*Ruth Nielsen, Steffen Lundsteen and Juliet Brodie*

# Seaweeds of Denmark

## 2

## Brown algae (*Phaeophyceae*)
## Green algae (*Chlorophyta*)

Det Kongelige Danske Videnskabernes Selskab
The Royal Danish Academy of Sciences and Letters

Seaweeds of Denmark Volume 2

Brown algae (Phaeophyceae) and Green algae (Chlorophyta)

# Synopsis

*Seaweeds of Denmark* is the most comprehensive Danish seaweed flora to date. All the marine macroscopic red, brown and green algae which have been recorded in Danish waters are described in text and photos, totalling about 373 species. It is a work that provides information about each individual species, and the many illustrations show their beauty and are a source of inspiration and pleasure.

The red algae are described in volume 1, and the brown and green algae in volume 2.

The introduction covers both the history of Danish algal research and the work of a significant number of Danish phycologists who became internationally recognised for their studies of the algae. These phycologists also contributed important and large collections to the algal herbarium, the Natural History Museum of Denmark. Conditions for the growth of algae in Danish waters are mentioned and there is a survey of the specific characters and structures which characterize and separate the red, brown, and green algae. Practical information is also given about collecting and pressing the algae in order to preserve them, and how to make slide-preparations.

*Seaweeds of Denmark* includes 165 red algae (Rhodophyta), 125 brown algae (Phaeophyceae) and 83 green algae (Chlorophyta). The order of species follows the modern systematic understanding and the species are placed in the higher systematic groups: phyla, classes, subclasses, and orders followed by families, tribes, genera, species, subspecies, forms and varieties.

The description for each species deals with the general appearance, construction, reproduction, seasonal variation, distribution and habitat in Danish waters, and there are references to additional literature. The illustrations include pictures of herbarium specimens, photos of microscopic details and a few habitat pictures. There are also maps with dots that indicate collection localities in Danish waters.

The pictures will be a great help for identification along with identification keys to genera. Most genera will also have identification keys to the individuals species.

Volume 2 contains a list of explanations to scientific terms used in the text and in the identification keys.

# Seaweeds of Denmark

## Volume 2
## Brown algae (Phaeophyceae) and Green algae (Chlorophyta)

*By*
*Ruth Nielsen, Steffen Lundsteen and Juliet Brodie*
*Map of collection localities: Karl Gunnarsson*
*English translation: Ruth Nielsen and Juliet Brodie*

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Illustration on front cover: *Chorda filum* and *Cladophora* sp.
Illustration on back cover: *Petalonia fascia* and *Bryopsis hypnoides*

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# Foreword

I'm delighted that Ruth Nielsen and Juliet Brodie have prepared this English translation and revised edition of *Danmarks Havalger* (Seaweeds of Denmark, 2019). This comprehensive two-volume beautifully illustrated book reveals the richness of the seaweed flora of Danish waters. Covering the 373 seaweed species recorded from Danish waters, including 165 red, 125 brown and 83 green algae, the flora reflects the region's habitats such as the distinctive stone reefs with mobile gravel and sand, coupled with the particular environmental conditions including a range of salinity gradients.

Here in the UK, we have had a long history of seaweed study, but in comparison with our near neighbour Denmark, we have never had a guide to the whole seaweed flora illustrated with macroscopic and microscopic photos. Some groups have been covered and the later Rhodophyta volumes of Seaweeds of the British Isles (1993, 2003) were documented with photographs, as was the Green Seaweeds of Britain and Ireland (2007). Francis Bunker (with Juliet Brodie, Christine Maggs and Anne Bunker) filled the gap to some extent with the Seasearch guide to macroscopic seaweeds of Britain and Ireland (2017). However, we do not have a guide in the British Isles equivalent to that of the Danish seaweed flora. Personally, I continue to use this and other European guides, particularly the flora of Helgoland (Kornmann & Sahling, 1977), to compare microscopic features of our seaweeds, making some (hopefully good!) guesses in my translations from the original languages.

Now we will have a guide that combines the superb photographs in Ruth and Steffen's book in Danish (sadly Steffen passed away in 2018) with a new English translation of the diagnoses and notes. This will be a fantastic resource for all those working on macroalgae in Britain and Ireland, and across the rest of the Atlantic European coastline. I believe all field workers will wish to have a copy of this landmark work to hand to help with identification of those difficult species.

The introduction to the history of phycology in Denmark is interesting and provides information about key people whom we may know only from the authorities associated with Latin species names. This publication represents many years of work by Ruth Nielsen and a major effort by Juliet Brodie to bring it to a wider audience. I know the audience will be delighted to welcome it.

Christine Maggs
February 2022

# Table of Contents

## Volume 2

# Class: Phaeophyceae – Brown algae

**Class: Phaeophyceae · Subclass: Ishigeophycidae · Order: Ishigeales · Family: Petrodermataceae**

## *Petroderma maculiforme*

**(Wollny) Kuckuck**

Rock Skin

**Appearance:** Small yellow-brown to dark brown slightly raised more or less circular patches, 0.5-13 mm in width, or more extended crusts. They are closely attached to the substratum and have a solid, jelly-like consistency.

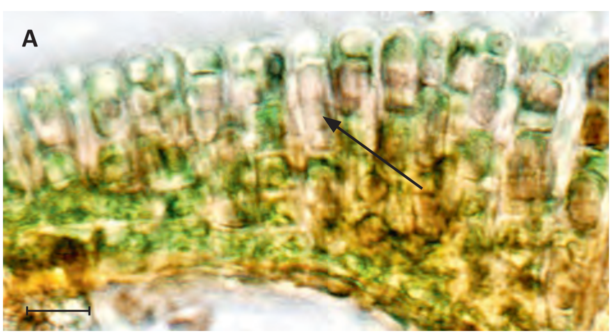
**Structure:** Monostromatic basal layer consists of radiating coherent filaments, which completely cover the substratum. Upright filaments arise from the basal layer and are loosely connected so they easily separate by light pressure. Upright filaments are unbranched or sparsely branched and consist of a few or up to 30 cells (Wilce et al., 1970). Cells are c. 8.5 µm wide and 1-2 times as long as wide. Each cell contains a curved, plate-shaped plastid in the distal end of the cell, without a visible pyrenoid. Brown algal hairs with sheaths may occur, and are scattered and apical on vegetative filaments, but rare according to Wilce et al. (1970) and have not been recorded on Rock Skin (*P. maculiforme*) from Danish waters. Special cells (ascocysts) containing fucosan sometimes occur. They are elongate and apical or intercalary in the upright filaments, occurring individually or several in a series. Filaments commonly grow through empty sporangia-walls, so remnants of old walls appear on the filaments.

**Reproduction:** Sporangia are apical on the upright filaments, closely packed and form extended spots (sori) without vegetative cells (paraphyses) between them. Unilocular sporangia are short ellipsoid, 10.5-12 µm wide and 17.5-19 µm long. Plurilocular sporangia are not recorded in Danish waters.

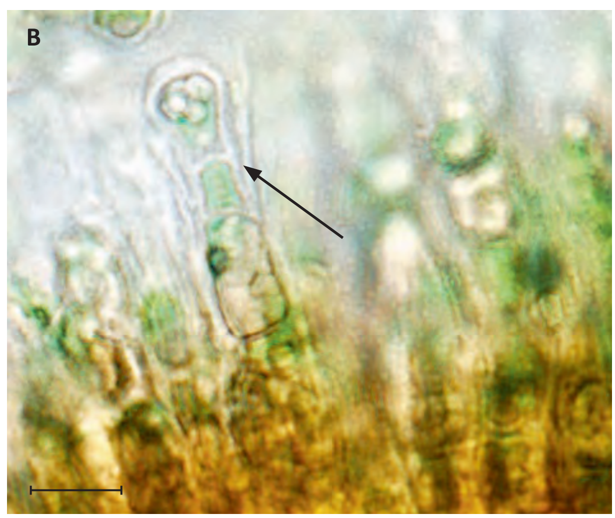
**Seasonal variation:** Occurs all year. Unilocular sporangia recorded in February.

