouth, had empty corbulae on 16 October 1974.

Collecting dates of non-European fertile material have not been recorded.

Habitat and ecology.— Nearly all the *Aglaophenia parvula* colonies seen had been growing on sponges, although many of the older museum specimens lacked evi-

dence of a substrate. One colony from Bilbao was on a *Mytilus* shell, another on barnacles. Most of the Spanish material was from semi-shaded situations (I. Isasi, in litt.), as was that from British Isles and Brittany (personal observation). Two South African colonies were recorded on algae, the rest being taken from sponge substrates. In S Australia *A. parvula* has been reported on sponges among holdfasts of the large brown alga *Ecklonia* (J. Watson, pers. comm.).

The range of water temperature in areas of S Australia from which *Aglaophenia parvula* has been recorded is wide, 13-25° C, and is similar in both S Africa (Millard, 1978) and Europe. The distribution in N Europe would seem to be limited by temperature.

Seasonal fertility in the species may well be induced by rising temperature but the relation of colony branching to temperature is as yet unclear. Dr N. A. H. Millard (in litt.) reported a different cause of branching. Cormoids with unbranched branches occur abundantly in wave-washed areas where they form a cover over rocks, barnacles, mussels and other substrates, whereas branched colonies occur in deeper water.

Distribution.— Near Melbourne, Victoria (Bale, op. cit.); several S Australian and Queensland localities (J. Watson, in litt.); no records yet from W Australia; in S Africa from Natal around the Cape to Namibia (Gili, Vervoort & Pagès, 1989, and literature cited therein; St Paul I, S Indian Ocean (Vanhöffen, 1910; Millard, 1975). No records from Madagascar so far. Material now in the BMNH and RMNH comes from 19°2'S, 12°29'E, Rocky Point, Namibia, comprising dichotomous intertidal colonies. Recorded also from Mauritania (present material) and Morocco (Casablanca, Patriti, 1970, also present material; Tangier, off submarine telephone cable, ex A. M. Norman colln, BMNH 1910.10.19.1).

First recognized European specimens collected from Bilbao (Isasi, 1985; Isasi & Saiz, 1986); here recorded also from N Spain, NW France and the British Isles (present material). A specimen now about 250 years old in the Linnaeus Collection in London was probably also collected in the British Isles (p. 39).

The present material from Ireland (Eire), Wales, England, France, Mauritania and Namibia comprises the first published records from those countries. That from Cap Blanc, Mauritania, is from a locality virtually on the frontier with Spanish Sahara, so that the species seems likely to occur all along the west coast of Africa.

Remarks.— This species seems widely distributed in warm to temperate waters of the world but has hitherto often been confused with the closely similar *Aglaophenia pluma*. Identification is treated elsewhere (pp. 10-11, also caption to fig. 10). A comparison of British-collected *A. parvula* and *A. pluma* has been made recently by Thorpe, Ryland & Cornelius (unpublished) who compared both morphological criteria and a total of fourteen enzyme loci coding for eleven different enzymes using starch-gel electrophoresis.

Several specimens from the collection of the South African Museum [SAM], collected by the University of Cape Town and determined by Dr N. A. H. Millard as *Aglaophenia pluma parvula* and *A. pluma dichotoma*, were re-examined. They included unbranched intertidal specimens with extremely small cormoids and cormidia (from Isipingo, Natal, SAM 2093, and Port Elizabeth, SAM 2090); and some slightly larger ones, with cormidial internodes up to 300 µm in length and with a tendency to branch irregularly (False Bay, 5 m, SAM 2086) or dichotomously (intertidal, Rocky Point, SW Africa, SAM 2098; also Luderitz Bay, SW Africa, hydrothecal rims with

marked subsidiary cusp). However, in large dichotomously branched colonies with internodal length exceeding 300 μm the subsidiary cusp is smaller in material so far examined and such specimens are intermediate in this respect between *A. pluma* sensu stricto and *A. parvula* (intertidal, Strandfontain, False Bay, SAM 210; 47 m, Aghulas Bank, SAM 138). Such 'subsidiary cusps' in dichotomous colonies were recognized by Millard (1975) who considered that such material should be referred to *A. pluma dichotoma*. The shape and prominence of these additional cusps may prove to be related to the force of water movement, as might also be the occurrence of dichotomous branching in some other *Aglaophenia* species.

***Aglaophenia picardi* Svoboda, 1979**
(fig. 11)

?*Aglaophenia* sp. Picard, 1955: 190.

Aglaophenia pluma f. *typica*; Riedl, 1959: 660.

Aglaophenia pluma var. *teissieri* Svoboda, 1970: 676 (nom. nud.).

Aglaophenia picardi Svoboda, 1979: 70, figs 12b, 13b, 15b, 16b.

Material.— Type: 1 cormoid with 2 corbulae, Rovinj, Yugoslavia, landward side of hydrographic station, 2 m, 6.viii.1971, coll. A.S., in spirit, plus 1 microslide of 1 hydrocladium, NHM Vienna 13.215, RMNH Coel. 25292. Several hundred cormoids from same sample deposited as paratype (NHM Vienna 13.216) plus hydrocladial fragments of holotype in RMNH Coel. 25292.

Measurements of holotype (from microslide prep. no. 807): hydrotheca length $274 \pm 10 \mu\text{m}$, breadth $180 \pm 7 \mu\text{m}$, length of cladial segment $306 \pm 17 \mu\text{m}$.

Non-Type: NE ATLANTIC: N Spain: Ciervana, Bilbao, 3 m, 12.vii.1984, coll. I. Isasi, RMNH Coel. 25261 (subsample in BMNH 1988.4.6.27); Canary Is (first records): S Punta Taliarte, Gran Canaria, 1 m below 'low tide level', coll. K. Hiscock, RMNH Coel. 25283; Punta de las Arenas, Gran Canaria, 15 m, 1975, coll. K. Hiscock, RMNH Coel. 25284; MEDITERRANEAN: Malta: Sliema Tower, 0-8 m, viii.1971, coll. H. E. Schmidt, RMNH Coel. 13529; Italy: Isola Lachea, Sicily, 32 m, 13.x.1973, coll. F. Krapp, RMNH Coel. 13528, 13530; Naples, 1852-1853, coll. M. Sars, ex Oslo Mus. F1170 (subsample in RMNH Coel. 13531); Pta Barabarca, Capo Liveri, Elba, 2-4 m, 20.vii.1988, coll. A.S., RMNH Coel. 25257; Pta S. Pietro, Porto d'Ischia, 5 m, 14.viii.1974, coll. A.S., RMNH Coel. 25259; Rear part of Grotta del Mago, Ischia, 2-4 m, 30.viii.1974, coll. A.S., RMNH Coel. 25260; Israel: Akhziv, 26.vi.1960, coll. C. Lewinsohn, Univ. Tel Aviv coll. NS 20181 (subsample in RMNH Coel. 25213, slide 607); Off Bardawill, $31^{\circ}15'N$, $32^{\circ}41'E$, 31.x.1975, Univ. Tel Aviv colln NS 20308 (subsample in RMNH Coel. 25237, slide 594); No data, Univ. Tel Aviv colln NS 20181-2, (subsample in RMNH Coel. 25238, 2 slides nos 628); Tantara, 8.vii.1954, coll. C. Lewinsohn, Univ. Tel Aviv colln NS 20196. BLACK SEA: Turkey: $41^{\circ}16'N$, $29^{\circ}12'W$, 45 m, coll. Prof. Zernov, via S. D. Stepanyants, RMNH Coel. 25690.

Description.— Stolons densely branched, giving rise to up to 5 cormoids per cm^2 . Up to 4 stolonal roots on base of cormoid. Caulus monosiphonic, never regularly branched; rarely, with apical stolons; up to c. 50 mm high (c. 80 segments); basal region short, occasionally segmented by horizontal septa; *no prosegment developed* on bases of cladia bearing caulus segments; caulus segments with cladia and corbulae arising as alternatives, having 3 cauline nematothecae and an abortive hydrotheca. Cladia with up to c. 20 cormidia. Hydrotheca deep, slender, length/breadth ratio c. 1.5-2; *mesial nematotheca* gutter-shaped, *arising from about middle of hydrotheca*, short; tops of lateral nematothecae just at level of hydrothecal rim; cusps on rim 9, small, uniform, sharply pointed; intrathecal ledge inconspicuous to missing. Colonies dioecious, usually with 2-4 corbulae per cormoid; proximal pairs of ribs of corbula often free, following 6-9 pairs in female fully fused, in male with small openings between nematothecae.

Reproductive season.— Mature colonies found in Mediterranean Sea April–November (Svoboda, 1979: 21); in Bilbao, N Spain, July (Isasi, 1985: 95).

Habitat and ecology.— *Aglaophenia picardi* is most often found in partly shaded to dark locations subject to moderate wave action and/or strong currents. In depth profile it clearly settles below *A. octodonta*, and in caves further in than does that species. *A. picardi* is commonly collected on bare rock, balanomorph barnacles, *Mytilus*, sponges, many red algae and occasionally the stipes of *Posidonia oceanica*. It is common at 3–10 m depth, and has been recorded in strong current from Strait of Messina at c. 30 m.

The species is occasionally predated by a small nudibranch, *Doto coronata* (J. G. Gmelin, 1790), which is difficult to detect because it resembles a corbula and hence perhaps itself escapes predation from labrid fish. Caprellids apparently catch still living prey from the hydranths of this and other aglaophenians, even snatching it from the tentacles when the struggling of the prey attracts their attention (A.S., personal observation).

Symbiotic algae.— None (Svoboda, 1979: 73).

Distribution.— Whole Mediterranean Sea; two records Canaries (present material) and recently Bilbao, N Spain (Isasi, 1985: 95). Also recorded Black Sea (present material) and Cape Verdes (Svoboda, 1979).

Remarks.— *Aglaophenia picardi* is the only species of the genus known to lack a prosegment. The developmental significance of this is unclear and comparative rearing of this and other species has yet to be done.

Aglaophenia pluma (Linnaeus, 1758)

(figs 10f, 12, 13a–g, 19a–b, 24a–b)

Sertularia pluma Linnaeus, 1758: 811.

Plumularia cristata Lamarck, 1816, 125 (nom. nov. for *Sertularia pluma* Linnaeus, 1758); Johnston, 1838: 143–145, pl. 19 figs 1–3, pl. 20 fig. 1; Johnston, 1847: 92–94, pl. 23, figs 1–3.

Aglaophenia cristata; McCrady, 1857, 202–203.

Plumularia pluma; var. *dichotoma* Sars, 1857: 164 [nom. nov. for *P. cristata* sensu Johnston (part, as defined here)].

Aglaophenia pluma; Hincks, 1868: 286–288, fig. 37, pl. 63 fig. 1 (part); Vervoort, 1946a: 190, figs 80–81 (part); Svoboda, 1979: 98–102, figs 15j(1–4).

Aglaophenia dichotoma; Kirchenpauer, 1872: 13, 25, 30, pls 1–2, 3 fig. 7 (part).

Material.— Type: Svoboda (1979) designated as lectotype a specimen from the Linnean Collection in London but since it is highly probable that Linnaeus received the material after 1758 (Cornelius, 1979: 309; Cornelius & Wells, 1988) the material cannot be regarded as type and the designation is invalid [ICZN, 1985: Article 74a(v)]. The identity of the Linnean specimens is treated below (p. 38).

To facilitate comparison with *Aglaophenia parvula* we designate neotype material of *A. pluma* as follows: colony with 10 cormoids, Gannet's Rock Pinnacle, Lundy I, SW England, 20 m, 23.viii.1982, coll. B.E.P., material in spirit (BMNH 1985.8.3.10) plus one microslide preparation in BMNH and a second in RMNH Coel. 25297. The colony has infertile corbulae. Some of the cormoids have developing side branches near the base of the caulus.

Non-Type: NE ATLANTIC: British Isles: Ireland: Off Carrigathorna, coast S of Lough Ine, SW Cork, coll. K. Hiscock, RMNH Coel. 13435 (18 m, 18.vii.1972) & 13429 (depth unknown, 24.viii.1971); Spanish I, Roaringwater Bay, W Cork, 2–5 m, 21.viii.1975, coll. K. Hiscock, RMNH Coel. 13394; Off Truhane Pt, W coast of Sherkin I, Roaringwater Bay, 14 m, 25.viii.1975, coll. K. Hiscock, RMNH Coel. 13395; Rosslare Harbour, Wexford, 3 m, ix.1976, coll. A.S., RMNH Coel. 13393; N Wales: Corinell Head, Anglesey, 18.vi.1971, 10 m, coll. K. Hiscock, RMNH Coel. 13436; St Tudwall's I, 0.5–3 m,

22.v.1974, coll. K. Hiscock, RMNH Coel. 13428; Menai Strait, below Menai Bridge road bridge, 1 m, coll. K. Hiscock, RMNH Coel. 13414; Same, 1 m, 7.vii.1972, coll. K. Hiscock, RMNH Coel. 13416; Same, 1 m, 22.i.1974, coll. K. Hiscock, RMNH Coel. 13408; Same, 1 m, 13.x.1974, coll. A.S., RMNH Coel. 13406; S Wales: 3 m, North Haven, Skomer, Pembrokeshire, on steeply sloping rock, 9.viii.1975, coll. K. Hiscock, RMNH Coel. 13396; England: Carmine Philomena, Lundy I, Bristol Channel, 8 m, 2.viii.1974, coll. K. Hiscock, RMNH Coel. 13424; Needle Rock, Lundy I, Bristol Channel, 15 m, 3.viii.1974, coll. K. Hiscock, RMNH Coel. 13420; Clayne Cove, Ilfracombe, N Somerset, 6 m, 1.vi.1974, coll. K. Hiscock, RMNH Coel. 13419; Seals' Rock, Lundy I, Bristol Channel, 8 m, 28.vii.1974, coll. K. Hiscock, RMNH Coel. 13418; Eddystone Rock, off Plymouth, 2-8 m, 16.x.1974, coll. A.S., RMNH Coel. 13390; Brook Bay, Isle of Wight, 'low tide level', 6.ix.1974, coll. Jacky Garfath, RMNH Coel. 13412; NW France: Glénan Is, 1964, coll. A. Castric-Fey, BMNH 1988.4.1.43-64, duplicates in RMNH Coel., A.S. Hydrozoa subcollection, microslide preparations nos 418, 426, 427, 430, 432, 434-6, 438, 440-1, 443, 445-7, 450, 453-6, 463, 468; N Spain: Ciervana, Bilbao, 5 m, 17.vii.1984, coll. I. Isasi, RMNH Coel. 25287; Same, 12 m, 15.vii.1984, RMNH Coel. 25288; La Galea, Bilbao, 7 m, 23.vii.1984, coll. I. Isasi, RMNH Coel. 25289; Same, 15 m, 25.vii.1984, RMNH Coel. 25037; Musques, Bilbao, 10 m, 13.viii.1984, coll. I. Isasi, RMNH Coel. 25290; Portugal: Pt de Luz, Algarve, 5 m, viii.1987, coll. V. Petriconi, RMNH Coel. 25033; Morocco: Atlantic coast, 35°41'40"N, 6°16'00"W, 27-32 m, 25.vii.1969, coll. J. Stirn, RMNH Coel. 13432; MEDITERRANEAN: S Spain: Porto de Baños, Marbella, 20 m, 24.viii.1975, coll. A.S., RMNH Coel. 13551; Pta Carnera, near Algeciras, 10-17 m, 25.viii.1975, coll. A.S., RMNH Coel. 13552; La Parra, Almeria, 5-10 m, 13.vi.1975, coll. A.S., RMNH Coel. 13426; Almeria, 10 m, 21.vi.1975, coll. A.S., RMNH Coel. 13398; Almeria, 6 m, 19.vi.1975, coll. A.S., RMNH Coel. 13400, also RMNH Coel., A.S. Hydrozoa subcollection microslide preparation no. 486, Almeria, ?depth, 26.vii.1975, coll. A.S., RMNH Coel. 13426; S France: Harbour and breakwater, Cette (Sette), coll. 'Dr Collins', ex Zoologische Staatssammlung, Munich, RMNH Coel. 25291, ex A.S. slide coll. nos 380, 471, 487.

Description.— Stolon branching frequently or following branchings of substrate alga, often *Halidrys siliquosa*. Erect stems irregularly spaced, up to about 80 mm; short unsegmented basal region followed by 1-3 prosegments, each with one frontal nematotheca, delimited by oblique annuli; rest of erect stem comprising 30-50 internodes, or up to several thousand internodes in tall, dichotomously branched specimens up to at least 150 mm; 3 cauline nematothecae and one abortive hydrotheca on each stem internode. Hydrocladia up to c. 9 cormidia long; basalmost cormidium shortest, its hydrotheca being the least deep; hydrothecal depth differing also between localities. Hydrothecal length/breadth ratio c. 1.5; rim with 9 cusps of varied length; outermost or adjacent longest; mesial nematotheca branching off between middle and upper third of hydrotheca, free part 50-120 µm, gutter shaped (not tubular), with foramen to hydrotheca clearly visible; lateral nematotheca bordering rim at level of rear cusps, often hiding cusps in side view.

Colonies dioecious; male corbula with slit-like openings between ribs; female corbula usually with ribs fused, occasionally one free; corbula in both sexes typically comprising 5-10 but sometimes more ribs on each side of corbula rachis.

Hydranth small, transparent, column cylindrical to tapering basally, broadening out just below tentacles; hypostome held at level of hydrothecal rim, rounded, low; column 160 x 60 µm, hypostome 110 x 110 µm; tentacles 10, each 210 µm long when fully extended, 18 µm wide at base and tapering gradually to 12 µm wide at blunt tip; held approximately horizontally, in 1 whorl; tentacles emerging between cusps of hydrothecal rim (Roscoff, August 1982; Cornelius, in prep. 1).

Most colonies are unbranched, and this is especially so in the populations around the British Isles. However, although dichotomously branched colonies are not rare in British and Irish waters they seem more characteristic of the Atlantic coast of Europe from SW England to Portugal and of the western Mediterranean. At present it seems

that dichotomous colonies might be produced in response to summer sea-water temperatures, since there have been only a few records of such colonies in winter; but there is a relative paucity of winter-collected material. *A. tubiformis* appears to respond in the reverse manner (see Remarks).

Reproductive season.— Svoboda (1979) recorded that in S England (Plymouth, Isle of Wight, Lundy I), N Wales (Anglesey), SE Ireland and NW France corbulae occur May to October, but there is little winter-collected material and seasonal limits are hence imprecisely known. Teissier (1965) reported fertile material April-September at Roscoff. However, it is possible that some of his records related to colonies of *A. tubiformis* which also occurs on *Halidrys* in that region (see next section and Remarks).

Habitat and ecology.— Often on the brown alga *Halidrys siliquosa* but reliably recorded also on rock and gravel, *Sargassum* spp. and occasionally on stipes of *Laminaria* spp. Lower shore, deep pools and sublittoral to c. 20 m. Recorded often on *Halidrys* at MLWS amongst eel-grass beds near Roscoff (Teissier, 1965) but confusion there with *A. tubiformis* is not excluded. In Irish waters *A. pluma* is the common shallow-water species, occurring intertidally and in very shallow sublittoral depths on *Halidrys* except in exposed sites, typically at 5-10 m, when on rock (B.E.P.); also on *Halidrys* in intertidal rapids and pools (Ireland, B.E.P.; Isle of Wight, the late Jacky Garfath; Roscoff and Ile de Callot, NW France, P.F.S.C.).

Symbiotic algae.— None. The closely similar *A. tubiformis* has zooxanthellae but most species in the genus lack them.