**Habitat:** On small stones and pebbles, 0.5-14.5 m depth.

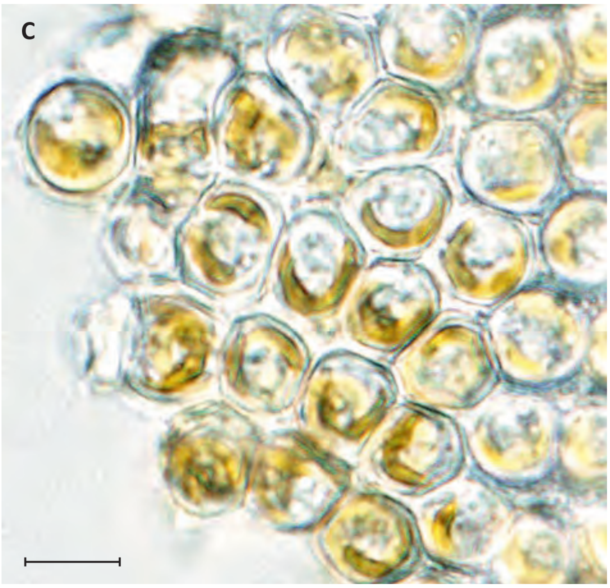
**References:** Fletcher (1978, 1987), Pedersen (2011), Wilce et al. (1970), Wærn (1952).




A: *Petroderma maculiforme*. Basal layer, upright filaments with ascocyst (arrow). Hirsholm, 1 m, 9.7.1992. Scale 10 µm.




B: *Petroderma maculiforme*. Filament with remnants of old walls (arrow). Tangen, 7.5 m, 15.9.1996. Scale 10 µm.




C: *Petroderma maculiforme*. Vegetative cells, each with a curved plastid, part of crust in surface view. Scale 10 µm. C-E: On a small stone, harbour basin, Frederikssund, 0.5 m, 11.2.2014.


D: *Petroderma maculiforme*. Upright filaments, apical ellipsoid unilocular sporangia. Scale 10 µm.


E: *Petroderma maculiforme*. Sorus of unilocular sporangia. Scale 10 µm.

**Subclass: Dictyotophycidae · Order: Dictyotales · Family: Dictyotaceae**

## *Dictyota dichotoma*

**(Hudson) J.V.Lamouroux**

Brown Fan Weed

**Appearance:** Yellow-brown ribbon-shaped fronds, up to 26 cm in height and 5-6 mm in width. Fronds are regularly dichotomously branched. Sections of the fronds are uniform in width, but gradually become slightly narrower towards the apex of the frond to nearly filiform in some individuals. There is no midrib. Basal part is cylindrical with many rhizoids which attach the alga to the substratum.

**Structure:** Fronds consist of 3 cell layers, 100-125 (-135) µm in width. There is a central medulla of large colourless cells, covered on each side by a layer of small cortical cells with several disc-shaped plastids. Growth occurs from a large apical cell, which is transversely divided by longitudinal growth. Apical cells are longitudinally divided at branching points where two uniformly large cells develop. Each of them become apical cells in new branches (genuine dichotomous branching). True brown algal hairs form tufts on both sides of the frond.

**Reproduction:** Life history comprises isomorphic sexual dioecious gametophytes and vegetative sporophyte. Reproductive structures develop on both sides of the frond. They form from surface cells, which are transversely divided, and reproductive structures develop from the outermost cell. Sexual reproduction is oogamous with immobile eggs and moving sperm cells with flagella (spermatozoids), which form in antheridia. Sexual structures form oval spots (sori) on the gametophytes. Sori protrude slightly above the surface of the thalli. Sori on male gametophytes, are surrounded by a border of sterile cells. Antheridia divide into many small cells, each with a spermatozoid. Oogonia on female gametophytes are obovate, each with a single egg-cell which is released prior to fertilization which takes place in the water. Zygotes grow into diploid sporophytes, which have scattered sporangia, occurring either individually or in small groups. Sporangia are approximately spherical with a thick wall, 120-125 µm wide at maturity. Meiosis takes place in the sporangia and 4 haploid spores are formed. These germinate and develop into male and female gametophytes. Spores develop into diploid individuals in some cases, according to Lund (1950).

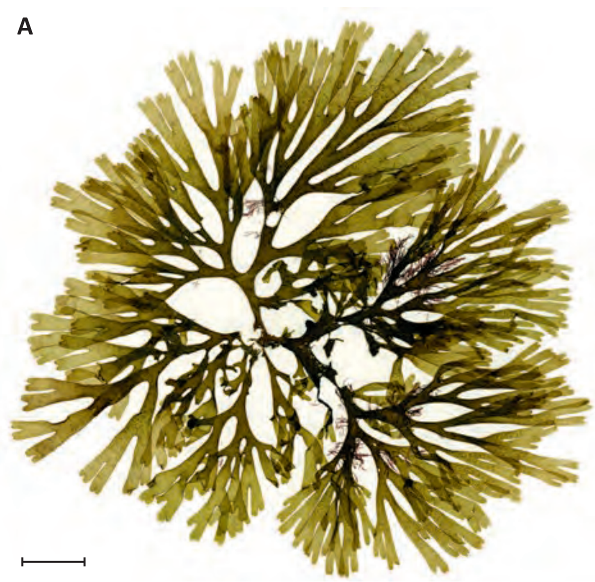
**Seasonal variation:** Collected in April, July-October. Antheridia recorded in August, oogonia in July-August and sporangia in July-August and October.

**Habitat:** On small stones, and shells of Blue Mussel (*Mytilus edulis*), epiphytic on Wrack (*Fucus*), 0.15-4.5 m depth.

**Comment:** Brown Fan Weed (*D. dichotoma*) in Danish waters, only occurs in the western part of the Limfjord, where it was first collected in 1939. It probably arrived after 1920, the year of the previous investigation of this area, at which time the species was not observed.

**References:** Lund (1950), Tronholm et al. (2008, 2010).

A



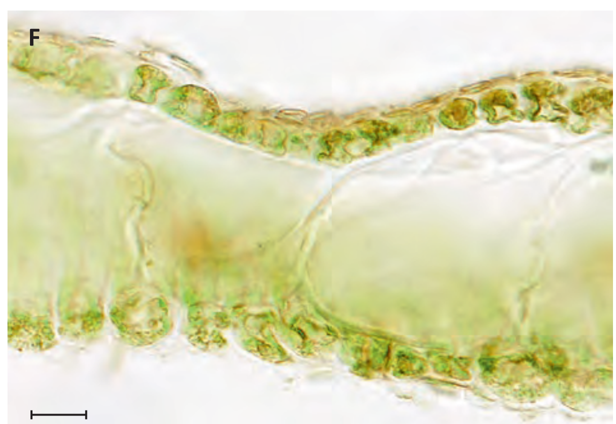
A: *Dictyota dichotoma*. Thallus of ribbon-shaped, dichotomously branched frond. Scale 2 cm. A-K: Tile works, Helligsø, 3.5 m, 22.8.2005.


B: *Dictyota dichotoma*. Narrow ribbon-shaped frond. Scale 2 cm.


C: *Dictyota dichotoma*. Wide ribbon-shaped frond. Scale 2 cm.


D: *Dictyota dichotoma*. Longitudinal division of apical cell. Scale 20 µm.


E: *Dictyota dichotoma*. Apex with genuine dichotomous branching. Scale 20 µm.




F: *Dictyota dichotoma*. Large pale medullary cells with a layer of small assimilating cortical cells on both sides. Transverse section. Scale 20 µm.

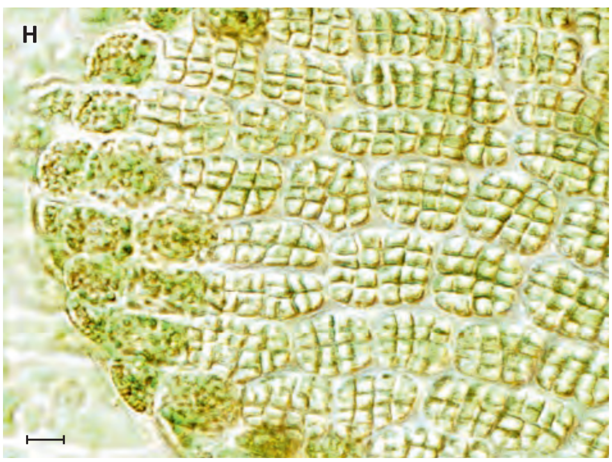
G: *Dictyota dichotoma*. Surface of male gametophyte with sori which have a margin of sterile cells. Scale 100 µm.

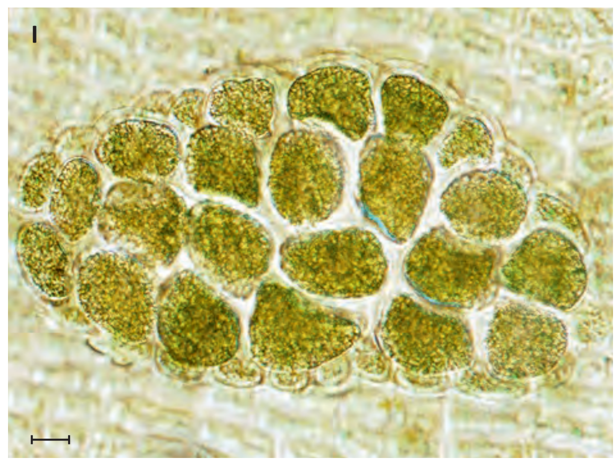
H: *Dictyota dichotoma*. Part of antheridial sorus. Scale 10 µm.

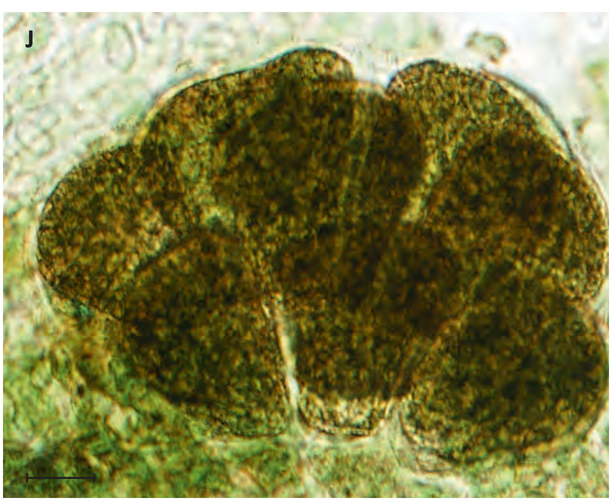
I: *Dictyota dichotoma*. Sorus of oogonia. Scale 20 µm.

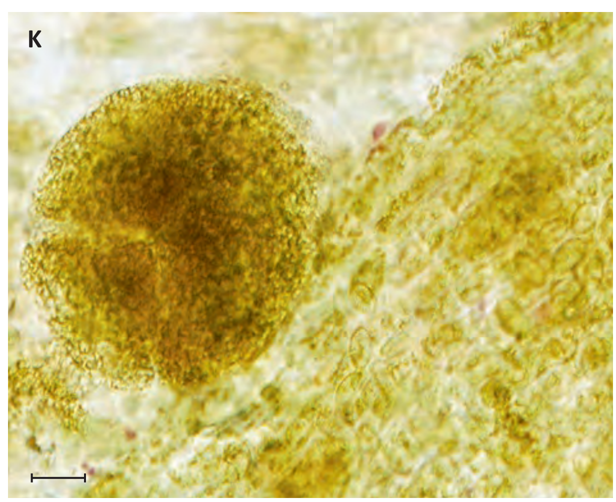
J: *Dictyota dichotoma*. Obovate oogonia. Oblique transverse section. Scale 20 µm.

K: *Dictyota dichotoma*. Tetrahedrally divided sporangium. Scale 20 µm.

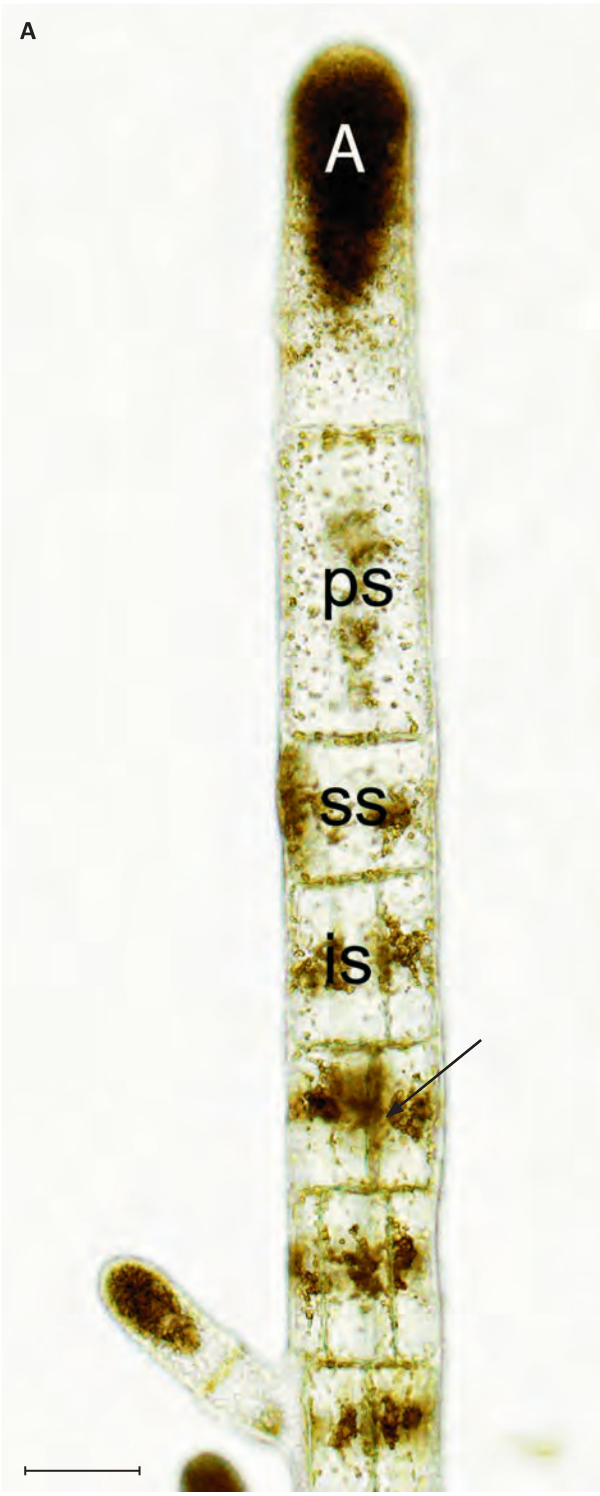



## Order: Sphacelariales




Spacelariales includes parenchymatous algae with apical growth. An apical cell is large, and a primary segment is cut off after cell division. This extends and divides into a superior and an inferior secondary segment. Below the apex, the segments are divided by longitudinal cell walls and the thallus becomes parenchymatous. Longitudinal cell walls might be radial or parallel to the surface (pericline), in which case central medullary cells are formed. In some families the cells are divided by secondary transverse cell walls. Segments of the family Cladostephaceae become both longer and wider away from the apex and develop many whorled branches with restricted growth. Segments of the family Sphacelariaceae do not increase in length or in width below the apex. Some species develop very narrow branches (rhizoids), which may form a dense cover or be loosely attached to the branches. They grow downwards in some cases and contribute to the attachment of the thalli. Stolons are creeping branches, constructed as the uprights, but commonly unbranched. Some species have, special cells (pericysts) which contain fucosan. They are transparent in fresh individuals, but in dried individuals or after fixation in formalin, they become a dark brown colour.

A: Pompon Brown Feather Weed (*Sphacelaria cirrosa*). Large apical cell (A), primary segment (ps), superior secondary segment (ss), inferior secondary segment (is), longitudinal wall (arrow). In each of the cells, many disc-shaped plastids. Horneks Odde, Læsø, drift, 24.8.2016. Scale 50 µm.

## Family: Cladostephaceae

# *Cladostephus spongiosus*

**(Hudson) C.Agardh**

Hairy Sand Weed

**Appearance:** Dark brown bushy thalli, with irregularly dichotomously branched main axis, which has short closely packed branches in whorls. Uprights, up to 12 cm in height and 0.5 cm in width, arise from a leather-like basal crust, approximate 0.5 mm in thickness.

**Structure:** Growth from the apical cell, and a primary segment is cut off, stretches and divides into a superior and an inferior secondary segment. Segments below the apex, grow both longitudinal and transversely, divided by many longitudinal and transverse walls. There are 8-24 branches in each whorl, they have restricted growth, 1-3 mm in height, are pointed, decrease slightly in width towards the base and are curved inwards (sickle-shaped).