Distribution.— The species has its northern limit in British waters, albeit occurring perhaps as far north as the Shetlands, and it is convenient to discuss this area separately. Many of the following locality records are supported by the material cited above. British Isles: Occurs throughout Irish waters. Reliably recorded north at least to Anglesey and W Scotland on the west coast of mainland Britain, and as far east as the Isle of Wight on southern coasts. Possible confusion with other species makes assessment of more northerly records difficult. Joshua Alder (quoted in Evans, 1978) recorded '*Plumularia cristata*' from Northumberland in or prior to 1858 and Johnston (1847: 471) reported fertile material under the same name from the Orkneys collected in 1845: both were on *Halidrys siliquosa*, the usual substrate. A detailed survey of intertidal fauna in the Shetlands in 1974, in which the cnidarians were studied exhaustively by the late David Huxtable of the Department of Zoology, University College, Swansea, did not report *Aglaophenia* spp. (R. Earll, pers. comm.). A later survey (Berryman, 1980) reported *A. pluma* from a single locality in 1980 but the specimen was not kept (J. Berryman, pers. comm.) and we cannot confirm the species identification. Present evidence thus suggests that *Aglaophenia* might nowadays occur in the Shetlands but at least around 1974-1980 was scarce. Though *A. pluma* may occur there this has not been proved. Elsewhere: Reliably reported from N and S Spain (Garcia Coralles et al., 1978), S Spain and NW African coast (Svoboda, 1979) and also Portugal; in the Mediterranean Sea at least formerly found as far east as Cette (Sette), S France (Stechow, 1919, as *A. dichotoma*); and more recently Morocco (Patrity, 1970). The distribution in the Mediterranean basin may be governed at least partly by the absence of the normal substrate alga, *Halidrys siliquosa*, from that region (I. Tittley, pers. comm.). The eastern limit along the English Channel coast of mainland Europe seems to be in northern French waters. The species has been recorded from the coasts of Belgium (Leloup, 1952; J. Bouillon, pers. comm.) and The Netherlands (Vervoort, 1946a; pers. comm.) but from both

countries only when cast ashore on *Halidrys siliquosa*, the specimens maybe originating elsewhere. There are no records from Danish waters (Kramp, 1935) and no Danish specimens in the Zoological Museum, Copenhagen (K. W. Petersen, pers. comm.). A report by Segerstedt (1889) that Linnaeus (1761: 541) recorded the species from the west coast of Sweden is unfounded. Linnaeus gave the 'locality' as 'In Oceano' but seems to have been guessing that the species might be found in Swedish waters. There are no other Scandinavian records.

There are reports of the species from many other countries but we have not been able to evaluate them. These include: Italy (Rossi, 1971; Morri, 1981), Egypt (Shoukr, 1982), Cape Verde Is, Congo, Luderitz Bay, Azores, Canaries (Stechow, 1925), South Africa (Rees & Thursfield, 1965; Millard, 1975), Patagonia (Stechow, 1912), Japan (Rees & Thursfield), Enewetak Atoll (Cooke, 1975), and Australia (Millard), but so far as we know not from New Zealand. The species has been recorded also from the western but not the eastern seaboard of the U.S.A., unless a single *A. dichotoma* record from Florida is regarded as of this species (E. Leloup, in Fraser, 1944). Van Gernerden-Hoogeveen (1965) gave a single Caribbean record, from Bimini, but Vervoort (1968) gave no others. Van Gernerden-Hoogeveen also cited records from the 'entire African coast', Tanzania, Indonesia, tropical W America and Portugal. However, many of the *Aglaophenia* species which have become well known in recent years have rather limited distributions (Svoboda, 1979) and the near-cosmopolitan impression of *A. pluma* given by these records might well prove invalid. Nevertheless, *A. parvula* apparently has a wide distribution and the situation is unclear.

Remarks.— In contrast to the other species treated here, *A. pluma* has no peculiar diagnostic characters and its distinction from some other species has not always been clear. It is paradoxical that it is also the commonest aglaopheniinid in British waters from whence the species has long been considered well known.

The species as now conceived might include more than one morphologically similar sibling species. Techniques such as electrophoresis and nematocyst studies might contribute to a resolution of this question. A first attempt at employing electrophoresis has already been made to support the separation of *A. parvula* (by Thorpe, Ryland & Cornelius, unpublished). The similarity of *A. octodonta* Heller, 1868, recorded from the whole Mediterranean, is also striking, but that species has not been found to branch dichotomously. Populations identified as *A. octodonta* apparently replace *A. pluma* in the eastern Mediterranean.

Dichotomously branched colonies were first described and illustrated by Johnston (1838; 1847) under the invalid species name *Plumularia cristata*. Sars (1857) introduced the epithet *dichotoma*, and the variety was upgraded to species rank by Kirchenpauer (1872). Bedot (1919) discussed variation in *A. pluma* and provided perhaps the best available illustration of the dichotomous habit. Illustrations of the bifid form additional to those of Johnston and Bedot have been provided by Kirchenpauer (1872), Hincks (1868) and Cornelius (in prep. 2).

A. pluma has been thought to produce dichotomously branched colonies in warm water. In contrast, the Mediterranean *A. tubiformis* is suspected of producing bifid colonies below 16° C and usually produces unbranched colonies at warmer temperatures in the summer (p. 35). Exceptionally, in a relatively cool upwelling at Ganzirri in the Strait of Messina, bifid colonies of *A. tubiformis* have been found in the summer (BMNH 1988.4.6.38, coll. & det. A.S.).

There seems no need to recognize *Aglaophenia pluma* var. *dichotoma* Sars, 1857, as a distinct variety. Sars's material came from Naples and Messina, Italy, and was collected in the winter of 1852/53 (Oslo Mus. B1171). It comprises badly-preserved fragments of *A. kirchenpaueri* from Messina (without substrate preserved) and of *A. octodonta* and *A. picardi* (both off *Posidonia* rhizomes) from the Naples area. It seems certain that Sars studied dichotomously branched *A. tubiformis*, which occurs at Messina all the year round but was at that time not yet regarded a distinct species.

Aglaophenia dichotoma sensu Kirchenpauer, 1872, was based on a mixed series comprising 'dichotomous' material of *A. pluma*, *A. tubiformis* and probably *A. parvula*.

We interpret Millard's (1975: 413) description under the name *Aglaophenia pluma dichotoma* as based on a mixed series comprising *A. pluma* and *A. parvula*, since characters of each were indicated in her description.

Notes on the growth of the colony from the planula were provided by Leloup (1933a), on unusual growth forms of the colony and of the corbula also by Leloup (1933b), and on the corbula and on gonophore development by Faure (1960).

***Aglaophenia tubiformis* Marktanner-Turneretscher, 1890** (figs 14, 25a)

Plumularia pluma var. *dichotoma* Sars, 1857: 164 (part, only the specimens from Messina).

Plumularia cristata; Heller, 1868: 39, pl. 2 fig. 1.

Aglaophenia pluma; Graeffe, 1884: 23; Marktanner-Turneretscher, 1890: 269-270, pl. 7 figs 1-2, 18; Pausinger, 1900: 4; Broch, 1912: 32, fig. 9, 34, fig. 10 (part, dichotomously branched specimens only).

Aglaophenia tubiformis plus var. *Marktanner-Turneretscher*, 1890: 269-270, pl. 7 figs 4, 5, 6, 17.

Aglaophenia tubiformis; Schneider, 1897: 487; Neppi, 1920: 11; Neppi, 1922: 82; Svoboda, 1979: 90, figs 12h, 13h, 14d, 15h, 16h, pl. 5a, b, 6, 8, 9a(1,2).

Aglaophenia elongata; Broch, 1912: 32, fig. 9, 34, fig. 10 (part, dichotomously branched specimens only).

Aglaophenia nanella Stechow, 1919: 147.

Aglaophenia pluma plus var. *dichotoma*; Neppi, 1920: 10-11, pl. 1, figs 7-9.

Aglaophenia tubulifera; Stechow, 1923: 249.

Aglaophenia pluma f. *typica*; Broch, 1933: 44 (specimen no. 2, loc. Split), fig. 18b, no. 1 (loc. Dujmovaca).

Aglaophenia dichotoma f. *gracilis* Broch, 1933: 55 (loc. Poljud, Split).

Aglaophenia elongata Broch, 1933: 56, no. 5 (loc. Prizidnice, Ciovo).

Material.— Type: Gulf of Rijeka, N Adriatic Sea. The lectotype (Svoboda, 1979) was collected by Lorenz v. Liburnau (Vienna NHM cat. no. 13.221 (formerly 6022) plus two microslide preparations nos 829, 833 and subsample in RMNH Coel. 25295) and lacks details of locality, depth or date. It comprises one dichotomously branched cormoid in spirit, lacking corbulae but with several apical stolons. It was selected in preference to other specimens from Marktanner-Turneretscher's collection since it was figured by him. The paratypes comprise 7 fragments from the same sample as the lectotype under the same catalogue number. A microslide preparation of a single cladium is preserved in the RMNH, Leiden (Coel. 25295).

Non-Type: NE ATLANTIC: NW France: Roscoff, 20.vi.1978, on *Halidrys*, coll. Lehrstuhl für Spezielle Zoologie, Bochum (Excursion Ruhr-Universität Bochum), RMNH Coel. 25268, duplicate in BMNH 1988.4.6.35; Toulbroch, Berthaume, 16 m, 28.vii.1982, coll. A. Castric-Fey, RMNH Coel. 25269; Glénan Is, 1964, coll. A. Castric-Fey, RMNH Coel., A.S. Hydrozoa subcollection, microslide preparations nos 422, 444, 504; NW Spain: Arredonda, Ria de Ferrol, Galicia, 12.xi.1985, coll. F. J. Ramil Blanco, RMNH Coel. 25274; Agiuno, Ria de Arosa, Galicia, coll. F. J. Ramil Blanco, RMNH Coel. 25275; El Grove, Ria de Arosa, Galicia, N Spain, coll. I. Iglesias, subsample in RMNH Coel. 25276; Portugal: Ericeira, 17.iii.1972, intertidal, ex Zool. Mus. Lisbon, subsample in RMNH Coel. 13460; MEDITERRANEAN: S Spain: RMNH Coel., A.S. Hydrozoa subcollection, numerous microslide preparations;

Cabo de Gata, Almería, 6-10 m, 10.viii.1975, coll. A.S., RMNH Coel. 13477; La Parra, Almería, 7 m, 4.viii.1975, coll. A.S., RMNH Coel. 13454; Italy: Ganzirri, Str Messina, Sicily, 20-30 m, coll. F. Krapp, 4.x.1973, RMNH Coel. 13447; Secca del Capo di Fonza, Elba, 4 m, 31.vii.1988, coll. A.S., RMNH Coel. 25044; Cala Dragunara, Capo Caccia (east), Sardinia, 24.iii.1982, coll. J. Schmitting, RMNH Coel. 25270; Capo Caccia (east), Sardinia, 1.v.1982, coll. J. Schmitting, RMNH Coel. 25271; Cala Dragunara, Capo Caccia (east), Sardinia, 2 m, 24.iv.1982, coll. J. Schmitting, RMNH Coel. 25272; Cala Dragunara, Capo Caccia (east), Sardinia, 1.5 m, 28.iii.1982, coll. J. Schmitting, RMNH Coel. 25273; Malta: Sliema Tower, 8-12 m, 9.ix.1973, coll. H.-E. Schmidt, RMNH Coel. 13456; Yugoslavia: Malinska, Krk, 12-15 m, 29.vii.1987, coll. A.S., RMNH Coel. 25032; Greece: Pointe Gayia, Gulf of Volos, 40 m, 25.iv.1960, coll. J. Laborel, ex mv Calypso MSE1541, RMNH Coel. 13404; Same, 30-40 m, 25.v.1960, RMNH Coel. 13409; Thasos, same collector, MSE 589, before 1960, RMNH Coel. 13413 (ex coll. A.S.). Israel: Numerous samples, region of Tantura and Atlit, no depths recorded, dates from 1946 to 1976; Univ. Tel Aviv colln NS 20.183-6, 188, 200, 203, 205, 222, 224, 637; subsamples in RMNH Coel. 25210 (slide 630), 240 (slide 615), 209 (slide 608), 239 (slide 622), 207 (slide 602), 241 (slide 619), 242 (slide 606), 637 (no slide), 208 (2 slides, 603).

Description.— Stolon of colony comprising dense, criss-crossing network when on flat surface but more elongated when on the usual substrate of sargassacean algae. Cormoid length c. 50-150 mm in sheltered places, decreasing with increasing water movement to just a few mm. Stems erect, monosiphonic, basal unsegmented part a few mm in length above which is one prosegment with oblique, deep annulation and, in unbranched specimens, 20-80 cauline segments bearing cladia or corbulae; up to several hundred cladia in dichotomously-branched cormoids. *Hydrothecae deep, narrow*, length/breadth ratio c. 1.4-2.0, tending to be highest in colonies from deeper water, decreasing light and decreasing water-movement but with considerable variation along W European coast. Rim with 9 equal cusps, often rounded; intrathecal ridge well developed in wave-exposed specimens, less so in those from sheltered areas. Mesial nematotheca arising between middle and upper third of hydrotheca, free part 30-100 μm , gutter shaped; lateral nematothecae slightly overtopping hydrothecal rim.

Colonies dioecious (exceptions reported by Faure, 1960); corbulae comprising 4-8 pairs of ribs, the first pair often free; ribs in female corbulae completely fused laterally, in male corbulae with slits between.

The species branches dichotomously in wave-sheltered areas at water temperatures below 16° C and is hence commonly unbranched in the summer (exceptions occur: Israel, no depth recorded, RMNH Coel. 25240, 243; Strait of Messina in cold upwelling at 30 m (Svoboda, 1979: 95, RMNH Coel. 13447)). Dichotomous colonies have been recorded in the Atlantic as far north as Galicia (RMNH Coel. 2173) but none has yet been found in Brittany.

Reproductive season.— Fertile specimens recorded February-October, Adriatic (Svoboda, 1979); April-September, Galicia (NW Spain, Blanco, 1988). Other records, for example from Brittany, are unreliable owing to possible confusion with *A. pluma*.

Habitat and ecology.— In Adriatic Sea preferentially settling on certain Sargassaceae (*Cystoseira* and *Sargassum* spp.) but in W Mediterranean often on bare rock as well. Off Morocco recorded on *Cystoseira* at 7-27 m, and off Galicia and Brittany commonly (on *Halidrys* sp.) down to 10 m. In N Adriatic recorded from 0.5 m in extremely wave-exposed areas down to 20 m in weak currents. Down to 40 m in clear waters [for example mid-Adriatic, Broch, 1933 (RMNH Coel. 13475); eastern Greece (RMNH Coel. 13404, 409)].

Symbiotic algae.— All endodermal tissues, including eggs and developing plan-

ulae, contain intracellular zooxanthellae of the species *Symbiodinium microadriaticum*. Their role in nutrition has been described (Svoboda, 1981). The density of zooxanthellae in the tissues increases with water depth over the approximate range 20-40 x 10⁵ algal cells per mm² tissue (Svoboda, 1979: 36).

Distribution (from Svoboda, 1979, and present material).— Recorded in E Atlantic from Morocco N to Brittany; all parts of Mediterranean Sea but not Black Sea; apparently not reaching British Isles.

Remarks.— Only three species of *Aglaophenia* are known to harbour symbiotic algae in their tissues: the present species, *A. harpago* which is endemic to the Mediterranean, and *A. cupressina* Lamouroux (sensu Millard, 1975) which occurs widely in warmer parts of the Indo-Pacific. The last-named alone has polysiphonic cormoids.

Aglaophenia tubulifera (Hincks, 1861)

(figs 15-16, 19c-d, 24c-d)

Plumularia tubulifera Hincks, 1861: 256, pl. 7 figs 1-2.

Aglaophenia tubulifera; Hincks, 1868: 288-289, pl. 63 fig. 2, pl. 64 fig. 3; Svoboda, 1979: 86-87, figs 12f, 13f, 15f(1-4), 16f, pl. 5 figs g-i; Gili, Vervoort & Pagès, 1989: 95-96.

Material.— Type: Coast of Cornwall, on the gorgonian *Eunicella verrucosa* (Pallas, 1766) (record after Hincks, 1861). Cornelius & Garfath (1980: 287) indicated that part of the syntype series was in the BMNH but this was erroneous. The material from the Hancock Museum, Newcastle upon Tyne, which they listed is all that we have traced. The tube in that collection contained two cormoids, and bore three labels: '*Aglaophenia tubulifera* Hincks', '*Plumularia tubulifera*, Cornwall, Revd Hincks' and 'Dark specn, Connemara', the two last written by Joshua Alder and the author of the first not identified. The paler of the two cormoids, evidently from Cornwall, was shorter than the other and is the holotype. The second specimen, from Connemara, has no type status. Both were infertile, and only a few damaged cladia remained. The holotype specimen has now been preserved as a microslide preparation.

Non-Type: NE ATLANTIC: **British Isles:** Ireland: 23 m, Marlfield Bay, Strangford Lough, Co. Down, 54°24'35"N, 5°35'15"W, 13.v.1982, coll. C. M. Howson, BMNH 1985.8.4.1; 28 m, Coningbeg Rock, Saltee I, Co. Wexford, 52°4'0"N, 6°38'30"W, 26.v.1981, coll; B.E.P., BMNH 1985.8.4.2; 20 m, S side of Carrigmore Rocks, Sherkin I, Co. Cork, 51°27'1"N, 9°27'4"W, 20.viii.1981, coll. B.E.P., BMNH 1985.8.4.3; Off Carrigathorna, S of Lough Ine, Co Cork, 14 m, 24.viii.1971, coll. K. Hiscock, RMNH Coel. 13494; Same, 18 m, 18.vii.1972, RMNH Coel. 13435; Schull, SW of Long Island, Carriduff, 20-27 m, 03.viii.1991, coll. A.S., RMNH Coel. 16597 (♀), 16598 (♂); Scotland: Mull of Kintyre, 120 m, BMNH 1888.2.29.14; Loch Lorn, BMNH 1888.6.9.18; Oban, several plumes, BMNH 1899.5.1.188, ?mentioned, Hincks, 1868: 289, see Remarks; **Isle of Man:** Port Erin, BMNH 1961.11.4.128 [with epizoic *Ventromma halecioides* (Alder, 1859)]; **England:** 20 m, Lundy I, Bristol Channel, 2.viii.1968, coll. K. Hiscock, RMNH Coel. 13481; Same, 2.viii.1969, RMNH Coel. 13482 plus one slide (197); Same, Gannets' Rock, 17 m, 9.viii.1974, RMNH Coel. 13479; 33 m, Deep Point, St Mary's, Scilly Is, 1969, coll. M. W. Robins, RMNH Coel. 13484; **NW France:** Glénan Is, coll. A. Castric-Fey, RMNH Coel., A.S. Hydrozoa subcollection, microslide preparations nos 416, 421, 423, 433, 449, 457-8, 460, 469, 489, 496, 499, 503, 505-6, 509, 511 (subsamples of BMNH 1988.4.1.28-37, alcohol preserved); **N Spain:** Bilbao, 20 m, 16.vi.1984, coll. I. Isasi, RMNH Coel. 25287; **Portugal:** Sesimbra, near Setubal, 25-28 m, 7.viii.1969, coll. H. Zibrowius, RMNH Coel. 13486, 489; **Morocco:** 55-73 m, Tangier, BMNH 1903.4.29.7, 1910.10.19.1; 35°50'N, 6°34'40"W, 350 m, RMNH Coel. 13483; 35°41'40"N, 6°16'00"W, 27-32 m, RMNH Coel. 13487; **Guinea Bissau:** 11°39'N, 17°20'W, 131-157 m, 9.ii.1985, coll. J.-M. Gili, RMNH Coel. 25277 (Gili, Vervoort & Pagès, 1989). **SOUTHERN AFRICA:** Republic of South Africa Algoa Bay, BMNH 1899.7.1.6163. The specimen came from George Busk's collection. It comprises the only South African record and the though locality has been regarded as dubious this view may change (Millard, 1975: 416; see also Remarks); **MEDITERRANEAN:** E Morocco: Ceuta, 15 m, v.1986, coll. J.-M. Gili, RMNH Coel. 16593, together with *Gymnangium montagui* (Billard, 1912). S Spain: SW of Alboran, 35°4.9'N, 3°14.4'W, 79-84 m, 13.ix.1958, coll. mv Calypso, RMNH Coel. 13492, ex A.S. slide colln 280-282.