**Reproduction:** Sporangia with a short stalk occur on special branchlets which are pointed, approximately 300 µm in length and form a felty cover on the main axis. Unilocular sporangia are ellipsoid to spherical but have only been observed a few times in the alga from Danish waters. Plurilocular sporangia are rounded to cylindrical, 29 µm wide and 79 µm long at maturity, and have been observed several times.

**Seasonal variation:** Perennial, collected in March-April and July-December. Growth begins early in the year but is most vigorous in summer. Sporangia develop in autumn and winter. Unilocular sporangia recorded in December and March, plurilocular sporangia in September-November, and empty sporangia in spring.

**Habitat:** On stone and boulders, 0.5-4 m depth, by dredge in old collections, 10 m depth.

**Comment:** Probably a species that is declining in distribution in the Northern Kattegat, where the latest collections were 1934, at Hirsholm, and 1975 at Nordre Rønner, Læsø. Hairy Sand Weed (*C. spongiosus*) was looked for in vain at Hirsholm during numerous field courses in the last part of the 20th century and at Nordre Rønner, Læsø, in 2004. Herbarium material in the algal herbarium, Natural history Museum of Denmark, documents a vigorous population, at Fornæs Fyr, 1984.

**References:** Kylin (1947, *C. spongiosus* and *C. verticillatus*), Lund (1950, *C. spongiosus* and *C. verticillatus*), Prud'homme van Reine (1972, 1982).


A: *Cladostephus spongiosus*. Well-developed alga, with epiphytic *Trailliella*-phase of *Bonnemaisonia hamifera*. Tile works, Helligsø, 3 m, 16.8.1959. Leg.: T. Christensen. Scale 2 cm.


B: *Cladostephus spongiosus*. Smaller but well-developed specimens. Fornæs Fyr, 0.2 m, 16.9.1984. Leg.: L. Mathiesen. Scale 2 cm.


C: *Cladostephus spongiosus*. Branchlets with plurilocular sporangia. Scale 20 µm. C-D: Skiveren, drift, 2.11.1973.


D: *Cladostephus spongiosus*. Plurilocular sporangium on a short stalk. Scale 10 µm.

## Family: Sphacelariaceae

### *Battersia*

Batters Feather Weeds

Upright branches arise from a well-developed, several layers thick, disc-shaped base. Branches are more or less covered by downward-growing rhizoidal filaments. Secondary segments are divided by periclinal cell walls and have one or a few medullary cells. Secondary transverse walls are common, so medullary cells are surrounded by small surface cells. There are uni- or plurilocular sporangia with stalks of one- or several cells. They emanate from the upright branches or the disc-shaped base. No propagules.

**Identification key to species of *Battersia***

| | | |
|---|---|---|
| 1a. | Thalli appear as dark brown tufts | *B. arctica* |
| 1b. | Thalli have feather-like branches | *B. plumigera* |

## *Battersia arctica*

**(Harvey) Draisma, Prud'homme & H.Kawai**

Batters Arctic Feather Weed

**Appearance:** Relatively stiff, dark brown tufts, 1-4 cm in height, that arise from a well-developed disc-shaped base.

**Structure:** Main branches look irregularly feather-shaped with both opposite and scattered branches, which might be distichous or in short uniseriate series. Rhizoidal filaments are loosely attached or more or less adpressed to the main branch, and the lower ones may contribute to the attachment of the alga. Segments have many secondary transverse walls.

**Reproduction:** Uni- and plurilocular sporangia are apical on short stalks, arising from all parts of the uprights, and occasionally from rhizoidal filaments. Branchlets with sporangia might resemble small racemes. Unilocular sporangia are ovoid, ellipsoid or spherical (41-) 45-53 (-62) µm long and (37-) 45-49 (-57) µm wide. Plurilocular sporangia are approximately cylindrical with a rounded apex.

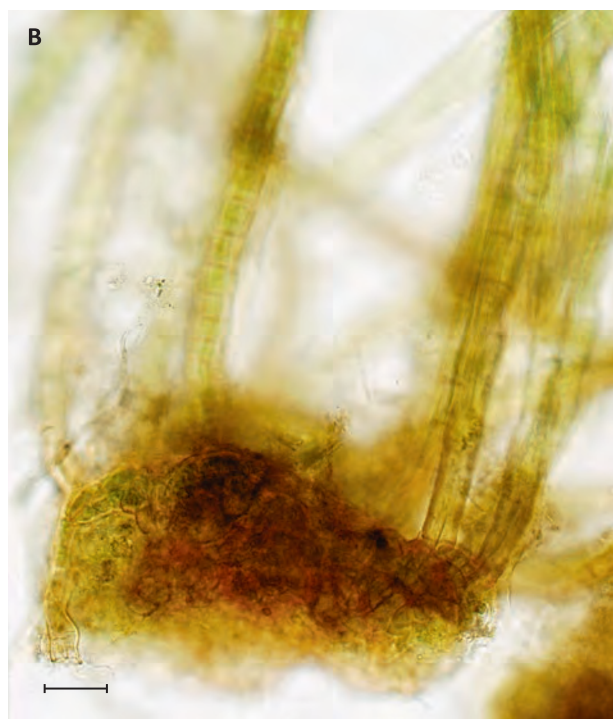
**Seasonal variation:** Perennial. Unilocular sporangia observed in February-March and plurilocular sporangia in March.

**Habitat:** On stone and mollusc shells, rarely on other algae, from the low water line to great depth. Most frequent around Bornholm, where it is collected by dredge to 37 m depth.

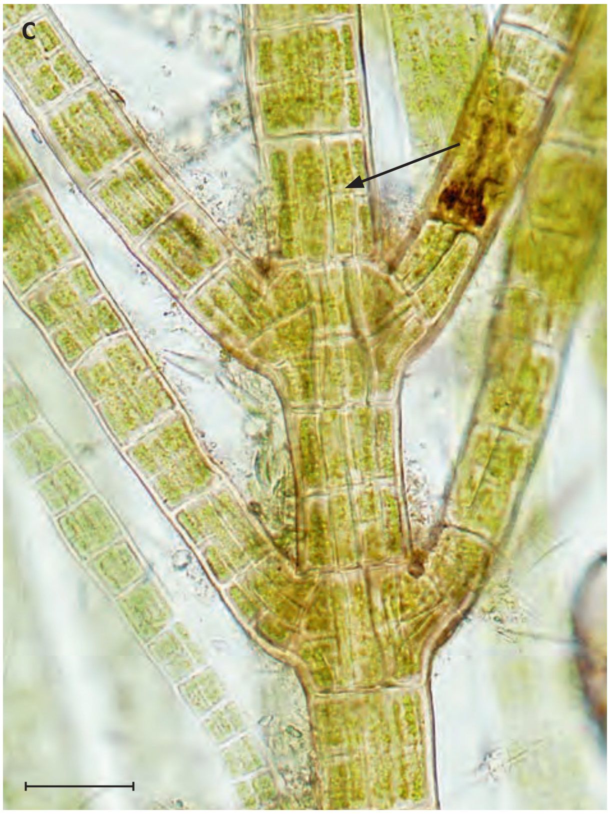
**Comment:** *Battersia racemosa* (Greville) Draisma, Prud'homme & H.Kawai probably does not occur in Danish waters. The sterile alga, 1 cm in height, from Aalborg Bugt, which was mentioned by Lund (1950) as *Sphacelaria racemosa* f. *typica*, was examined by Prud'homme van Reine (1982, p. 157) who found it to be similar to *B. arctica* (as *Sphacelaria*).