Description.— Stolon branching infrequently. Main stem erect, *only exceptionally branched*, monosiphonic, up to 60 mm, *not forming tall branched colonies*; spaced irregularly on stolon; basal region lacking annuli; prosegment with one frontal nematotheca and oblique nodes; subsequent internodes with 3 cauline nematothecae and one abortive hydrotheca. Normal hydrotheca (excepting basalmost on each hydrocladium) long, narrow, length/breadth ratio c. 1.7; rim 9-cusped, median cusp longest; intrathecal ledge indistinct. Most proximal cormidium with mesial nematotheca shorter than in those more distal and gutter shaped recalling those of *A. pluma*. *Subsequent mesial nematothecae along a cladium becoming tubular, closed in distal part; usually extending to level of hydrothecal rim or just beyond; subterminal region thickened with internal annulus, giving subspherical shape to distal region of lumen* (fig. 16c-d); mesial nematotheca adnate basally, arising below middle of hydrotheca, free part 120-200 μm ; distal closed part 70-100 μm ; foramen between it and hydrotheca clearly visible. Colonies dioecious; corbulae up to c. 12 per erect stem, commonly with some free ribs.

Hydranth: column short, cylindrical, when extended not projecting beyond hydrothecal rim; hypostome hemispherical, 90 x 90 μm ; tentacles 10, short, length extended 150 μm , width 12-15 μm , not tapering, tip rounded; held horizontal to 45° above, slightly down-curved; only c. 12 axial endoderm cells per tentacle; nematocysts inconspicuous (Roscoff, 1982; Cornelius, in prep. 1).

Reproductive season.— June-September at Roscoff (Teissier, 1965). In female corbulae the first rib is commonly free whereas the following ones are completely fused, normally overtopping the corbula considerably. In male corbulae, probably uniquely within the genus, the ribs stay completely unfused even in the mature state (although they form a basket). This was established in the samples from Schull, SW Ireland.

Habitat and ecology.— Recorded from depths of: 55 m, Mull, W Scotland; 20-40 m, Irish Sea; elsewhere c. 10-84 m (Svoboda, 1979). On rocks and boulders, 20-40 m in Irish Sea (K. Hiscock, in Svoboda); in Irish waters on silt-covered to clean rock and boulders in slight to moderate tidal streams, 20-50 m (B.E.P.); on pebbles and small rocks on sea bed off Roscoff, 60-80 m (Teissier, 1965; P.F.S.C.). Teissier's cited record on *Halidrys* in shallow water would need confirmation since in W Europe that substrate usually bears *A. pluma* and *A. tubiformis* and in the Roscoff area *A. tubulifera* is characteristic of deeper water.

Symbiotic algae.— None.

Distribution.— Recorded in NE Atlantic from cool and deep water, in the tropics (present material) rising to shallower depths in higher, temperate latitudes. Reaching northern limit in British Isles, northernmost record perhaps being Oban (Hincks, 1868). Published records from Connemara (type material), Irish Sea (Svoboda, 1979), Cornwall (Hincks, 1861, 1868), Plymouth (Svoboda), Lundy I & Scilly Is (present material). The BMNH collection includes specimens from Mull of Kintyre (1882.2.29.14) and Loch Lorn (W Scotland), Port Erin (Isle of Man), (1961.11.4.128) and the Scilly Is (1966.10.28.4) where recorded as widespread (Robins, 1969; present material). Occurs all round coasts of Ireland (B.E.P., unpublished). Elsewhere, reported from the Mediterranean only twice (Alboran, S Spain, Svoboda, 1979, and E Morocco; see Material section); in E Atlantic from Guinea Bissau (present material; also Gili, Vervoort & Pagès, 1989), Cape Verdes to Irish Sea; W to Azores (P.F.S.C.); also Mo-

rocco (Patrity, 1970). Common off Brittany coast (Teissier, 1965; Fey, 1969; Castric & Michel, 1982; P.F.S.C.).

Remarks.— The dubious 'Algoa Bay' material listed above is one of several unsubstantiated South African hydroid records based on nineteenth century George Busk material. Most were regarded suspect by Millard (1975: 260-261, 305, 313, 320, 416). The identity of the *A. tubulifera* specimen is not in doubt but the species has not again been reported from Southern Africa. However, as Gili, Vervoort & Pagès (1989) pointed out, the finding of the species along the coast of Guinea Bissau suggests that the Busk locality might after all prove correct.

Hincks (1868: 189) mentioned bifid colonies from Oban, from 30-40 m, but his material from there preserved in the BMNH (listed above) is not bifid and we cannot confirm his observation that such colonies occur in this species (but see below). It might be relevant that *A. acacia*, then unknown, has branching colonies and has now been recorded from nearby Loch Sunart (p. 14). But Hincks was already familiar with dichotomous colonies in *A. pluma* and would seem unlikely not to have noticed *A. acacia* material as distinct. His material may be the only 'dichotomous' colonies so far validly recorded in *A. tubulifera*.

J. S. Ryland showed P.F.S.C. a dense clump of some 20 cormoids of *Aglaophenia tubulifera* collected from the strand line at Oxwich Bay, S Wales, in which one caulus was forked. This seems quite exceptional, and possibly arose through damage to the primary rachis rather than to a 'genuine' branching as implied by Hincks' report.

The identity of the Linnean *Aglaophenia* specimens

The collection of hydroids once belonging to Linnaeus and now kept by the Linnean Society of London was catalogued by Savage (1945). Three of the herbarium sheets, numbered 1298.11-13, were both named by Linnaeus and listed by Savage as '*Sertularia pluma*' and in fact bear *Aglaophenia* material. The specimens are likely to have been collected by John Ellis (?1710-1776) from SE England but almost certainly did not reach Linnaeus until after 1758 (Cornelius, 1979: 309). Ellis was an accurate observer who wrote the first illustrated accounts of hydroids and other 'zoophyte' groups. He collected widely in SE England but also received material from elsewhere in the U.K. and overseas (Cornelius & Wells, 1988).

Linnaeus (1758: 811), when introducing the name of the nominal species *Sertularia pluma*, based his description largely on the illustrations of Ellis (1755: pl. 7 figs B, b) and probably not on specimens (Cornelius, 1979, loc. cit.; Cornelius & Wells, 1988). Hence any surviving Ellis material of *Aglaophenia* might be eligible for typification.

However, although the specimens now in the Linnean collection most likely came from Ellis, we have no evidence that Ellis saw them before he prepared his 1755 book. There is a strong possibility that Ellis collected material for Linnaeus other than his type material. Ellis may well have kept his type material separate since many important specimens were known to be in his collection when it was eventually sold in 1786 (Cornelius & Wells, 1988). Thus it seems improbable that Ellis would have sent all his original material to Linnaeus. Hence we assume that the London Linnean *Sertularia pluma* material is not in any sense type, and conclude that Svoboda's (1979) designation of one of the specimens as 'lectotype' of *A. pluma* is in-

valid. Newly collected material of *A. pluma* sensu stricto is designated neotype herein (p. 30).

However, there is some interest in all of the c. 250-year-old material on these herbarium sheets. It comprises 6 colonies on the 3 sheets; and in addition 4 microslide preparations of the material expertly made during the present study by our late colleague and friend Reginald H. Harris, formerly Chief Histologist in the Department of Zoology, BMNH. The sheets actually bear three species of *Aglaophenia* and we identify them as follows:

Sheet 1298.11: Four colonies, all probably *A. pluma*. Hydrocladial fragments from two of the colonies are preserved as two microslide preparations.

Sheet 1298.12: A single colony of *A. kirchenpaueri*. The characteristic intrahydrothecal septum is distinctly visible. There is a single microslide preparation of hydrocladial fragments.

Sheet 1298.13: A single dichotomously branched colony of *A. parvula* on an algal substrate. Although the material is not sufficiently well preserved for the diagnostic features of the hydrothecal rim to be easily seen, A.S. and P.F.S.C. jointly examined the single microslide preparation of hydrocladial fragments of the material and in a region of one fragment discerned the characteristic 'additional' cusp. In addition, the hydrothecae are much smaller than in *A. pluma*.

This material, almost certainly from Ellis, provides the earliest records in the British Isles of *A. parvula* by about 250 years (p. 28); of *A. kirchenpaueri* by about 80 years (p. 21); and of the better known *A. pluma* by several score years.

It is noteworthy that in the mid-eighteenth century Ellis was apparently able to collect these species from British waters, probably from SE England. Published records and old collections jointly show that many hydroid species that are limital within the British Isles have advanced or retreated northwards (depending on whether they are 'southerly' or 'northerly' members of the British fauna) during the past 150 years (P.F.S.C., unpublished); and certain cnidarian species formerly regarded as 'Lusitanian' have recently been recorded in British waters (Picton, 1985; Picton & Manuel, 1985; see also Cornelius, 1979: 306, and Cornelius, 1982: 113-115, for parallel cases). It is plausible that *Aglaophenia kirchenpaueri* and *A. parvula*, only recently recognized as British (along with *A. acacia*), were absent from British waters during part of the cooler intervening period: but we have not evaluated this. The question is mentioned also under *A. kirchenpaueri* (p. 21).

The coincidence that each of the three Linnean herbarium sheets bears a distinct species of *Aglaophenia* is remarkable. We have not pursued the possibility that Ellis might himself have suspected that the species were distinct. Not all the Ellis correspondence and manuscripts have been adequately studied (Cornelius & Wells, 1988) and an explanation of the coincidence might still be found.

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Table 1. Major identification features of the European and Mediterranean *Aglaophenia* species. Only the first five species have been reliably recorded from the British Isles. See also the text (pp. 10-13).

	Colony organization			Colour of living tissues*			Hydrotheca	
	No. of plumes per erect shoot	Branching pattern	Stem	Hydrocladium	Corbula	Prominent internal septem	Length: breadth at rim	Second pair cusps bifid
<i>A. acacia</i>	1-many	Trifid or unbranched	Brown	White	White	-	>1.8-2.0	No
<i>A. kirchsteuerei</i>	1	Unbranched	Brown, yellow in Adriatic	Brown, yellow in Adriatic	Brown, yellow in Adriatic	Thickened, recurved (fig. 4)	1-1.3	No
<i>A. parvula</i>	1-many	Unbranched/dichotomous	Dark brown	Translucent white	White	-	1.3-1.5	Yes usually
<i>A. piluma</i>	1-many	Unbranched/dichotomous	Brown	White	White	-	1.3-1.5, sometimes much more	No
<i>A. tubulifera</i>	1	Unbranched	Paler brown	Yellow, rarely white	Yellow, ripe gonophores white	-	1.5-1.7	No
<i>A. elongata</i>	Many	Irregularly bifid	Brown with yellow tips	Yellow	Yellow to white	-	Usually >1.8	No
<i>A. harpago</i>	1	Unbranched	Brown*	Brown*	Brown*	-	Usually >1.8, -1.4 W Mediterr.	No
<i>A. lophocarpa</i>	1	Unbranched	Brown	White	White	-	1.7-2.1	No
<i>A. octodonta</i>	1	Unbranched	Brown	White	Male white, female yellow	Often thickened ridges straight	1.1-1.4	No
<i>A. picardi</i>	1	Unbranched	Brown	Translucent	Translucent white	-	c. 1.5, sometimes longer	No
<i>A. tubiformis</i>	1-many	Unbranched/dichotomous	Brown*	Light brown*	Brown*	-	1.5-2, sometimes less	No

*The coloration of stems, hydrocladia and corbulae is in most species due to brown pigment(s) in the perisarc, but where indicated by an asterisk it is predominantly due to zooxanthellae.

Table 1. Continued.

	Mesial nematotheca			Other character states				Spacing of hydrocladia on stem (see figs)
	Easily reaching to level of hydrothecal rim	Arising in proximal/ distal half of hydrotheca	Portion of inner side typically free	Zooxanthellae present/ absent (+/-)	Usual substrate association	Prosegment(s) present/ absent (+/-)	With hooked terminal stolon	
<i>A. acacia</i>	No	Central	0%	-	None	+	-	Close
<i>A. kirchenpaueri</i>	Rarely	Distal	20-50%	-	None	+	-	Close
<i>A. parvula</i>	Occasionally	Distal	15-30%	-	None	+	-	Close
<i>A. pluma</i>	No	Distal	5-35%	-	<i>Halidrys sitiquosa</i> , facultative	+	-	Close
<i>A. tubulifera</i>	Yes	Distal	25-30%	-	None	+	-	Very close
<i>A. elongata</i>	No	Proximal (distal in some)	0-10%	-	None	+	-	Wide
<i>A. harpago</i>	No	Distal	0-30%	+	Seagrasses, obligate	+	In summer, usually	Very wide, conspicuously alternate
<i>A. lophocarpa</i>	No	Distal	0-30%	-	None	+	-	Wide
<i>A. octodonta</i>	No	Distal	10-30%	-	None	+	-	Close
<i>A. picardi</i>	No	Distal	0-25%	-	None	-	-	Wide, conspicuously alternate
<i>A. tubiformis</i>	No	Distal	5-25%	+	Sargassaceae, obligate in N Adriatic	+	-	Wide, conspicuously alternate

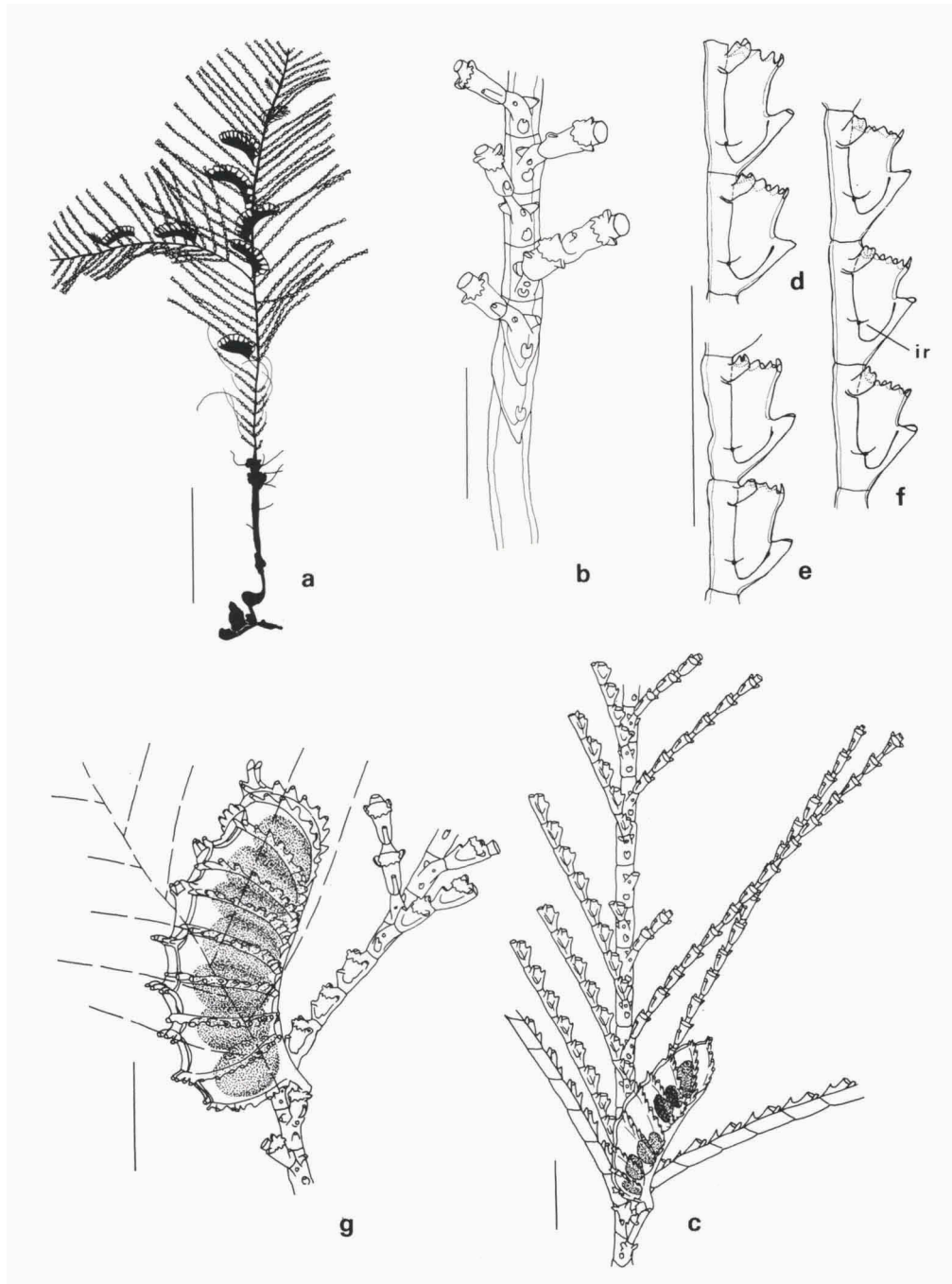


Fig. 1. *Aglaophenia acacia* Allman, Saltee I, Co Wexford, Ireland, BMNH 1985.8.1.1, 1a. a, whole cornus. b, hydrocaulus at region of basalmost hydrocladium. c, insertion of corbula on hydrocaulus. d-f, several cornidia. Note variation in level of origin of mesial nematotheca. g, corbula on hydrocaulus, with position of corresponding cornoid shown by broken lines. Note that pedicel turns corbula to overlie cornoid. (ir= intrathecal ridge). Scales (a) 10 mm, (b-g) 1 mm.

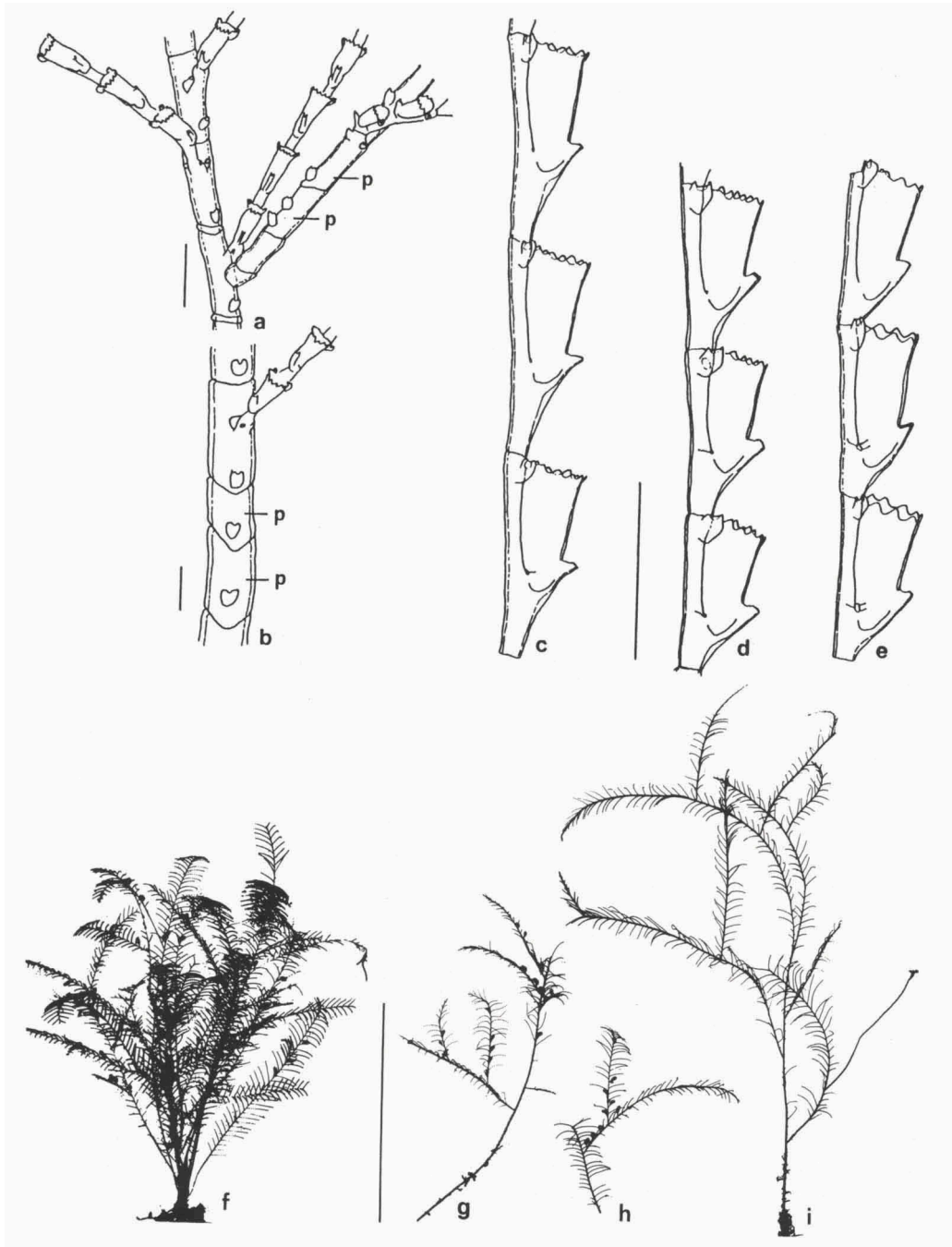


Fig. 2. *Aglaophenia elongata* Meneghini, a-b, from typically branched specimen, Banjole I., Rovinj, Yugoslavia, 30-40 m; redrawn after Svoboda (1979). a, with prosegments on ramus (diagnostic; p. 16). b, with prosegments on base of caulis. c, Scoglio Corbella, Capo Stella, Elba, Italy, 25-30 m; RMNH Coel. 25249. d, neotype specimen (see text). e, top of cladium, Haifa, Israel, 31 m, 32° 53' 30" N, 34° 59' E; Univ. Tel Aviv N.S. 20.254 (see text). f, complete cormus standing upright at slack water, Banjole I, 36 m; g, neotype cormoid, Banjole I, 35 m; h, fraction of neotype specimen with typical irregular branching pattern; i, infertile specimen collected in winter, Sv. Andrija, 42 m, RMNH Coel. 13576. Scales (a, b, c-e) 500 μ m, (f-i) 50 mm.