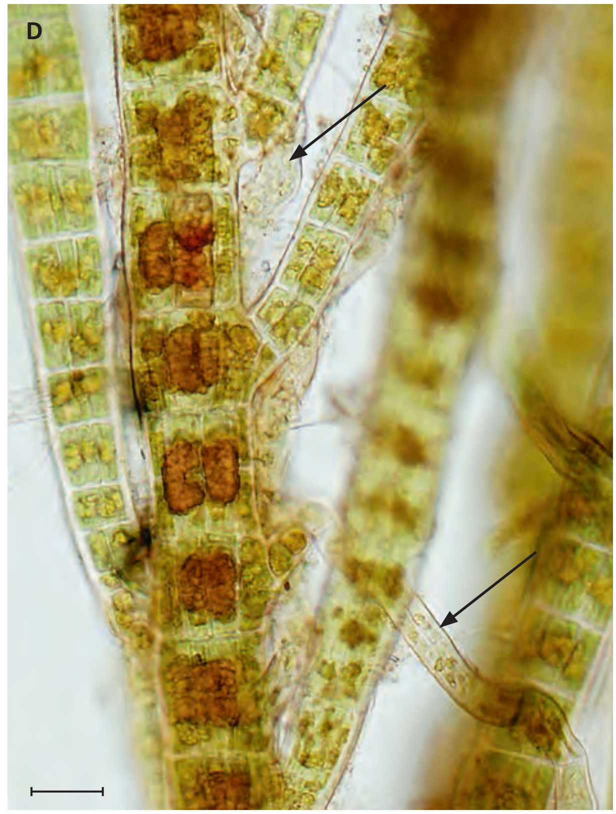
**References:** Draisma et al. (2010), Lund (1950, *Sphacelaria racemosa* f. *arctica*, f. *typica*), Prud'homme van Reine (1982, *S. arctica*), Wærn (1945, *S. arctica*).

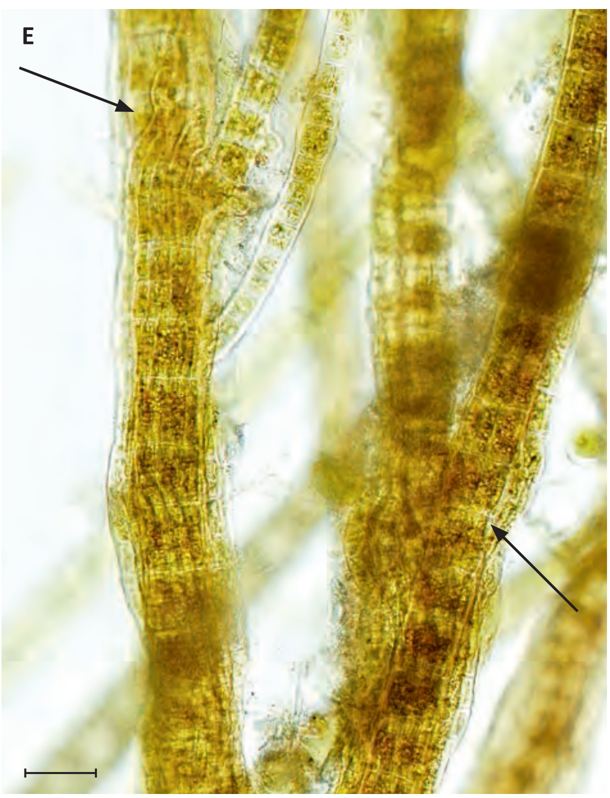

A: *Battersia arctica*. Dark brown tuft of closely packed branches. Scale 1 cm. A, H: Falske Bolsaks, 10.5 m, 5.3.1997.




B: *Battersia arctica*. Basal crust with upright branches. Scale 50 µm. B, E: Vejrø, 9 m, 26.3.1992.




C: *Battersia arctica*. Opposite branches, secondary transverse wall (arrow). Scale 50 µm. C, G: Vejrø, 11 m, 26.3.1992.

D: *Battersia arctica*. Scattered distichous branches and down-ward growing rhizoids (arrows). Scale 50 µm. D, F: Hatter Rev, 8 m, 7.3.1997.

E: *Battersia arctica*. Downward-growing rhizoids (arrows). Scale 50 µm.


F: *Battersia arctica*. Periclinal longitudinal walls, medullary cell (arrow), transverse section. Scale 10 µm.


G: *Battersia arctica*. Unilocular sporangia on stalks. Scale 20 µm.


H: *Battersia arctica*. Empty plurilocular sporangia. Scale 20 µm.

## *Battersia plumigera*

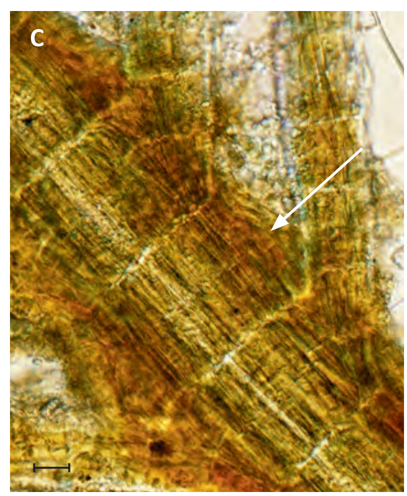
**(Holmes ex Hauck) Draisma, Prud'homme & H.Kawai**

Batters Long Feather Weed

**Appearance:** Light brown alga appears as a small feather with a distinct main axis and distichous branches of a uniform length. Main axis may be pseudodichotomously branched at irregular intervals. Thalli are soft and flexible, up to 11 cm in height in the northern part of Kattegat, but shorter in inner districts towards the Baltic Sea. Uprights from a small disc-shaped base.
**Structure:** Disc-shaped base of radiating confluent filaments, on which the surface gradually becomes covered by downward-growing rhizoids and slightly felty. Upright main axes have opposite, uniformly long branches, which arise from approximately all the superior secondary segments. Segments are as long as wide, with both longitudinal and secondary transverse walls. Rhizoids form below the apex and arise in the same plane as the branches. They are firmly attached to the main axes as a cortex, but do not cover the middle part of the main axis. True brown algal hairs sometimes present.
**Reproduction:** Unilocular sporangia are apical on slender branchlets which arise on the branches. They occur individually or in small raceme-like clusters. Sporangia are ovoid or spherical, 49-82 (-86) µm long and 41-66 µm wide.
**Seasonal variation:** Perennial, unilocular sporangia recorded in January, March and June.
**Habitat:** On stone and boulders, the sheltered side of harbour jetties, 0.5-1.5 m depth. In the algal herbarium, Natural History Museum of Denmark, there are older specimens collected by dredge to 26 m depth in the northern Kattegat and at Bornholm to 37.5 m depth.
**Resembles:** Reminiscent of Hair Plume Weed (*Chaetopteris plumosa*) but differs by the rhizoidal filaments not covering all of the main axis, which they do in this species (*C. plumosa*).
**Comment:** Lund (1950) mentioned a loose form in which the rhizoids were very sparsely developed. It was collected at considerable depth in the inner districts of the Danish waters. There are no newer collections of this form in the algal herbarium, Natural History Museum of Denmark.
**References:** Draisma et al. (2010), Lund (1950, *Sphacelaria plumigera*), Prud'homme van Reine (1982, *S. plumigera*).


A: *Battersia plumigera*. Upright thallus appears as a small, branched feather, main axes pseudodichotomously branched. Scale 2 cm. A, C: Sheltered side, southern harbour jetty, Frederikshavn, 1 m, 12.7.1972.


B: *Battersia plumigera*. Relatively long main axis. Sheltered side, near the head of the northern harbour jetty, Frederikshavn, 1.5 m, 11.1.1972. Scale 2 cm.




C: *Battersia plumigera*. Rhizoidal filaments (arrow) only between the opposite branches. Middle part of main axis without rhizoids. Rehydrated herbarium material. Scale 20 µm.

## *Chaetopteris plumosa*

**(Lyngbye) Kützing**

Hair Plume Weed

**Appearance:** Uprights, 4-10 (-12) cm in height, are feather-like and arise from a well-developed dark-brown crust. Main axes, up to 0.5 mm in width are dark brown with opposite branchlets of a lighter colour and individual branches have an elongate lanceolate outline. The young alga is light brown, regularly branched with opposite branches in one plane. The older alga is dark brown and main axes irregularly scattered or pseudodichotomous, without branchlets in the lower parts.

**Structure:** Secondary segments are divided by radial and periclinal longitudinal walls and have secondary transverse walls. Medulla of large cells and surface of small cells. Main axes covered by rhizoids which arise slightly below the apex. Rhizoids arise from scattered surface cells and cover all the main axes. True brown algal hairs may occur on branches. Polystromatic basal crusts consist of confluent radiating filaments which growth at the margin and upright filaments from intercalary cells. Strengthening of the crust may increase by downward-growing rhizoidal filaments which arise from upright branches.

**Reproduction:** Uni- and plurilocular sporangia occur mainly on different individuals. Sporangia have stalks and occur on small fertile branchlets which arise from cells of the rhizoidal cortex and form a felty cover on main axes. Unilocular sporangia are spherical, while plurilocular sporangia are short cylindrical.

**Seasonal variation:** Perennial, collected all year. Branches are shed at the end of the growing season, main axes overwinter and fertile branchlets develop. Growth of new branches begins in January. The alga is well-developed in April-September. Unilocular sporangia recorded in December and March, plurilocular sporangia in November-February, empty plurilocular sporangia in February, April-May and a single alga with remnants of plurilocular sporangia in August.

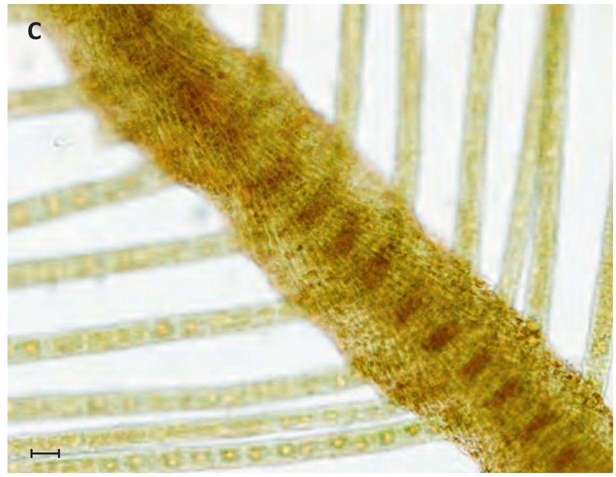
**Habitat**: On stone and mollusc shells, and epiphytic on haptera of Oar Weed (*Laminaria digitata*) and Forest Kelp (*L. hyperborea*), on stipes of Oar Weed (*L. digitata*), the lower part of Serrated Wrack (*Fucus serratus*) and on the basal crust of Brown Sea Oak (*Halidrys siliquosa*). Collected by divers to 19 m depth and by dredge, 30 m depth.

**References:** Christensen (1966), Draisma et al. (2010), Lund (1950), Prud'homme van Reine (1982).

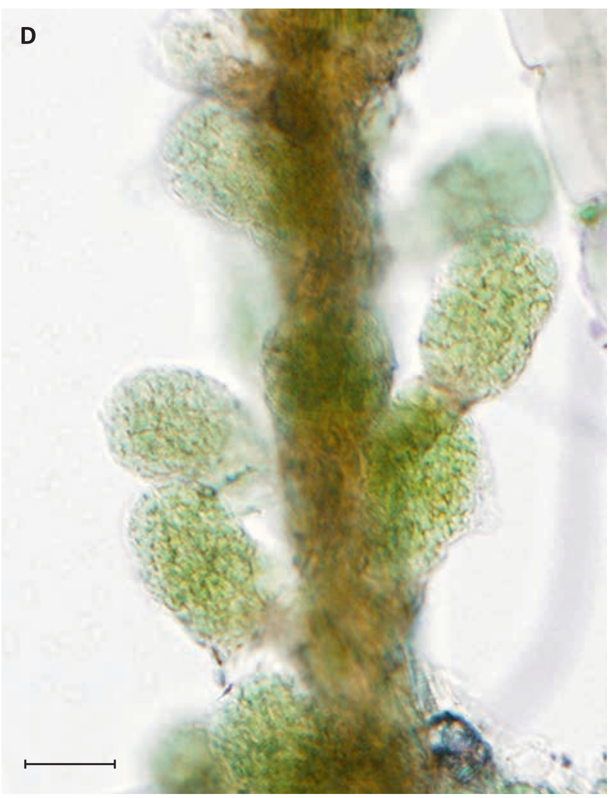
A

A: *Chaetopteris plumosa*. Dark brown feather-like alga, with epiphytic small Straggly Bushy Weed (*Rhodomela confervoides*) and Sea Oak (*Phycodrys rubens*). Tønneberg Banke, 16 m, 4.6.1989. Scale 2 cm.

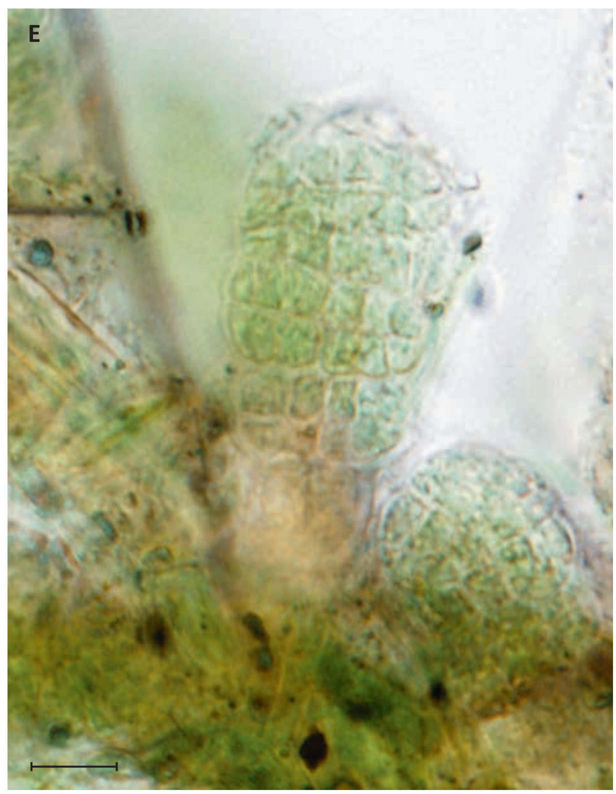

B: *Chaetopteris plumosa*. Winter form. Hirsholm, drift, 5.12.1973. Scale 2 cm.




C: *Chaetopteris plumosa*. Main axis completely covered by rhizoidal cortical filaments and with opposite branches. Herthas Flak, 18 m, 9.6.1991. Scale 50 µm.




D: *Chaetopteris plumosa*. Main axis with plurilocular sporangia. D-E: Hirsholm, Stålhage, 5.5 m, 3.2.1996. Scale 20 µm.




E: *Chaetopteris plumosa*. Plurilocular sporangium on short stalk. Scale 10 µm.

# *Sphacelaria*

Brown Feather Weeds

Segments are divided by longitudinal walls. Secondary transverse walls are rare. Propagules occur.

**Identification key to species of *Sphacelaria***

| | | |
|---|---|---|
| 1a. | Net-shaped, true dichotomously divided branches | *S. reticulata* |
| 1b. | Tufts of upright branches | 2 |
| 2a. | Main branches irregular feather-shaped, with opposite branches, propagules approximately triangular | S. *plumula* |
| 2b. | Few or no opposite branches | 3 |
| 3a. | Branches 17-36 µm in width | 4 |
| 3b. | Branches > 30 µm in width, in most cases twice this size | 5 |
| 4a. | Propagules with two cylindrical arms, which are symmetrical or of different length, one of them may be branched | *S. solitaria* |
| 4b. | Propagules approximately triangular | *S. tribuloides* |
| 5a. | Branches scattered, sometimes uniseriate or opposite, rhizoids may occur at the base. Propagules with an apical hair or a small lens-shaped cell; arms constricted at base | *S. cirrosa* |
| 5b. | Branches scattered on all sides, no rhizoids. Propagules with a small lens-shaped apical cell; arms not constricted at base | *S. fusca* |

# *Sphacelaria cirrosa*

**(Roth) C.Agardh**

Pompon Brown Feather Weed

**Appearance:** Stiff yellow-brown to dark brown tufts, up to 2 (-3) cm in height. Main upright branches with slightly narrower branches. Loose, spherical, pompon-shaped thalli also appear, up to more than 3 cm in diameter (f. *aegagrophila* C.Agardh).

**Structure:** Base of small mono- or polystromatic crusts from which stolons may arise from the margin and develop into new crusts, or base slightly endophytic in larger brown individuals. Uprights are irregularly branched on all sides, branches unilateral or distichous in short series and sometimes opposite. Main branches, (41-) 45-94 µm in width with narrower branches, some of which have stopped growing and terminate in a narrow apical cell. Segments have radial longitudinal walls, without medullary cells. Secondary transverse walls do not occur, or seldom a few in the very lowest part. True brown algal hairs are common. They develop from a small lens-shaped apical cell. Scattered rhizoids may occur in the lower part of the main axis. They twist loosely down the branches and may grow along the substratum and contribute to the attachment.