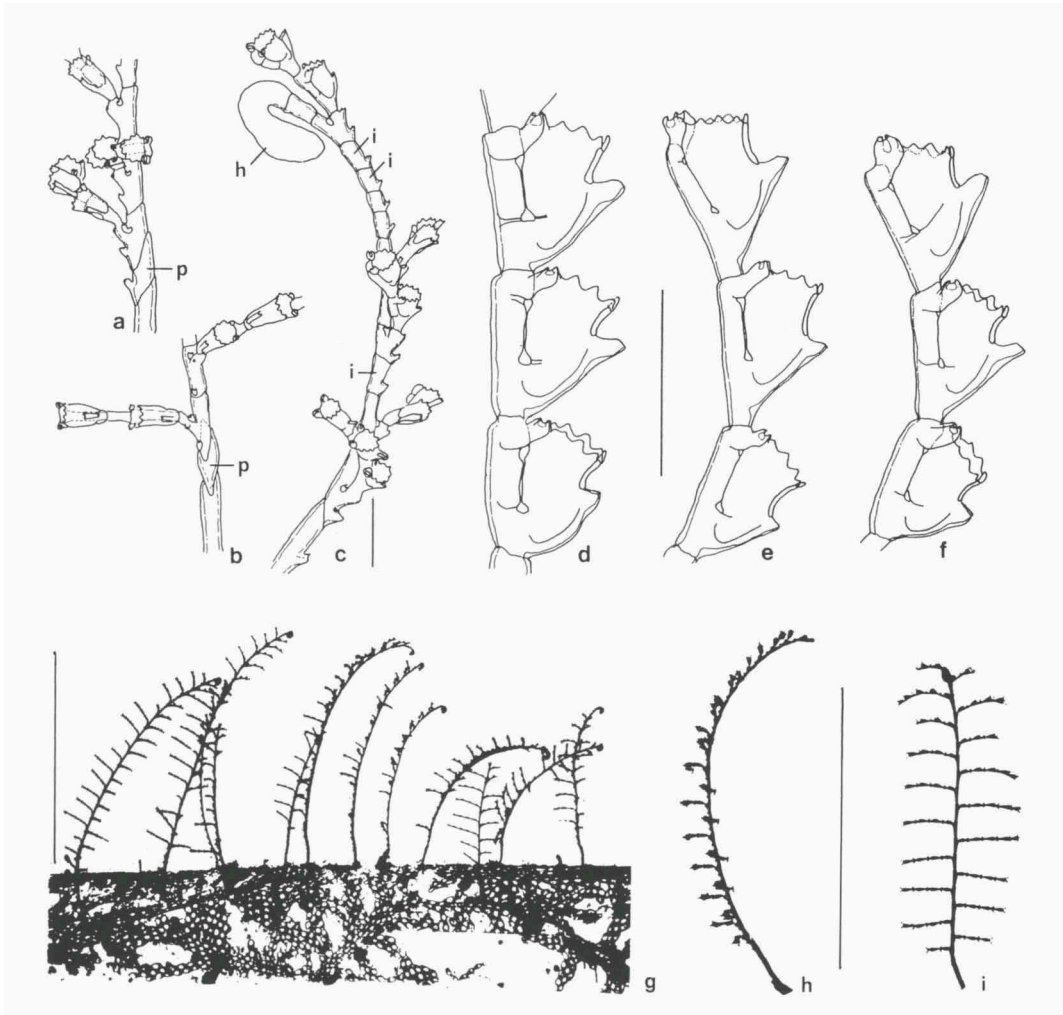


Fig. 3. *Aglaophenia harpago* von Schenck, a, basal region of caulus, lateral view, Figarola, Rovinj, Yugoslavia, 10 m, on *Cymodocea*; redrawn after Svoboda, 1979. b, same, frontal view. c, apical region with hook (h) and several intersegments (i), Zlarin, near Sibenik, Dalmatia, Yugoslavia, on *Posidonia*; RMNH Coel. 13519. e, complete cladium, Secca di Fonza, Capo Stella, Elba, Italy, 15-22 m, *Posidonia* field; RMNH Coel. 25039. f, complete cladium, Pta S. Pietro, Ischia, Italy, 6 m, *Posidonia* field; RMNH Coel. 25256. g, cormus growing on leaf of *Posidonia oceanica* (covered by Polyzoa); cormoids bending backwards at slack water, Prvic, Gulf of Rijeka, Yugoslavia, 15 m; h, lateral view of preserved cormoid, showing typically curved caulus of specimens growing in unidirectional current (flow from right to left), Cape Kriz, Rovinj, 10 m; i, frontal view of same, with cladia inserted at right angles, from *Cymodocea nodosa* leaves. Scales (a-c, d-f) 500 μ m, (g-i) 10 mm.

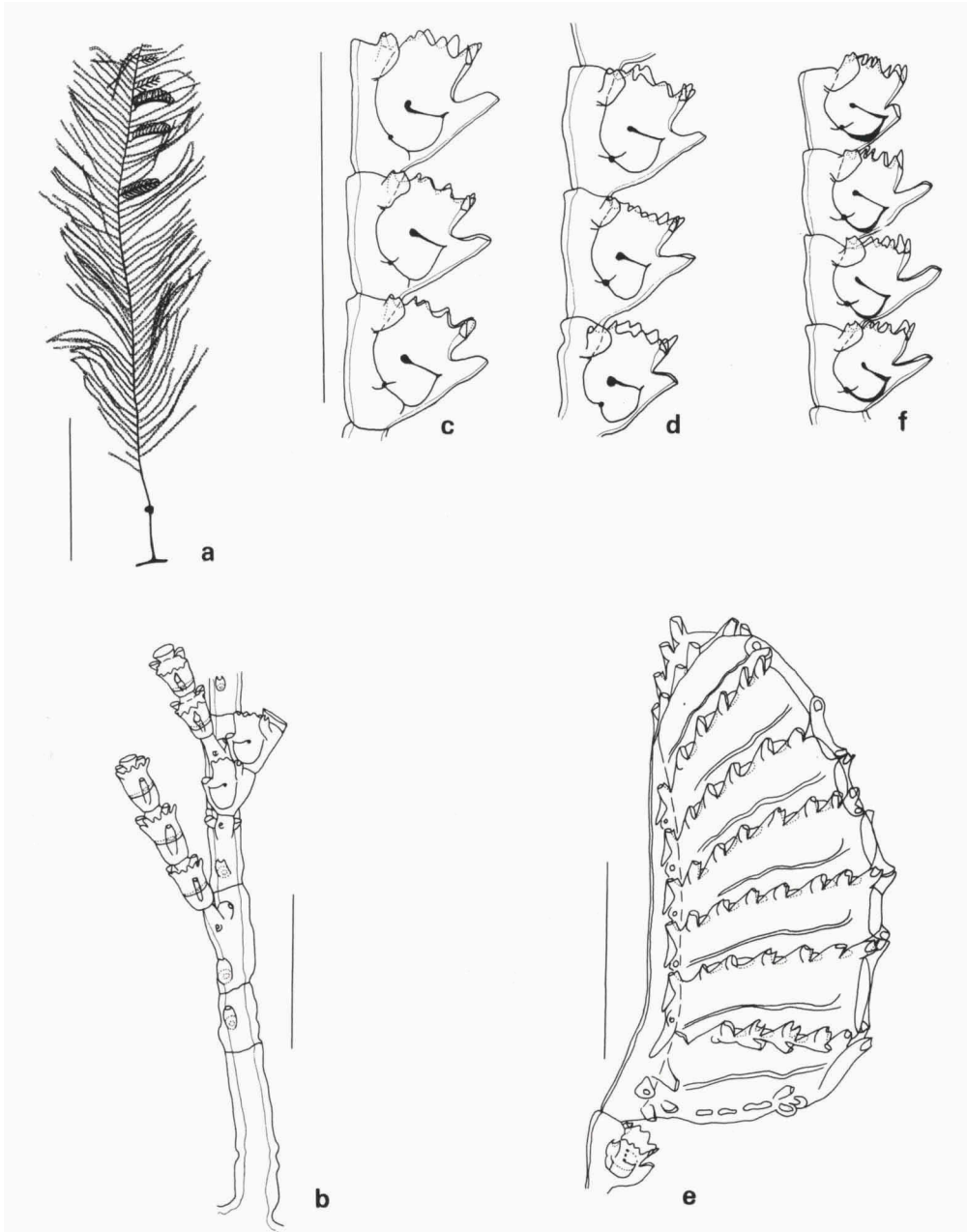


Fig. 4. *Aglaophenia kirchenpaueri* (Heller). a-e, Sherkin I, Co Cork, Ireland, 20 m; BMNH 1985.8.4.3, 3a. a, whole cormus. b, basal region of hydrocaulus, showing prosegment and bases of hydrocladia. c, end of cladium, and, d, its base. Note thickened septum originating from outer side. e, male corbula. f, no locality; Linnean herb., Linnean Soc., London, 1298.12. Four cormidia. See text (pp. 21, 39). Scales (a) 10 mm, (b-f) 1 mm.

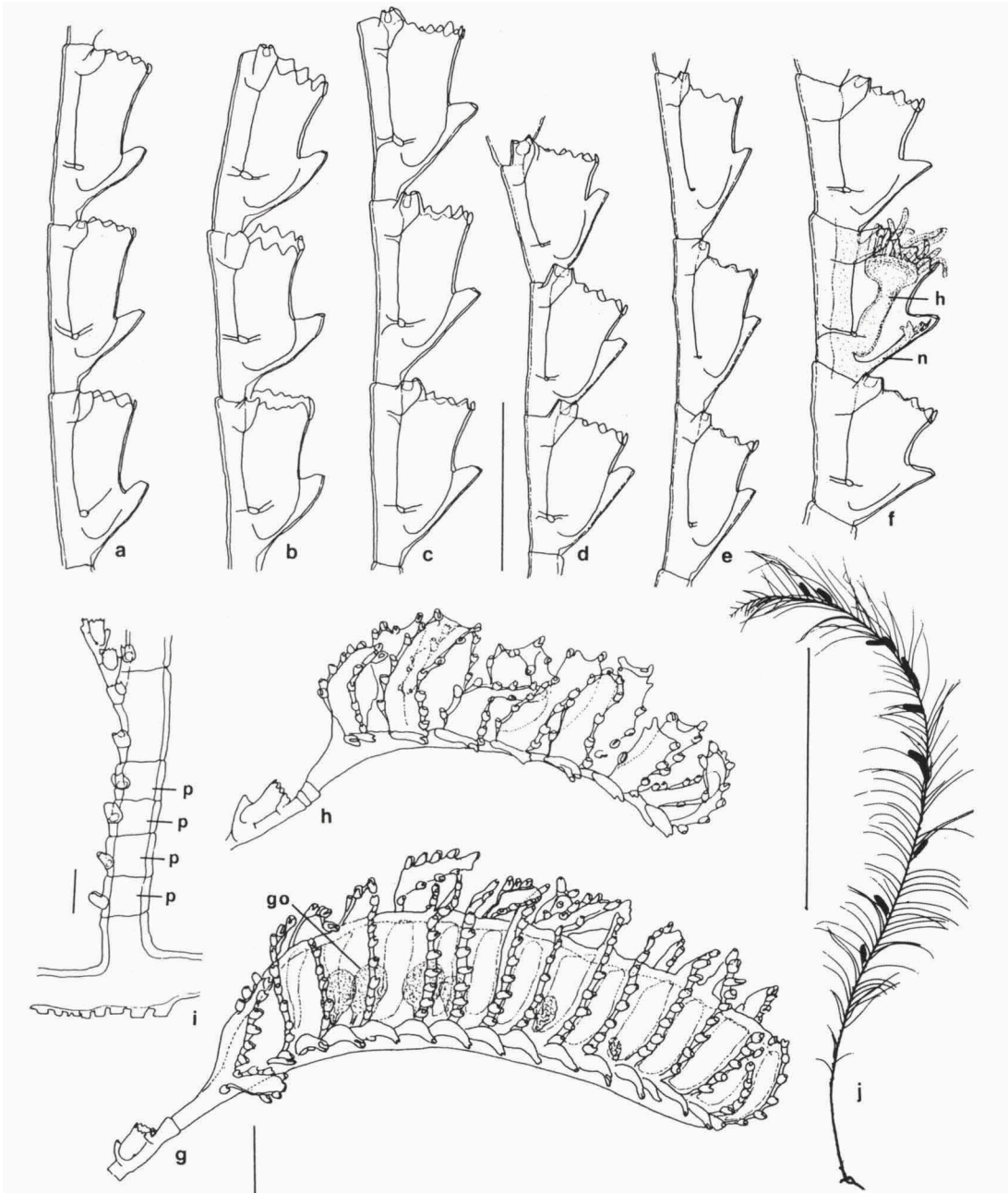


Fig. 5. *Aglaophenia lophocarpa* Allman. a, from microslide preparation of part of lectotype (see text). b, from microslide preparation of part of type of *A. apocarpa* Allman, 1877 (= *A. lophocarpa*); end of cladium (see text). c, end of cladium, Cap Creus, Costa Brava, Spain, 35 m; RMNH Coel. 25245. d, E side of Capo Caccia, Sardinia, Italy, 6 m, from wave-sheltered cave entrance; RMNH Coel. 25246 (= BMNH 1988.4.6.18). e, Isola Corbella, Capo Stella, Elba, Italy, 50 m, in slight current; RMNH Coel. 25042. f, Ganzirri, Strait of Messina, Sicily, Italy, 40-45 m, in strong tidal current; BMNH 1988.4.6.16. g, female corbula from lectotype (see text). h, fully-grown corbula with, abnormally, completely unfused ribs, from type specimen of *A. apocarpa* from the Caribbean which has all its corbulae abnormal in this way, but which may represent a male corbula as was established for *A. tubulifera* (see text). i, base of cormoid with 4 prosegments, Grosseto, Italy; RMNH Coel. 13545; redrawn after Svoboda, 1979. j, cormoid from area with low current speed, Portofino, Gulf of Genova, Italy, 50 m. (go= gonotheca; h= hydranth; n= nematophore; p= prosegment.) Scales (a-f, g-h, i) = 500 μ m, (j) 50 mm.

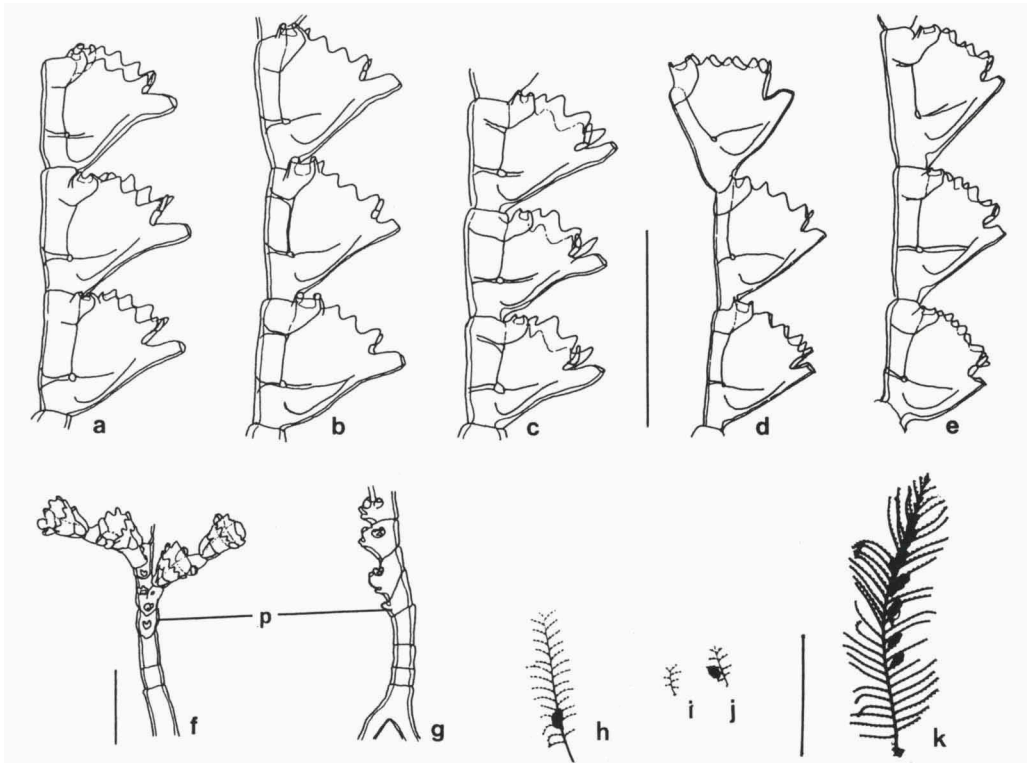


Fig. 6. *Aglaophenia octodonta* (Heller) a, end of cladium, 1 m, La Parra, Almeria, S Spain; RMNH Coel. 13520. b, S Pancrazio, Ischia, Italy, 10 m; RMNH Coel. 25263. c, specimen collected by M. Sars at Naples, Italy, off *Posidonia stipes* (see text). d, neotype; see text. e, basal region of cladium, Malinska, Krk, Yugoslavia, 1 m; RMNH Coel. 25256 (= BMNH 1988.4.6.19). f, lateral view of basal region of caulis. Banjole I., Rovinj, Yugoslavia. g, same as a, redrawn after Svoboda (1979). h, neotype specimen, Rovinj, 1 m; i-j, extremely wave-exposed dwarf specimens growing between branches of *Cystoseira spec.*, Banjole I., 0.5 m; k, large specimen from shipping channel, Lido di Albaroni, Venice, Italy, 1 m. (p= prosegment). Scales (a-e, f-g) 500 μ m, (h-k) 10 mm.

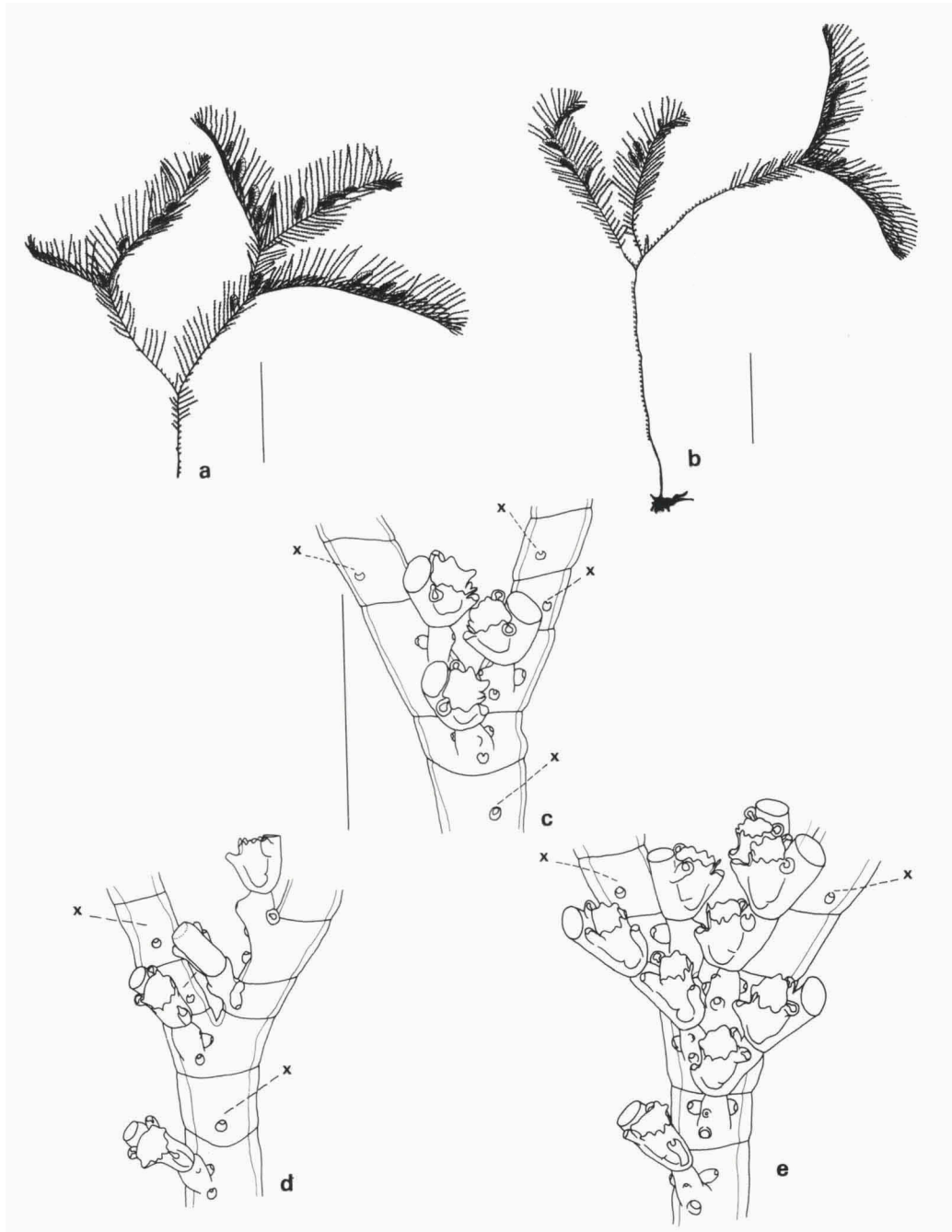


Fig. 7. *Aglaophenia parvula* Bale. Dichotomously branched cormi, Saltee I, Co Wexford, Ireland, 10 m; BMNH 1985.8.3.4, 4a. c-e, detail of forks. c, same locality, 10 m; BMNH 1985.8.3.2, 2a. d-e, Sherkin I, Co Cork, Ireland, 15 m; BMNH 1985.8.3.5, 5a. (x= base of corbula rachis.) Scales (a-b) 10 mm, (c-e) 1 mm.

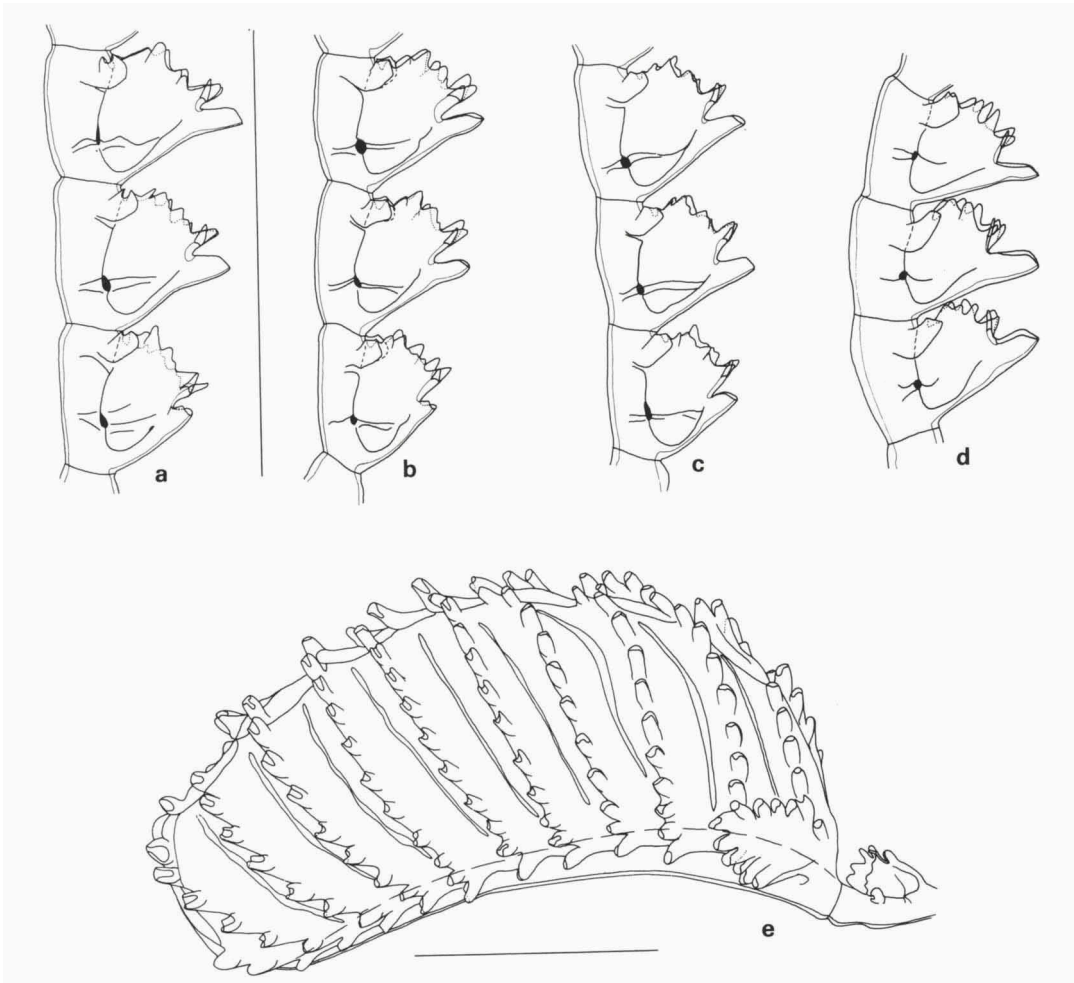


Fig. 8. *Aglaophenia parvula* Bale. a-c, branched form (concluded). Several cornidia. a, Saltee I, Co Wexford, Ireland, 10 m; BMNH 1985.8.3.2, 2a. b, same locality, 10 m; BMNH 1985.8.3.4, 4a. c, Sherkin I, Co Cork, Ireland, 15 m; BMNH 1985.8.3.5, 5a. d, Linnean herb., Linnean Soc., London, 1298.13 (p. 39). e, same specimen as (a), female corbula. Scales (a-d, e) 1 mm.

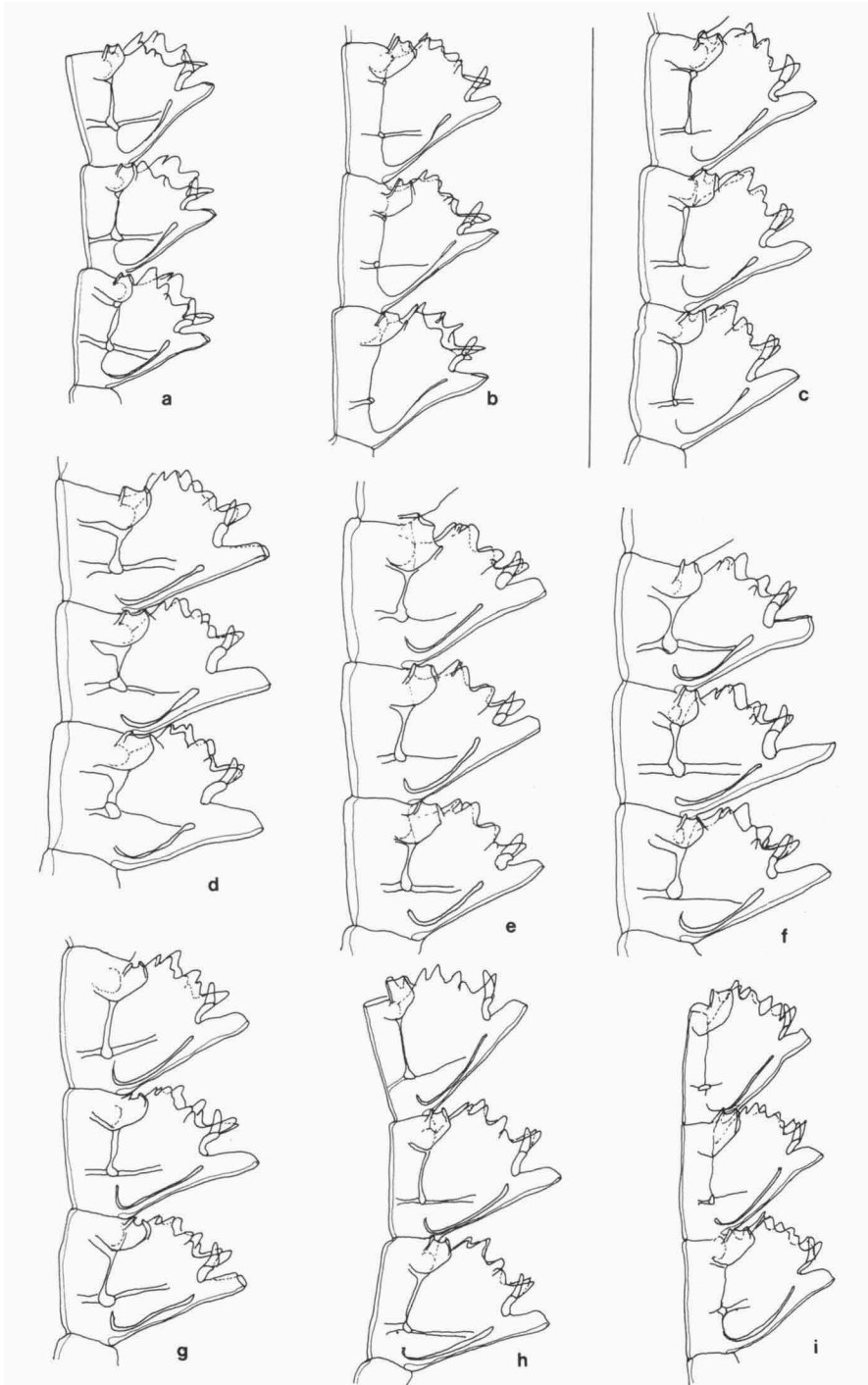


Fig. 9. *Aglaophenia parvula* Bale, lateral views of cormidia from various localities. a-c, Australia, d-f, southern Africa, g-i, Europe. a, part of unbranched specimen, Queenscliff, Melbourne, coll. Goldstein, ex W. M. Bale colln; lectotype (see text). b, part of bifid specimen, Port Phillip, New South Wales; coll. G. B. Wilson, ex W. M. Bale colln; Museum of New South Wales. c, part of bifid specimen, Gippsland coast, Victoria, coll. J. Watson. d, Port Natal, South Africa; coll. 'Mr Vahlberg', Stockholm Mus. colln. e, part of unbranched specimen, South Africa, coll. J. S. Ritchie; BMNH colln. f, part of bifid colony, Namibia, coll. J.-M. Gili. g, part of unbranched colony, Dingle Peninsula, Co Kerry, Ireland, coll. R. Bassindale; BMNH colln. h, part of dichotomous colony, Glénan Is, NW France, coll. A. Castric-Fey; BMNH colln. i, part of unbranched colony, Bilbao, Spain, coll. I. Isasi; BMNH colln. Scale (a-i) 1 mm.

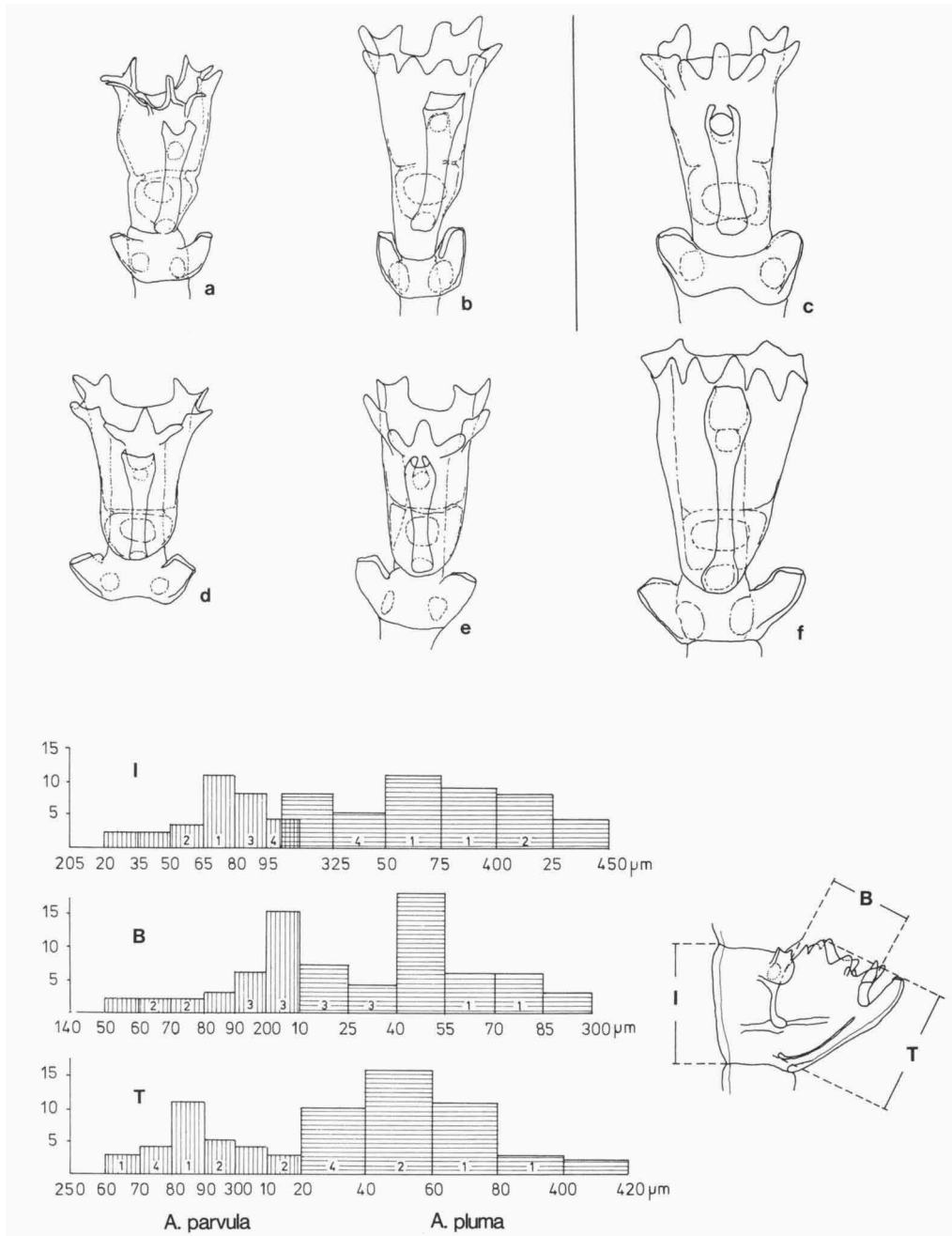


Fig. 10. *Aglaophenia parvula* Bale and *A. pluma* (Linnaeus). a-e, frontal views of cormidia of *Aglaophenia parvula*, lateral nematothecae omitted for clarity; f, same, *A. pluma*; below, biometric data. a, from specimen probably first dried then mounted in balsam, Queenscliff, Melbourne, ex W. M. Bale colln; Museum of New South Wales. Note 'additional' cusp on near edge of second paired cusp from front. b, Gippsland coast, Victoria, Australia, 12 m depth, 2 km offshore, coll. J. Watson. Note deep cleft between 'additional' cusp and main part of second one (cf. a). c, Port Natal, South Africa, coll. Vahlberg, (Continued on p. 58).

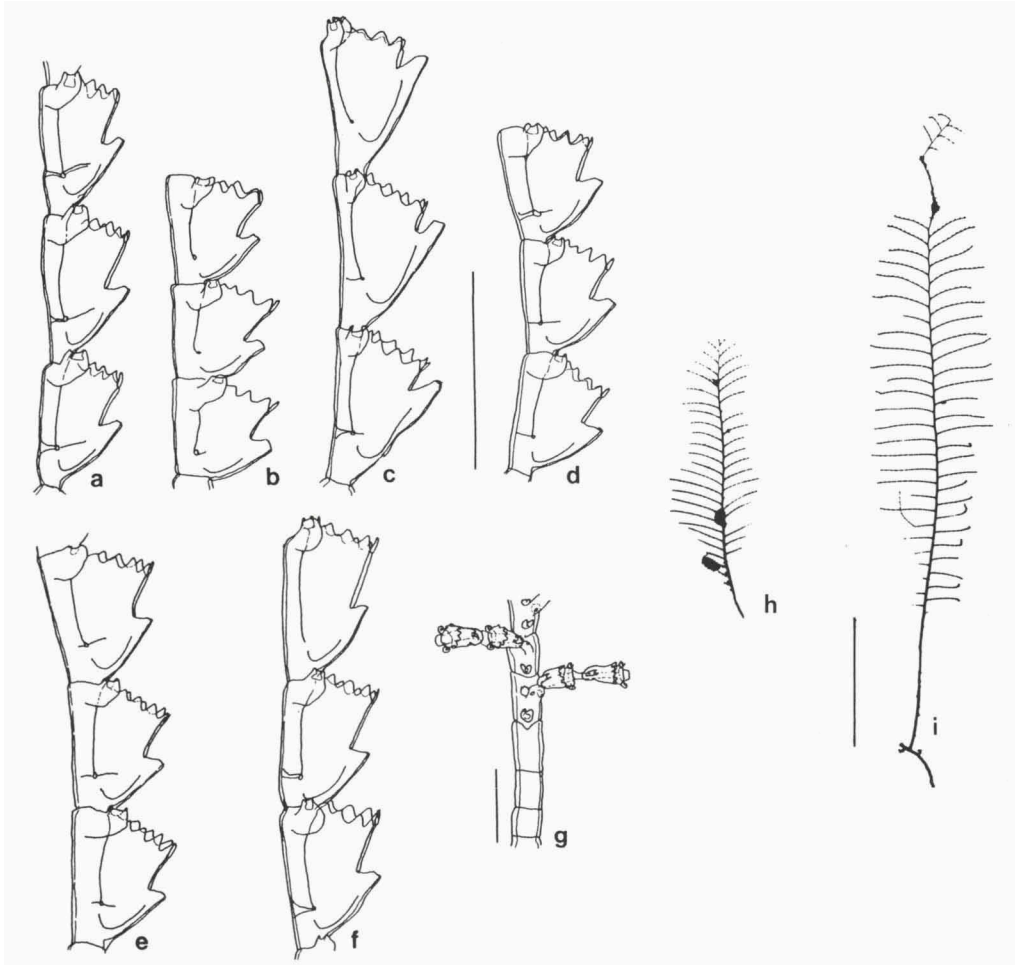


Fig. 11. *Aglaophenia picardi* Svoboda. a-f, portions of cladia. a, Punta de Taliarte, Gran Canaria, Canary Is, 1 m below MLTL; RMNH Coel. 25283. b, Ciervana, Bilbao, N Spain, 3 m; RMNH Coel. 25261. c, end of cladium, Isola Corbella, Capo Stella, Elba, Italy, 3 m; RMNH Coel. 25043. d, specimen coll. M. Sars, Naples, Italy, RMNH Coel. 13531 (see text). e, holotype, Rovinj, Yugoslavia, 2 m; RMNH Coel. 25292 (see text). f, Israel, 17 m; RMNH Coel. 25.237 (see text). g, basal region of caulus, Rovinj, Yugoslavia. Note absence of prosegment in this species. h, holotype specimen, Rovinj, 2 m; i, unusually long specimen from current-exposed cave bottom with tiny cormoid growing from apical stolon, Banjole I., Rovinj, 16 m. Note cormoid growing from apical stolon. Redrawn after Svoboda, 1979. Scales (a-f) 500 μ m, (h-i) 10 mm.