A

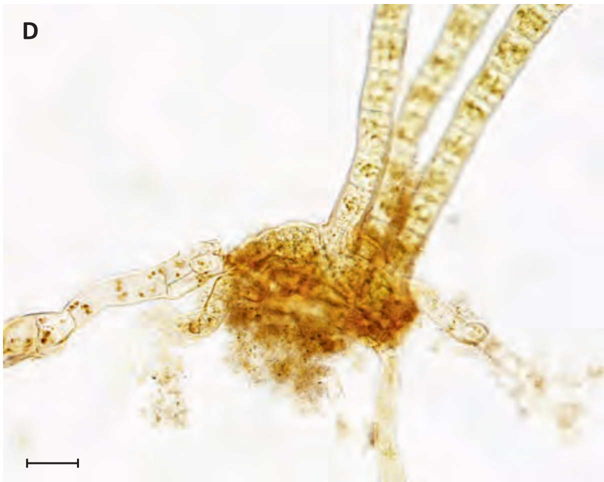
A: *Sphacelaria cirrosa*. Epiphytic on Brown Sea Oak (*Halidrys siliquosa*). Hirsholm, drift, 14.8.1974. Scale 2 cm.

B

B: *Sphacelaria cirrosa*. Winter specimens on Desmarest's Prickly Weed (*Desmarestia aculeata*). Tønneberg Banke, 14.5 m, 16.1.1997. Scale 2 cm.

C

C: *Sphacelaria cirrosa*. Spherical, pompon-shaped loose specimens. Beach north of Vesterø Havn, Læsø, 0.5 m, 11.7.1972. Scale 2 cm.

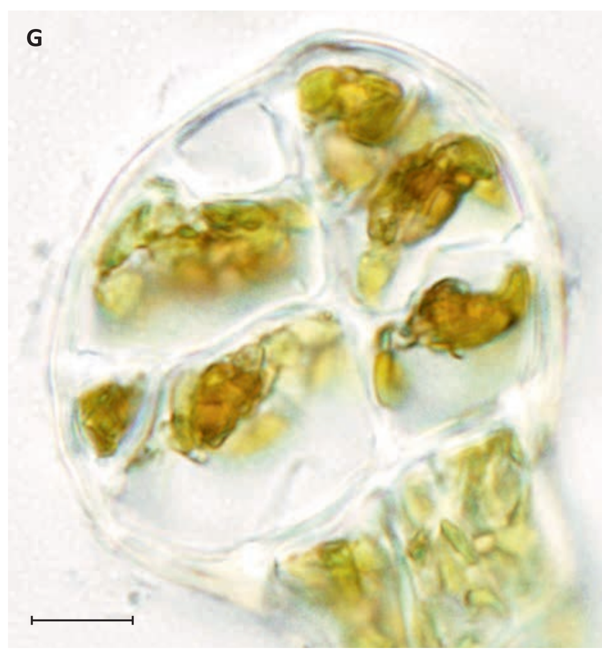



D: *Sphacelaria cirrosa*. Basal crust with stolons and uprights. Tat, Christiansø, 11 m, 16.6.2009. Leg.: C. Darling. Scale 50 µm.


E: *Sphacelaria cirrosa*. Main branch with opposite and scattered branches on all sides. Scale 50 µm. E-F: Horneks Odde, 0.5 m, drift, 24.8.2016.

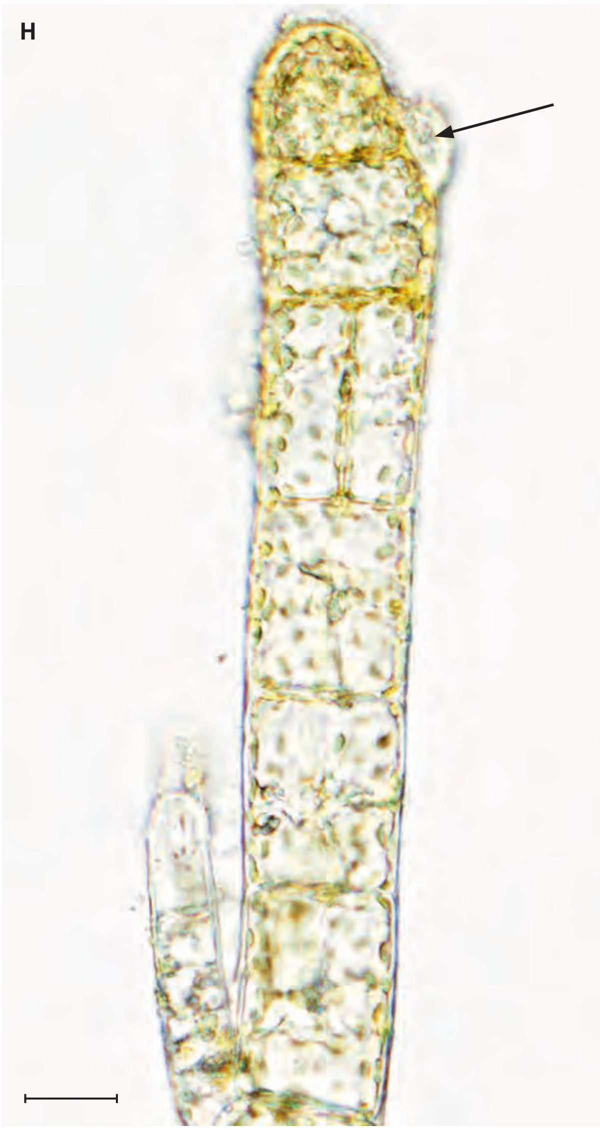
F: *Sphacelaria cirrosa*. Segments divided by longitudinal walls, no secondary transverse walls. Many disc-shaped plastids in each cell. Scale 10 µm.

G: *Sphacelaria cirrosa*. Radial longitudinal walls, no medullary cells. Oblique transverse section. Scale 10 µm.
G, N-Q: On Brown Sea Oak (*Halidrys siliquosa*), beach south of Vesterø Havn, Læsø, drift, 25.8.2016.

An unattached growing form (f. *patentissima* (Greville) S.Lund) may occur between Eelgrass (*Zostera marina*). It has short straight branches which arise at 90° angles.

**Reproduction**: Vegetative propagules are common. They have a multicellular stalk with (2-) 3 branches (arms) and typically an apical brown algal hair, occasionally an apical small lens-shaped cell. Arms of propagules develop successively and are cylindrical with a constriction at base. The basal stalk cell remains when propagules are shed, and new propagules may develop from this several times. Therefore, stalks may have a series of older stalk cells at the base, visible as cells with small remnants of cell walls (collars). Uni- and plurilocular sporangia occur on the same or different individuals. Unilocular sporangia are ellipsoid or spherical, (66-) 70-86 (-103) µm wide and have a unicellular stalk. Plurilocular sporangia are elongate ellipsoid, (62-) 86-94 (-107) µm long and (41-) 49-53 µm wide with a stalk of one or two cells.




H: *Sphacelaria cirrosa*. Apex, a new apical cell and a small lens-shaped cell (arrow), which becomes the initial cell of a true brown algal hair. On Brown Sea Oak (*Halidrys siliquosa*), beach south of Vesterø Havn, Læsø, drift, 1.5.2016. Scale 50 µm.

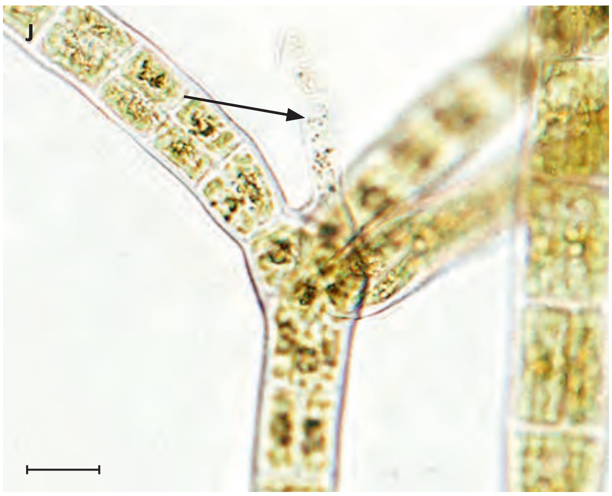

I: *Sphacelaria cirrosa*. Branch with downward-growing rhizoids. Scale 50 µm. I-J: Ebbeløkke, 9 m, 26.7.1994.