Fig. 10. Continued.

Stockholm Mus. colln. d, Plymouth, SW England, coll. A. M. Norman; BMNH colln. Note shallowness of 'additional' cusp. e, Dingle Peninsula, Co. Kerry, coll. R. Bassindale; BMNH colln. f, *A. pluma*, for comparison, 16 m, Lundy I, SW England, coll. B.E.P.; BMNH colln. Note absence of 'additional' cusp in this species. Scale (a-f) 500 μ m.

Below, size-classes of (I) internodal length of cormidium, (B) breadth of hydrotheca at rim, and (T) depth of hydrotheca, in *A. parvula* (vertical hatching) and *A. pluma* (horizontal hatching), data from various localities pooled. The small numbers within the blocks of the histogram represent the numbers of dichotomous colonies within each size class. Inset: distances measured.

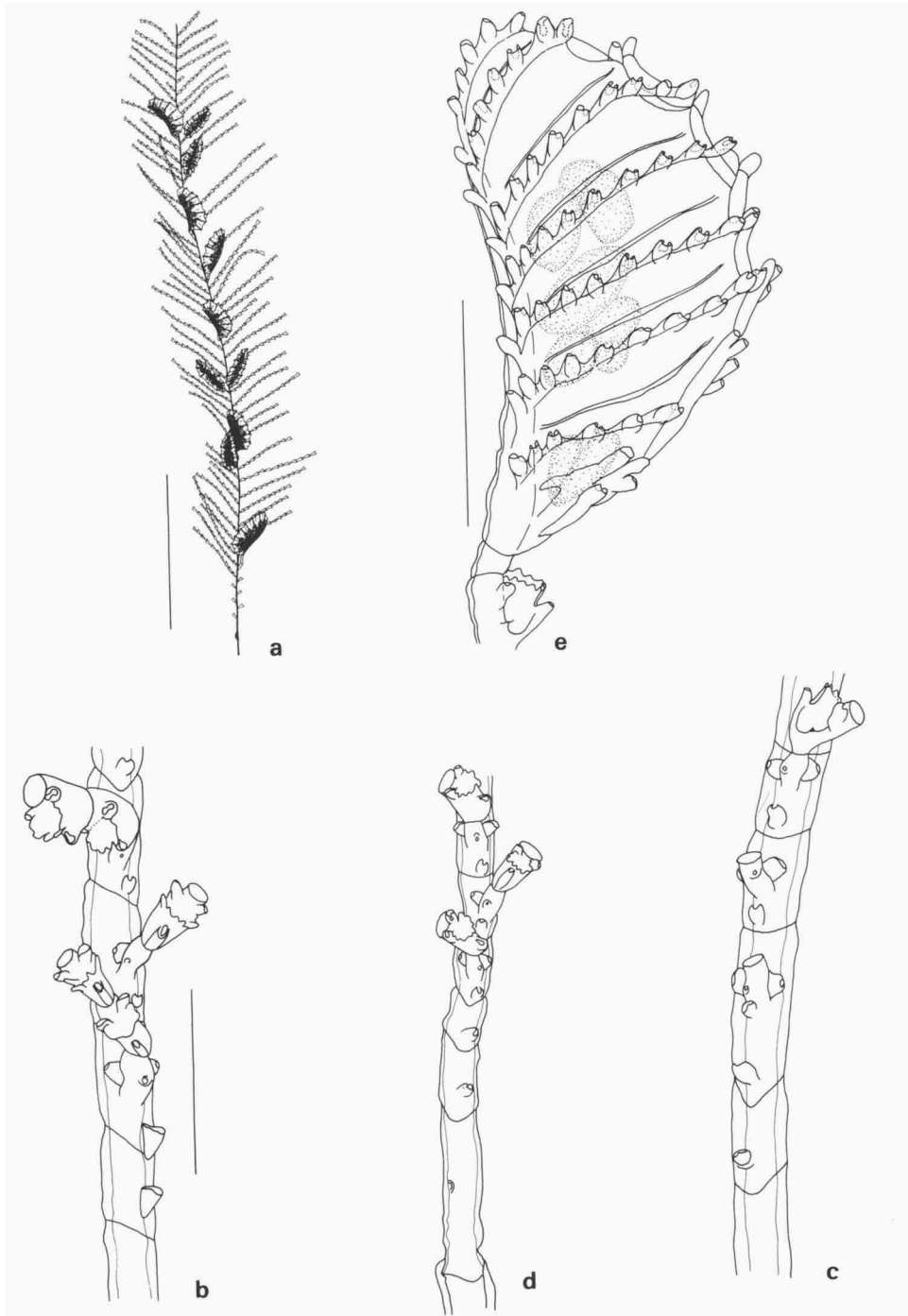


Fig. 12. *Aglaophenia pluma* (Linnaeus). From colonies with unbranched cauli. a, Whole cormus, Saltee I, Co Wexford, Ireland, 15 m; BMNH 1985.8.3.7, 7a. b-c, hydrocauline prosegments and (in b) origins of basalmost hydrocladia; Lundy I, SW England, 16 m; BMNH 1985.8.4.3, 3a. d, hydrocauline prosegments and origins of basalmost hydrocladia, Lundy I, 20 m; BMNH 1985.8.3.1, 1a. e, same, female corbula. Scales (a) 10 mm, (b-e) 1 mm.

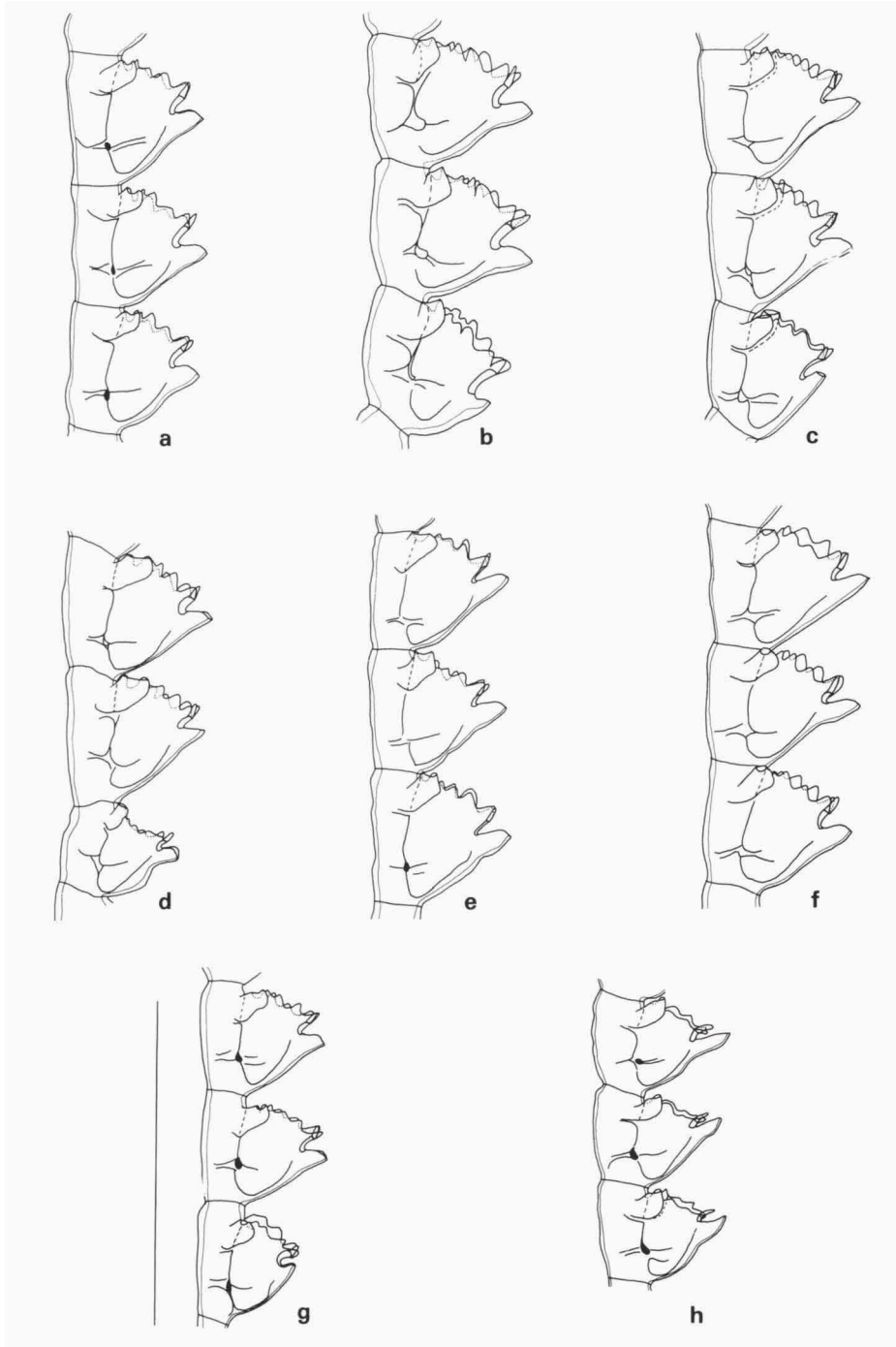


Fig. 13. *Aglaophenia pluma* (Linnaeus) and *A. parvula* Bale. a-g, *Aglaophenia pluma*. From unbranched specimens. Several cormidia. a, Lundy I, England, 16 m ; BMNH 1985.8.3.3, 3a. b, Saltee I, Co Wexford, Ireland, 8 m; BMNH 1985.8.3.9. c, same locality, 10 m; BMNH 1985.8.3.6, 6a. d, same locality, 15 m; BMNH 1985.8.3.7, 7a. e, part of neotype, Lundy I, England, 20 m; BMNH 1985.8.3.10, 10a. f, N Endskerd Rocks, Galway, Ireland, BMNH 1985.8.3.8, 8a. g, Lundy I, 20 m; BMNH 1985.8.3.1, 1a. h, *A. parvula* Linnean herb., Linnean Soc., London, 1298.11 (p. 38). Scale (a-h) 1 mm.

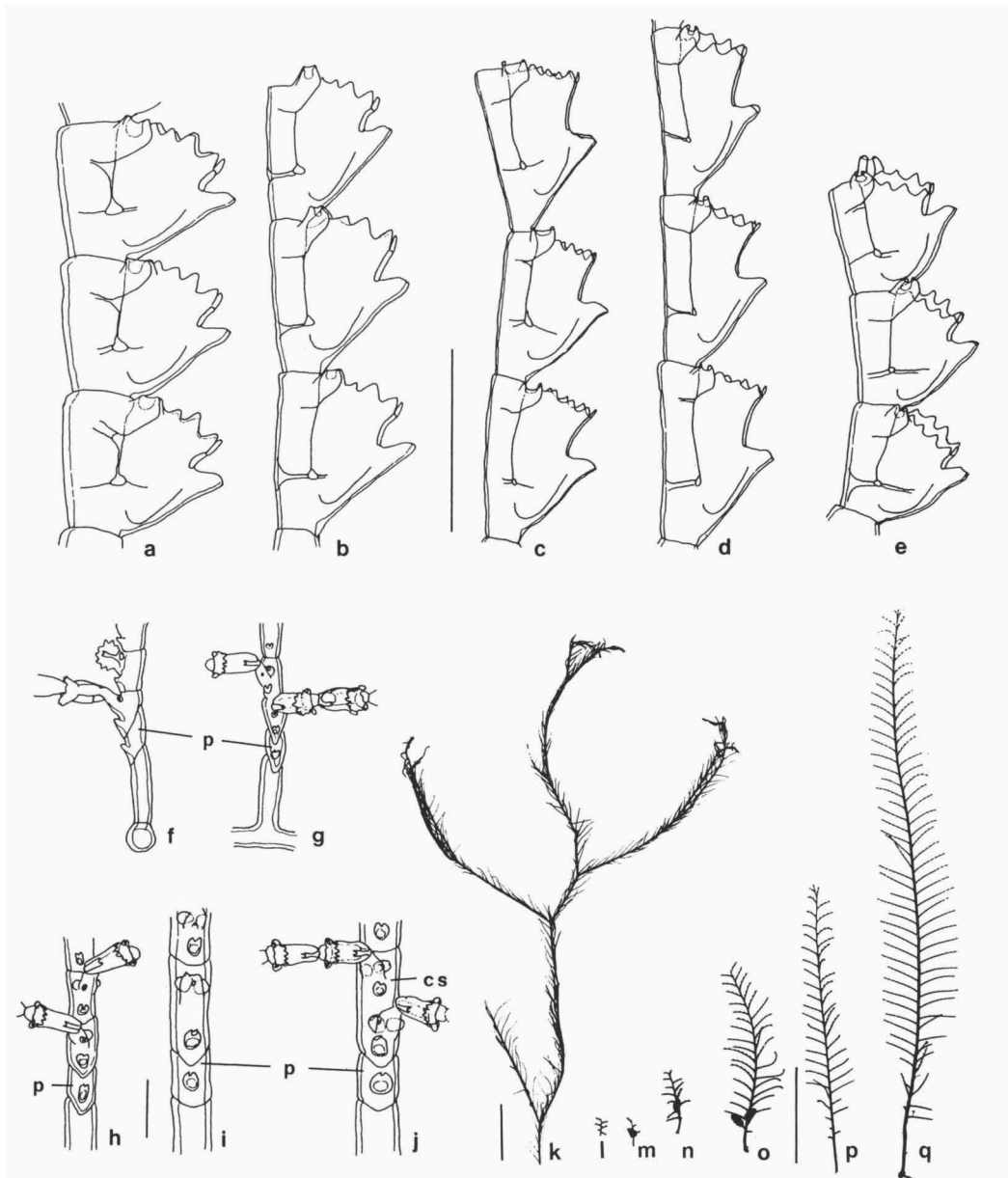


Fig. 14. *Aglaophenia tubiformis* Marktanner-Turneretscher. a-e, portions of cladia; f-g, basal regions of cauli; h-j, mid-regions of cauli. a-e, details in text; f-j, redrawn after Svoboda, 1979. a, Roscoff; RMNH Coel. 25268. b, distal region, N Spain; RMNH Coel. 25276. c, lectotype, Gulf of Rijeka, Yugoslavia, specimen dichotomously branched. d, distal region, dichotomous specimen, Gulf of Volos, Greece, 40 m; RMNH Coel. 13404. e, distal region, dichotomous specimen, Israel; Univ. Tel Aviv NS 20637, sample in RMNH Coel. 25208, ex slide 603. f-g, basal parts of dwarf specimens from *Cystoseira* on extremely exposed shore, Banjole I., Rovinj, Yugoslavia, 0.5 m. h, same, from 4 m depth; unbranched specimen. i, same, N side of Sv. Andrija, Rovinj, 4 m depth. j, same, but from unbranched specimen. k, lectotype specimen, Rijeka; l-m, extremely wave-exposed dwarf specimens growing between branches of *Cystoseira* spec. (compare with fig. 6 i-j), Banjole I.; n-q, size increase of specimens at gradually reducing current exposure from 2, 4, 7 and 20 m, Banjole I. Figs f-q after Svoboda, 1979. Scales (a-e, f-j) 500 μ m, (k-q) 10 mm. (cs= cauline segment; p= prosegment.)

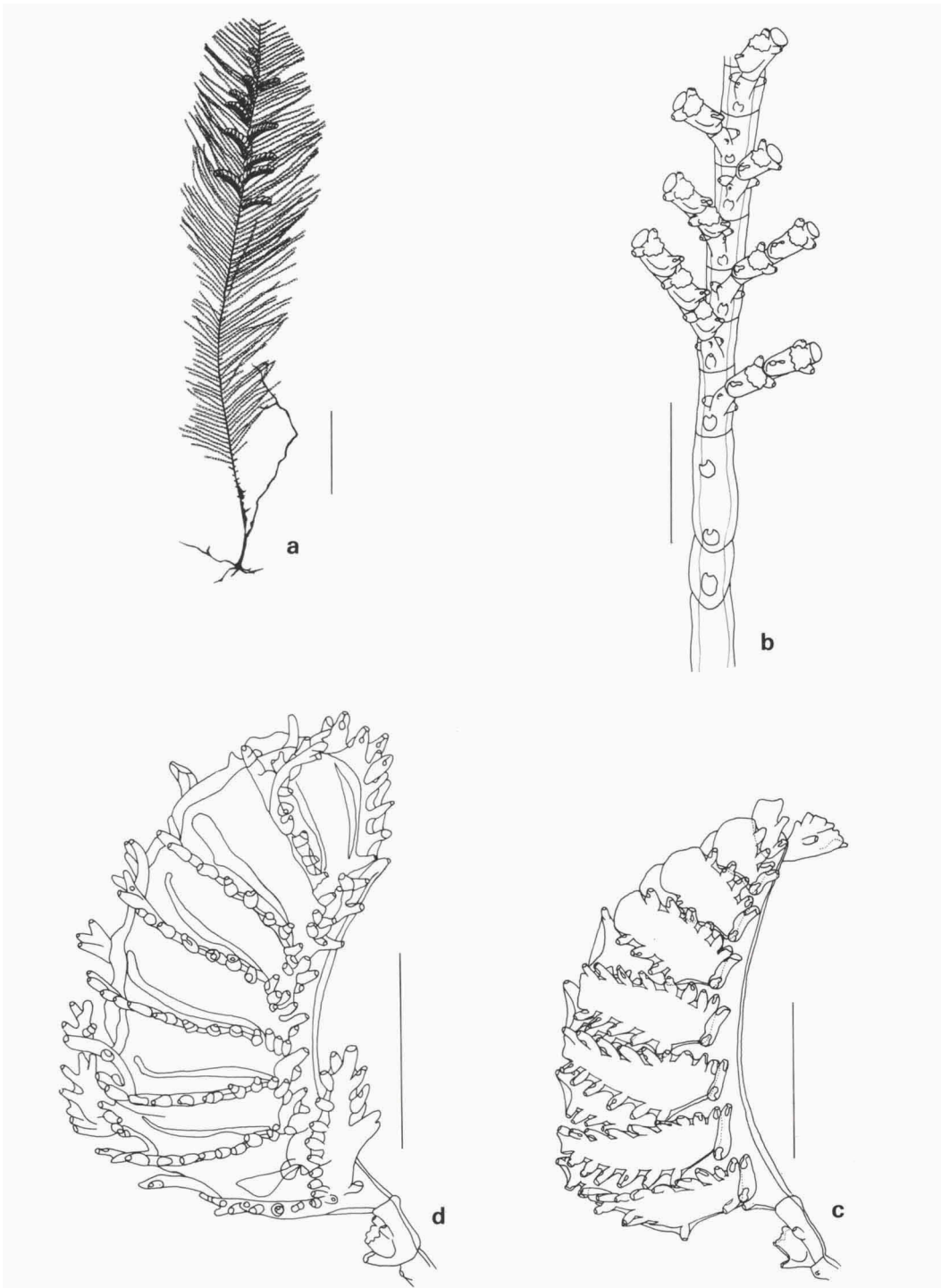


Fig. 15. *Aglaophenia tubulifera* (Hincks). a-c, Saltee I, Co Wexford, Ireland, 28 m, BMNH 1985.8.4.2, 2a. a, whole cormus. b, region of insertion of basalmost hydrocladia, including prosegments. c, male corbula. d, Lundy I, SW England, female corbula; redrawn after Svoboda (1979, fig. 16f). Note free proximal rib (corbulacosta). Scales (a) 10 mm, (b-d) 1 mm.

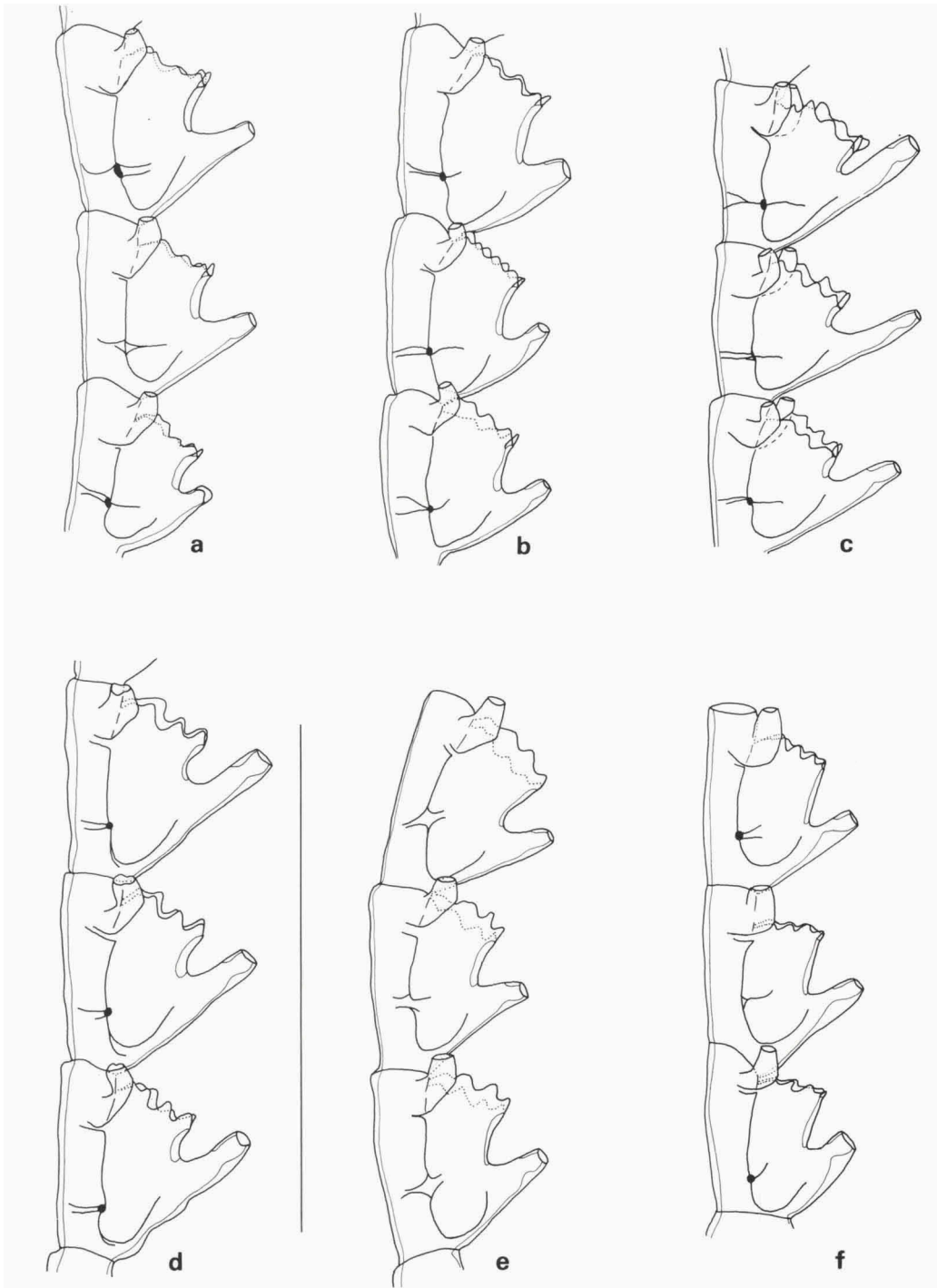


Fig. 16. *Aglaophenia tubulifera* (Hincks). a-f, several cormidia. Note range of variation, and subterminal thickening of mesial nematotheca. a, Sherkin I, Co Cork, Ireland; BMNH 1985.8.4.3, 3a. b, Loch Lorn, Scotland, '60-220 m', ex colln Sir John Murray, via J. Ritchie; BMNH 1888.6.9.18. c, Mull of Kintyre, Scotland, 120 m, ex colln Sir John Murray; BMNH 1888.2.29.14. d, Saltee I, Co Wexford, Ireland, 28 m; BMNH 1985.8.4.2, 2a. e, Strangford Lough, Co Down, Northern Ireland, 23 m; BMNH 1985.8.4.1, 1a. f, holotype, 'Cornwall' (see text). Scales (a-f) 1 mm.

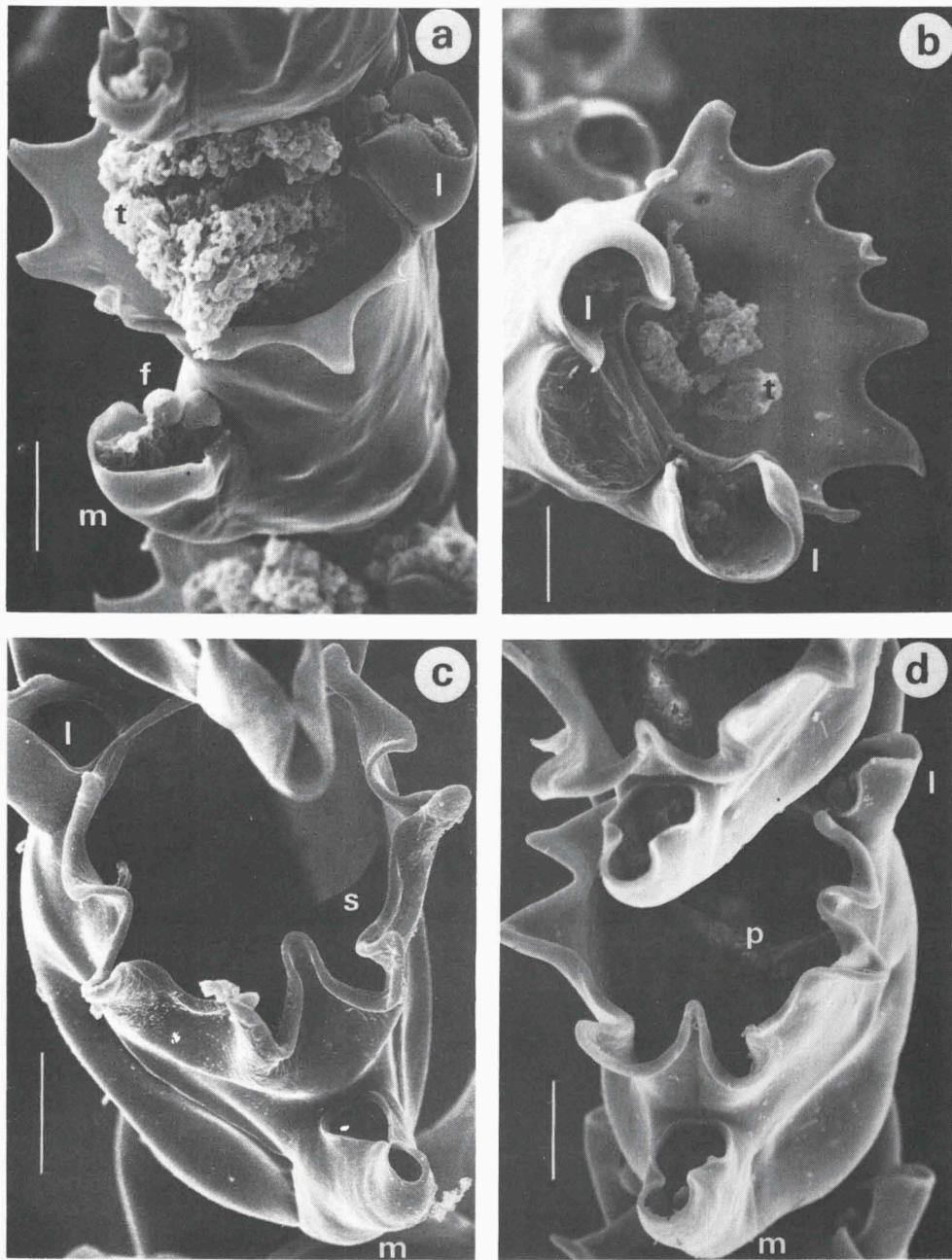


Fig. 17. Scanning electron micrographs of cormidia. a-b, *Aglaophenia acacia* Allman, c-d, *A. kirchenpaueri* (Heller). (f= foraminiferans; l= lateral nematotheca; m= mesial nematotheca; p= entrance to hydrothecal lumen beyond transverse septum; s= transverse septum; t= tentacle of hydranth). Scales (a-d) 25 μ m.

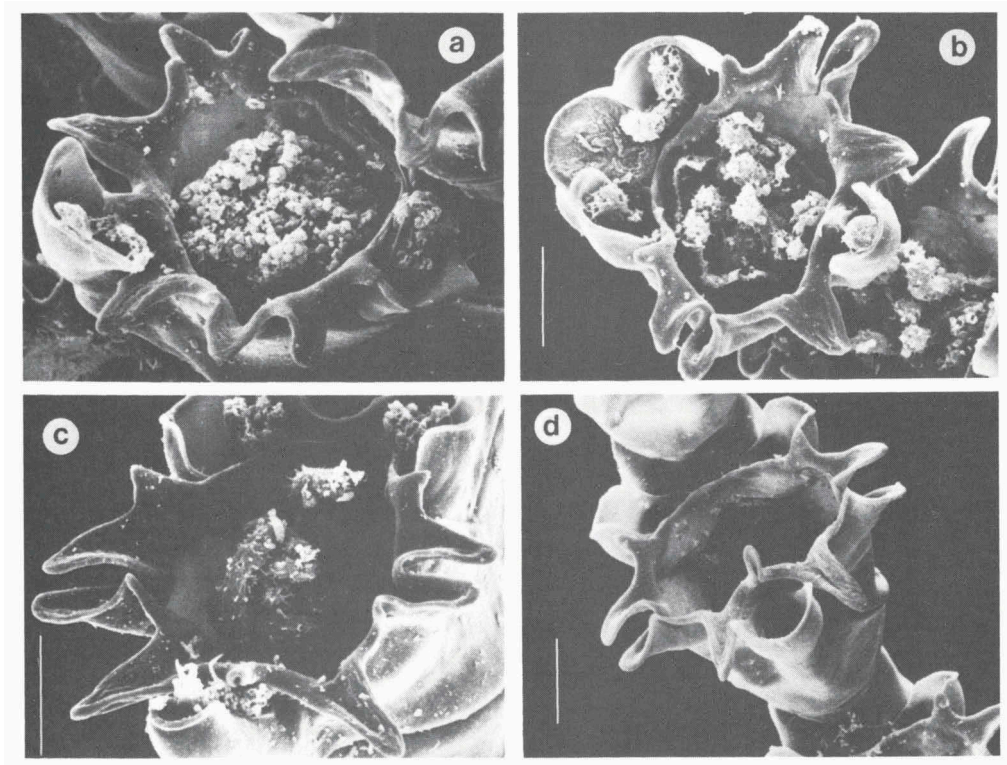


Fig. 18. *Aglaophenia parvula* Bale. Scanning electron micrographs of hydrothecal rims, critical-point dried material. a-b, southern Australia. c-d, Saltee I, SE Ireland. Note that second cusp and 'additional' cusp arising from it tend to be rolled longitudinally.

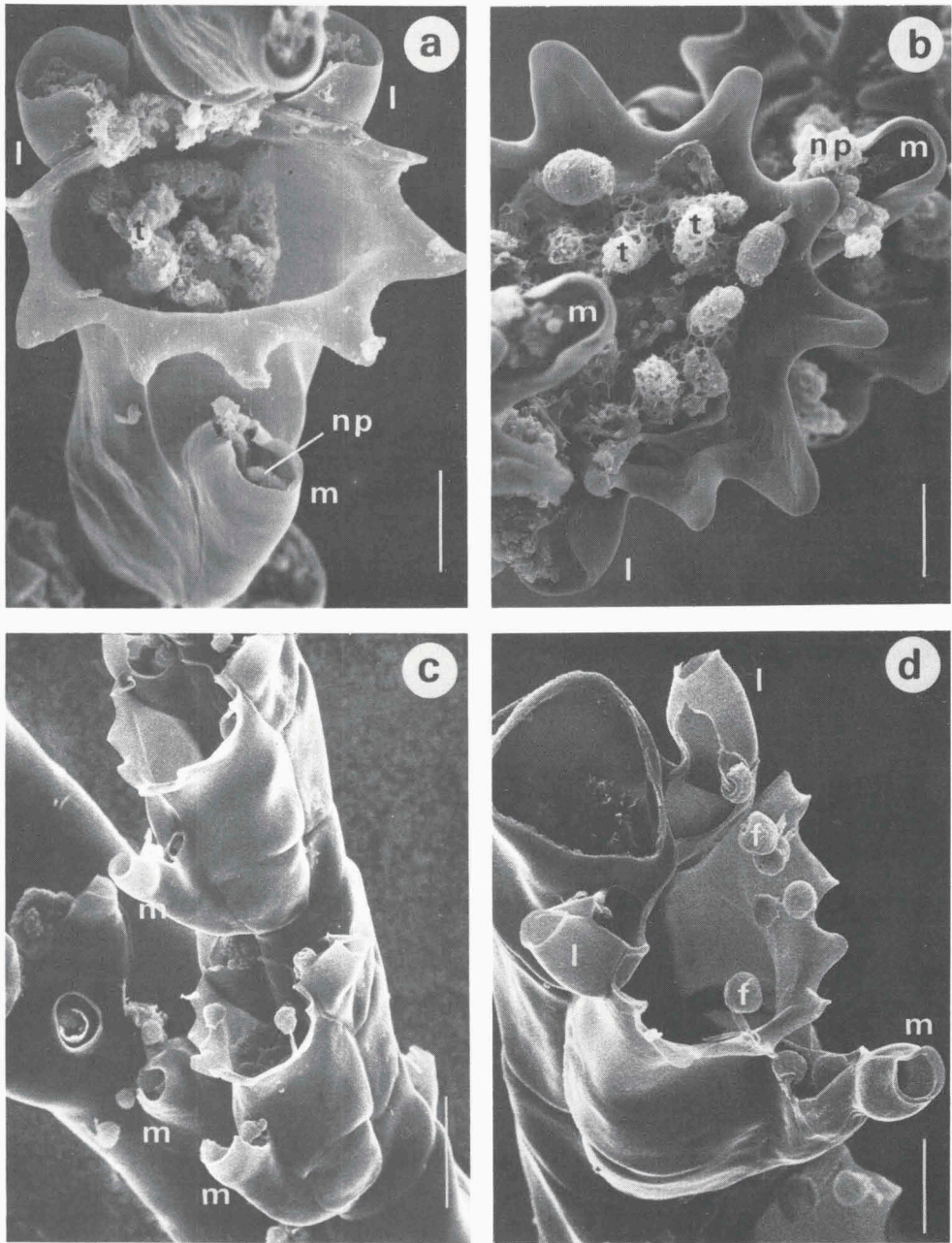


Fig. 19. Scanning electron micrographs of cormidia. a-b, *Aglaophenia pluma* (Linnaeus), c-d, *A. tubulifera* (Hincks). Note that in *A. tubulifera* the two sides of the elongate mesial nematotheca fuse in the midline. (cn= cnidostyle; st= sarcostyle; other labels as in fig. 17). Scales (a-b, d) 25 μ m, (c) 50 μ m.

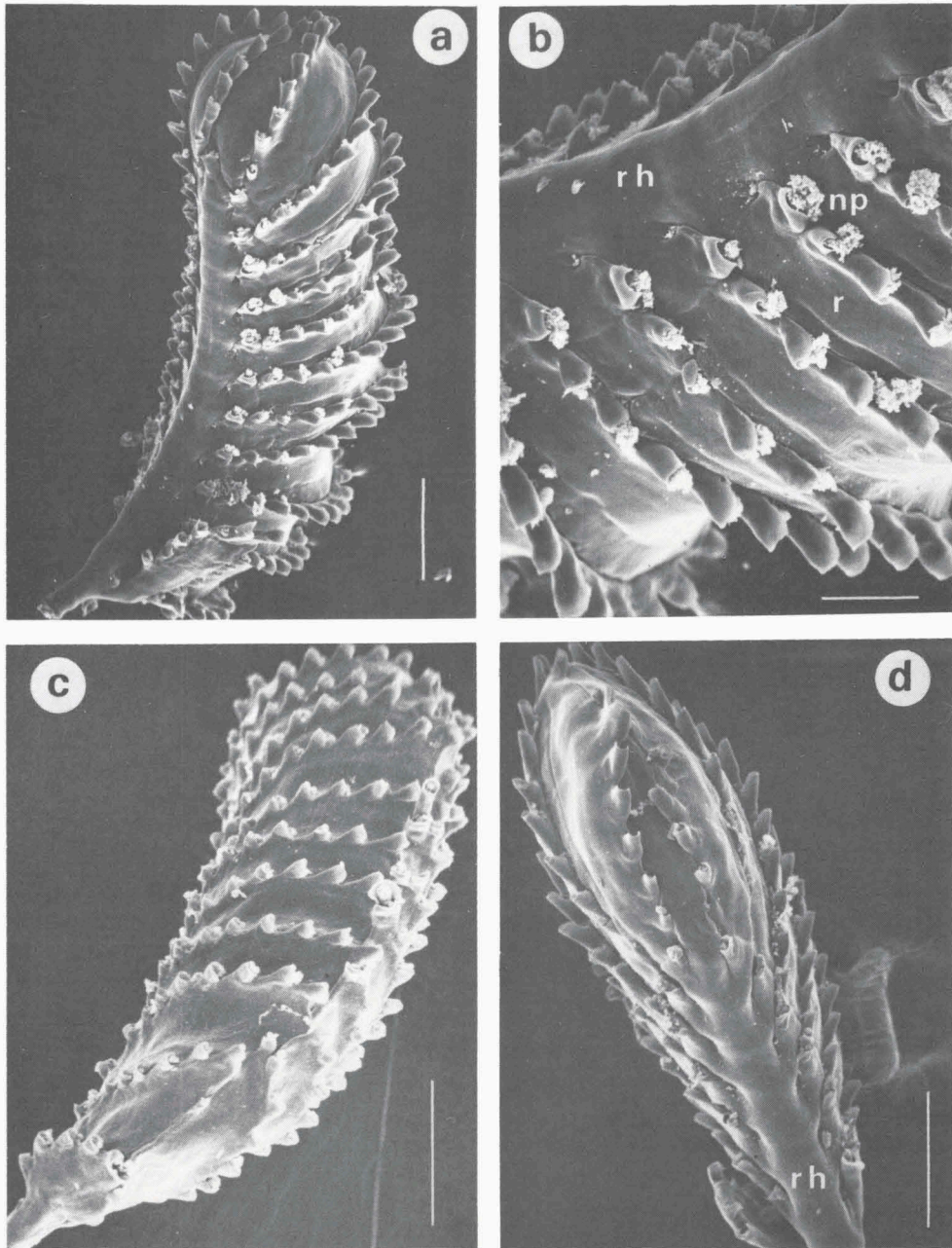


Fig. 20. Scanning electron micrographs of corbulae. a-b, *Aglaophenia acacia* Allman, c, *A. pluma* (Linnaeus), d, *A. kirchenpaueri* (Heller). (np= nematophore on rib (corbulacosta); r= rib; rh= rachis). Scales (a, c-d) 250 μ m, (b) 100 μ m.

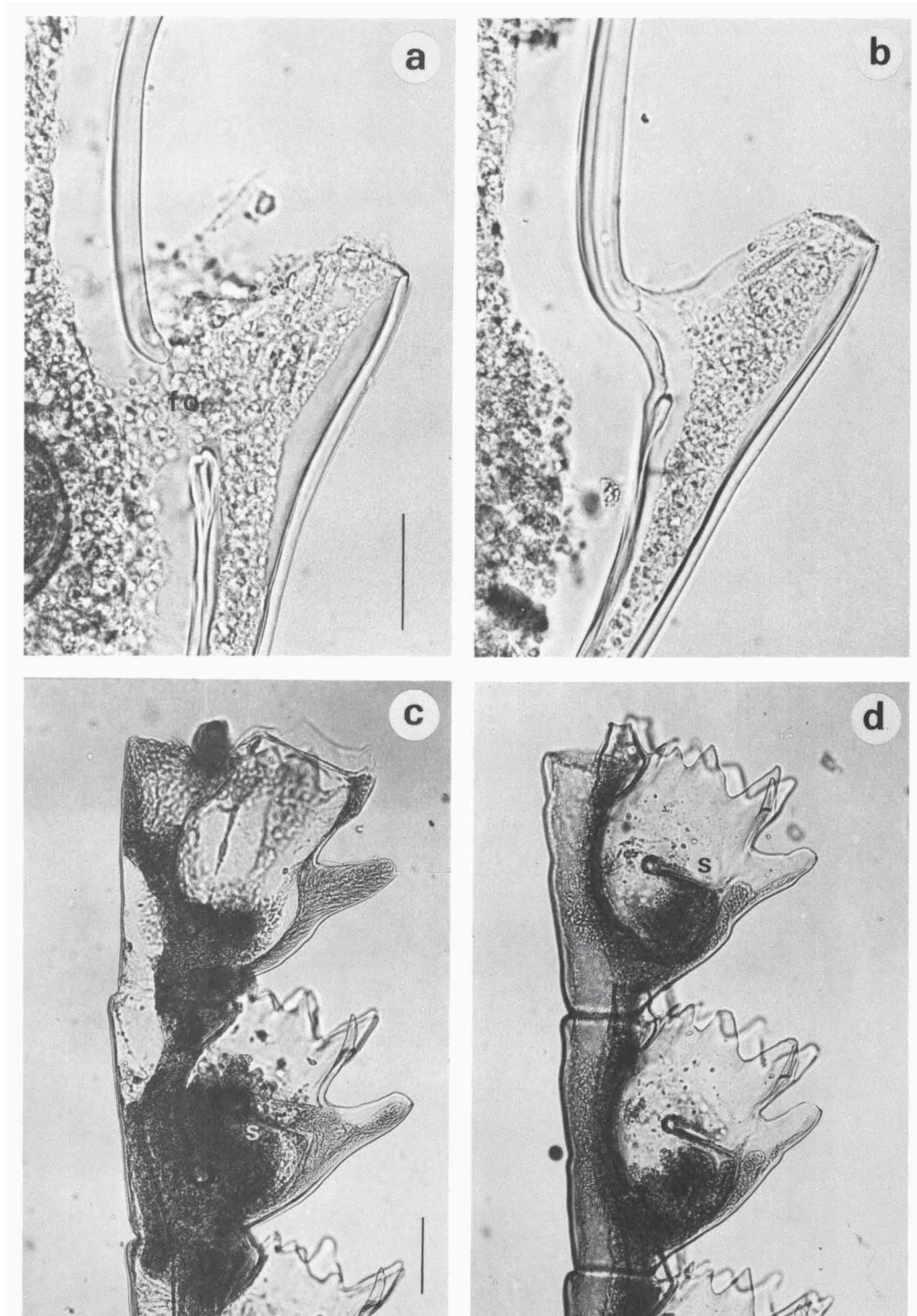


Fig. 21. *Aglaophenia acacia* Allman and *A. kirchenpaueri* (Heller). Transmitted light photomicrographs, preserved material. a-b, *Aglaophenia acacia*. Mesial nematothecae. a, Saltee I, Co Wexford, Ireland, 20 m; BMNH 1985.8.1.1, 1a. Foramen open. b, same, foramen closed by membrane. c-d, *A. kirchenpaueri* Lundy I, England, 20 m; BMNH 1985.8.2.1, 1a. cormidia showing intrahydrothecal septum characteristic of species: (c, upper) not yet formed, (c, lower) developing, (d) fully formed and thickened. (fo= foramen; s= intrahydrothecal septum.) Scales (a-b) 50 μ m, (c-d) 100 μ m.

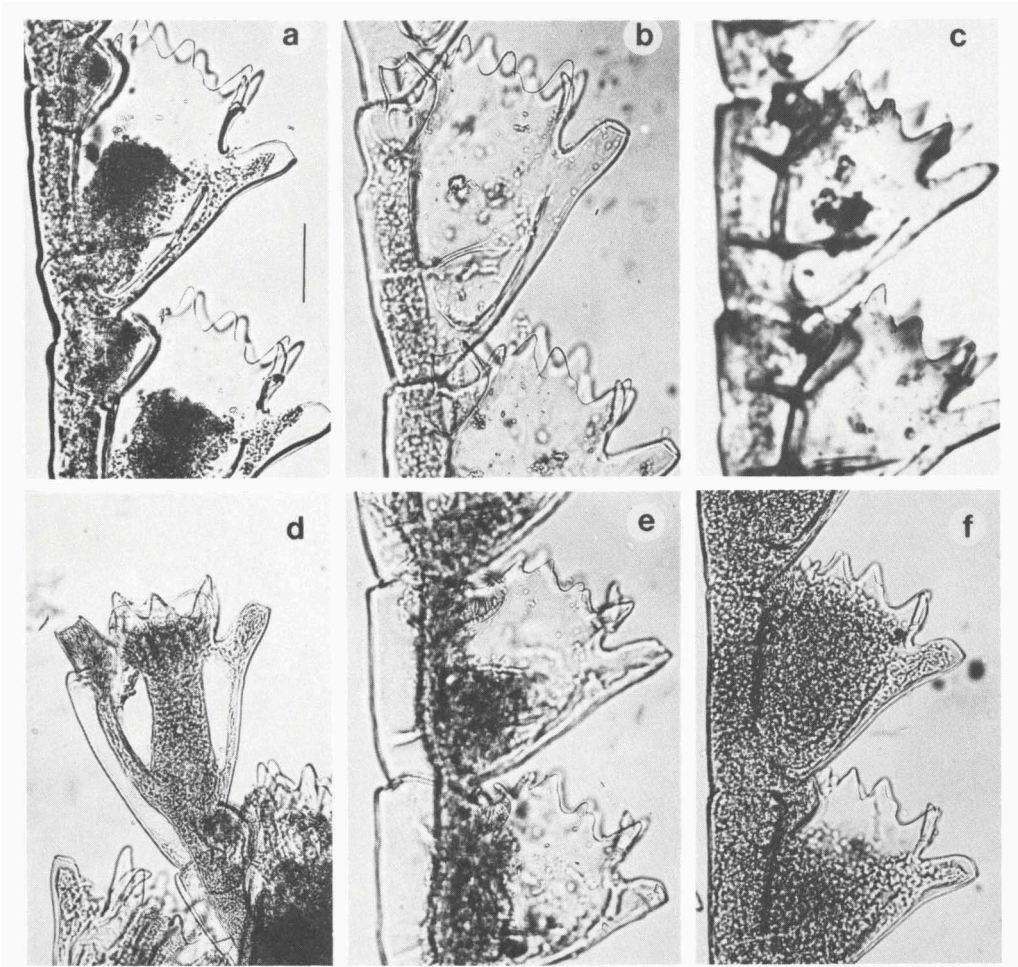


Fig. 22. *Aglaophenia parvula* Bale. Transmitted light photomicrographs, preserved material. a, S Ireland, coll. B.E.P.; BMNH colln. 1985. 8.3.5. b, S Ireland, coll. B.E.P.; BMNH colln 1985. 8.3.2. c, coll. R. Bassindale, BMNH colln. d, Gluet, Brittany, France, 6 m depth, developing cormidium from infertile colony, 19.viii.1984, coll. A. Castric; BMNH 1988.4.1.10. Note that the hydranth tentacles have yet to differentiate fully and that the diagnostic 'additional' cusp on the second main cusp from the front has also yet to form. e, ceiling of Bluinies Cave, Brittany, coll. A.S.; BMNH 1988.4.1.9. f, La Galea, Bilbao, N Spain, 6-9 m depth, coll. I. Isasi; BMNH 1988.4.6.24.

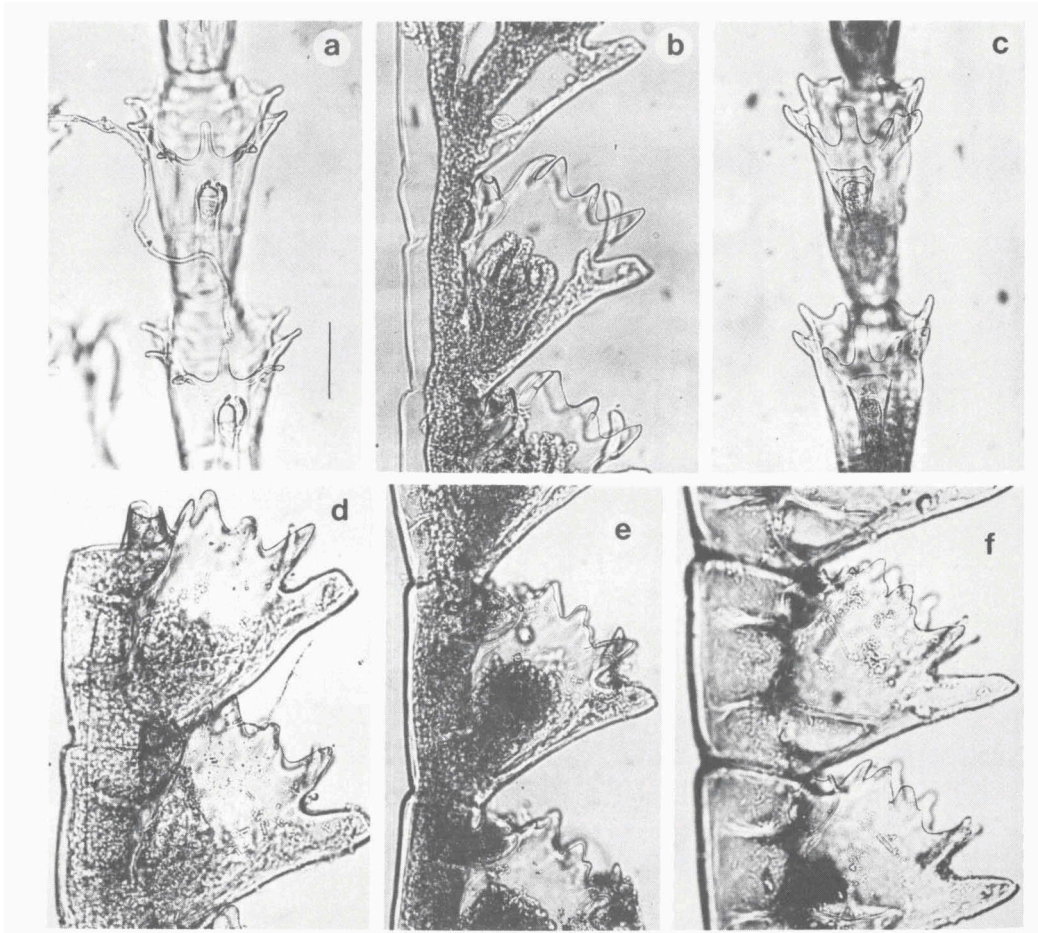


Fig. 23. *Aglaophenia parvula* Bale. Transmitted-light photomicrographs of preserved material. a, from dichotomously branched specimen, Port Phillip, Australia, ex colln W. M. Bale; Mus. Victoria slide F 53332. Note rolled-up mesial cusp due to desiccation. b-c, from dichotomously branched specimen, Victoria Reef, Gippsland coast, Australia, 12 m; coll. J. Watson, no. 1762. Note extreme bending inward of mesial and rear pair of cusps in (b), and the rather rounded mesial cusp in (c), compared with these structures in (a). d, Port Natal, South Africa, ex colln Vahlberg; Stockholm Mus. no. 3909 (see also Jäderholm, 1904). From specimen with mixture of irregular and dichotomous branching. e, from unbranched specimen, Saldanha Bay, South Africa, '50 m' but possibly shallower, coll. Discovery Expedition, 1902; BMNH 1956.9.25.6. f, from dichotomously branched specimen, Benguela Current, off W Africa, coll. J.-M. Gili. Scale (a-f) 100 μ m.

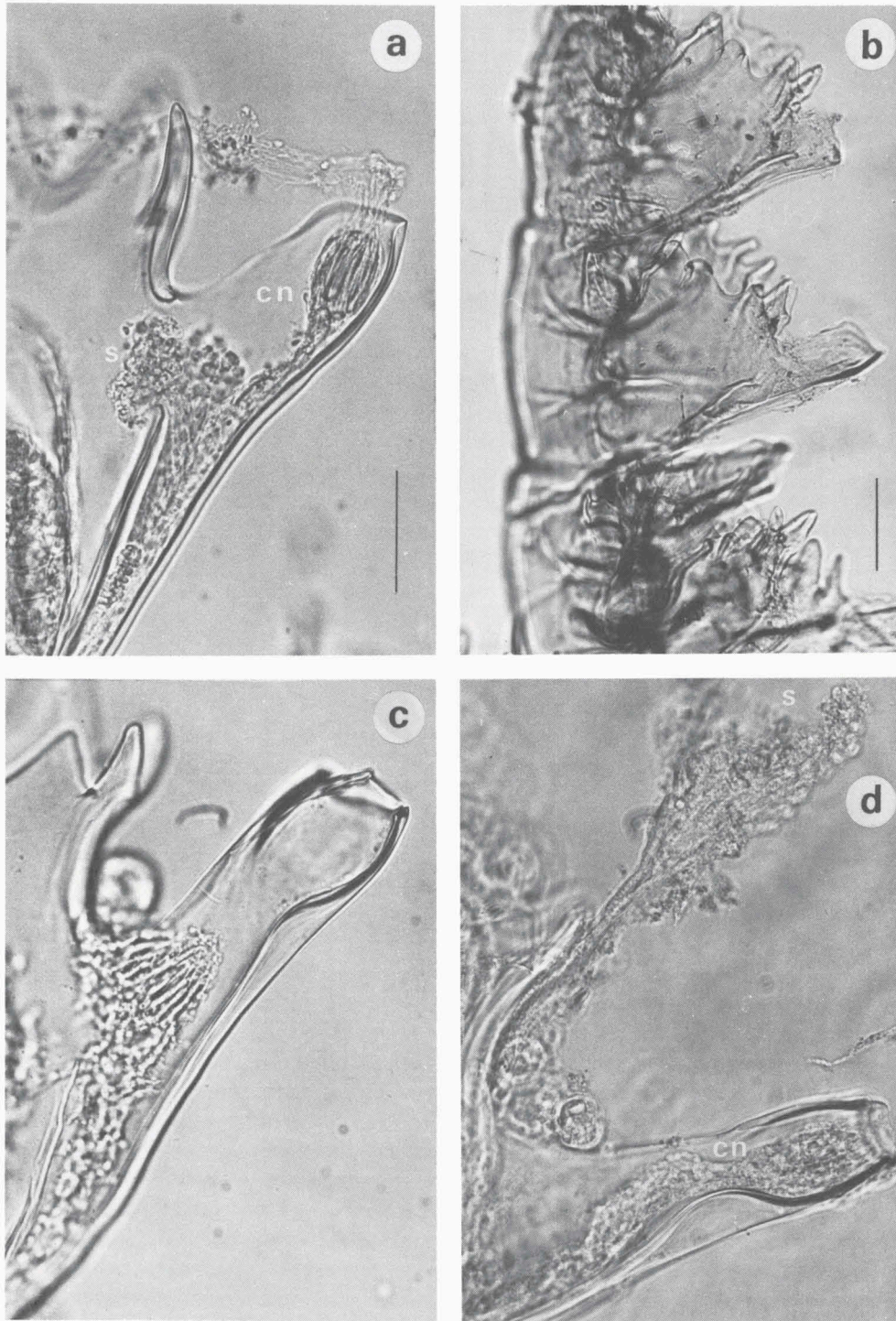


Fig. 24. *Aglaophenia pluma* (Linnaeus) and *A. tubulifera* (Hincks). Transmitted light photomicrographs, preserved material. a-b, *Aglaophenia pluma*. a, nematophore in nematotheca, Galway, Ireland; BMNH 1985.8.3.8, 8a. Note cnidostyle and threads of discharged nematocysts issuing through terminal aperture, and sarcostyle entering foramen into lumen of hydrotheca. b, fragment from specimen in Linnean (continued on p. 72).

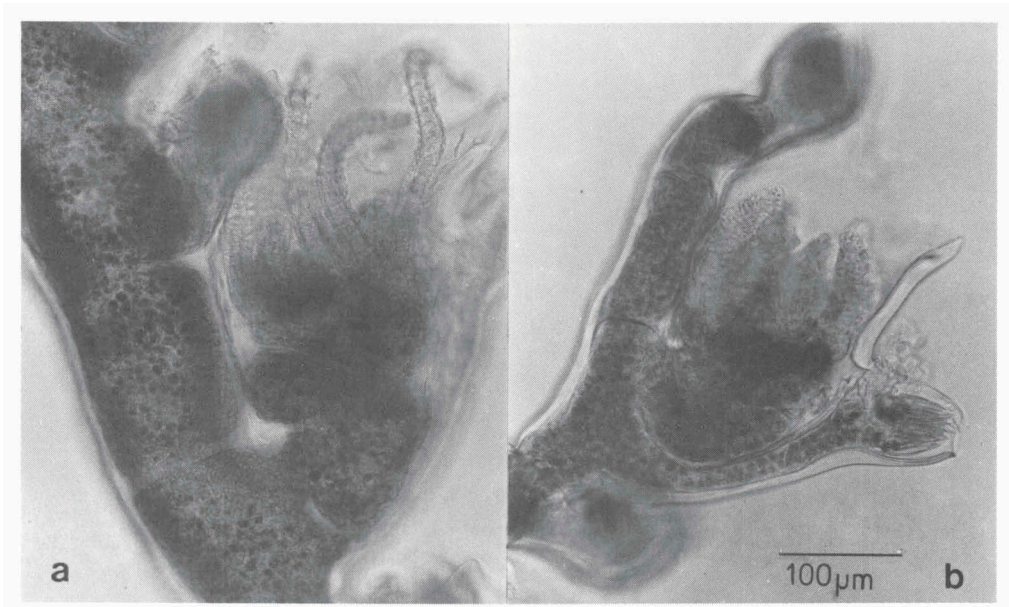


Fig. 25. Symbiotic zooxanthellae. Preparations stained 1 h with chlor-zinc-iodine solution (25 g $ZnCl_2$, 8 g H_2O , 8 g KI, 5 g I). The stain fades after several days. a, *Aglaophenia tubiformis* Marktanner-Turneretscher, Galicia, N Spain. b, *A. harpago* von Schenck, Ischia, Italy. Note that most of the symbionts occur in the cladial axis, and that there is none in the tentacles.

Fig. 24. Continued.

herb., Linnean Soc., London, 1298.13. c-d, *A. tubulifera*, mesial nematotheca and nematophore. Note subterminal thickening on lower inner side. c, Sherkin I, Co Cork, Ireland, 20 m; BMNH 1985.8.4.3, 3a. Note that upper surface of nematotheca is closed distally, open proximally. d, Saltee I, Co Wexford, Ireland, 28 m; BMNH 1985.8.4.2, 2a. Note same features, and that sarcostyle and cnidostyle are issuing from their respective orifices. (cn= cnidostyle; s= sarcostyle.) Scales (a, c-d) 50 μm , (b) 100 μm .