**Seasonal variation:** Perennial, collected in January and April-November. Worn down in winter, and with new light brown uprights in January. Propagules recorded in January and April-November, sporangia in January, April and June-November. Loose spherical, pompon-shaped thalli are common in late summer.

**Habitat:** Epiphytic on other algae, on mollusc shells and stone, 0.5-20 m depth and in the North Sea collected by dredge at 25 m depth. Frequent on Desmarest's Prickly Weed (*Desmarestia aculeata*), fig. A page 49, and Brown Sea Oak (*Halidrys siliquosa*).

**Comment:** Morphological variation comprises *S. bipinnata* (Kützing) Piccone, previously considered a separate species, common on Brown Sea Oak (*Halidrys siliquosa*).

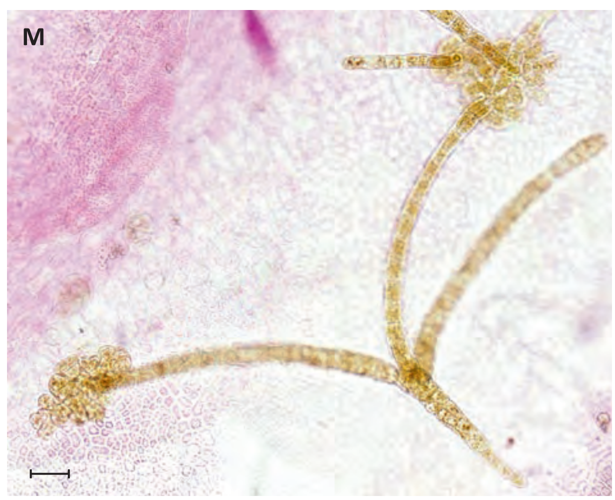
**References:** Lund (1950, *S. cirrosa* and *S. bipinnata*), Prud'homme van Reine (1982, 1993).




J: *Sphacelaria cirrosa*. Propagule with 3 arms and apical hair (arrow). Scale 20 µm.

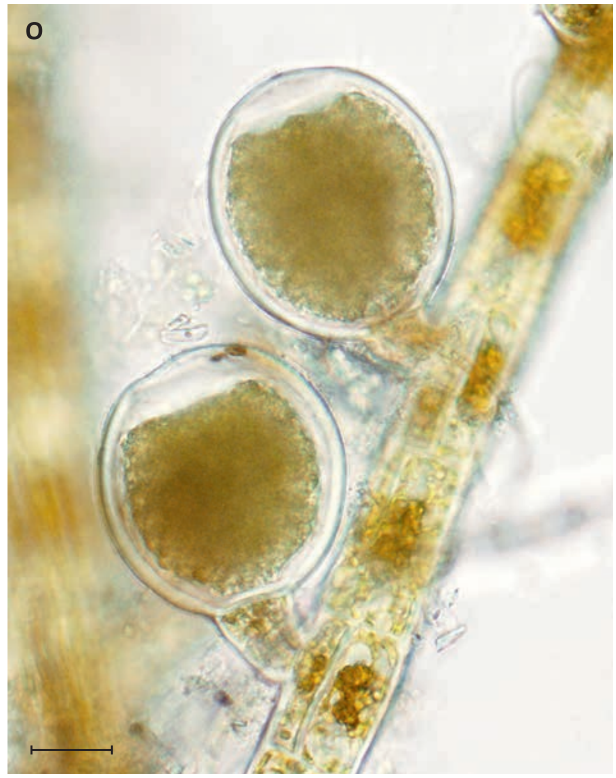

K: *Sphacelaria cirrosa*. Propagule with 3 arms and small apical cell (arrow). Arms with a basal constriction. Torup Flak, 6.5 m, 25.7.1994. Scale 20 µm.


L: *Sphacelaria cirrosa*. Propagule, lower part of stipe with a series of old stipe cells with collar (arrow). Middelflak, 10 m, 15.9.1991. Scale 50 µm.




M: *Sphacelaria cirrosa*. Propagule on Veined Tongue Weed (*Apoglossum ruscifolium*). Two of the arms have developed new basal crusts. Tønneberg Banke, 14 m, 27.8.2013. Scale 50 µm.


N: *Sphacelaria cirrosa*. Young ellipsoid unilocular sporangia on unicellular stalk. Scale 20 µm.




O: *Sphacelaria cirrosa*. Spherical, almost mature unilocular sporangia. Scale 20 µm.


P: *Sphacelaria cirrosa*. Plurilocular sporangia. Scale 20 µm.


Q: *Sphacelaria cirrosa*. Empty and almost mature plurilocular sporangium. Scale 10 µm.

## *Sphacelaria fusca*

**(Hudson) S.F.Gray**

Tufted Dark Brown Feather Weed

**Appearance:** Small irregular, dark brown or reddish brown tufts or hemispherical cushions. The thallus is 0.5-3 cm in height.

**Structure:** Upright branches arise from a mono- or polystromatic crust. Main axes with scattered branches on all sides. Branches are relatively coarse, (20-) 30-80 (-90) µm wide, without rhizoids. Secondary segments are divided by radial longitudinal cell walls which develop a parenchyma without medullary cells. Secondary transverse walls are rare. Hairs occur individually and might be common in the youngest branches.

**Reproduction:** Propagules have a straight stalk with 2-3 protruding uniformly long arms, and in continuation of the stipe a small lens-shaped apical cell. Arms are cylindrical without basal constriction.

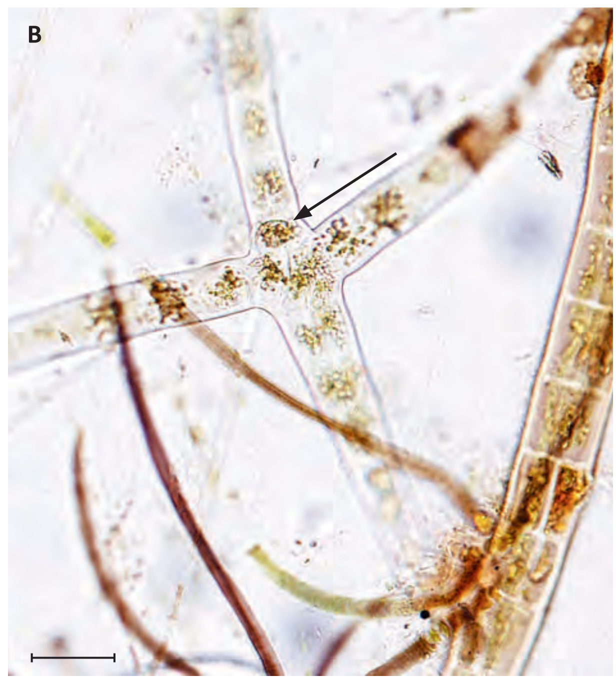
**Habitat:** Epiphytic or on stone at shallow water.

**Resembles:** Reminiscent of Solitary Brown Feather Weed (*S. solitaria*) but the lower part of main axis is particularly coarser. Differs from Pompon Brown Feather Weed (*S. cirrosa*), by the arms of the propagules which are cylindrical without basal constriction. Propagules have a terminal small lens-shaped cell and no hair as in Pompon Brown Feather Weed (*S. cirrosa*).

**Comment:** Prud'homme van Reine (1982, s. 222) mentioned a single collection from Danish waters, but the locality was not very precise: "Jylland, materiale Grunnow 19597 in W [Wien]". Since then, there is only a single collection of the species from Danish waters.

**References:** Prud'homme van Reine (1982, 1993), Keum et al. (2005).


A: *Sphacelaria fusca*. Small tufts. Scale 2 cm. A-B: On stone, west of Nordre Rønner, Læsø, 5 m, 19.8.2005.




B: *Sphacelaria fusca*. Propagule, three cylindrical arms without basal constrictions and a lens-shaped apical cell (arrow). Scale 50 µm.

# *Sphacelaria plumula*

**Zanardini**

Plume Brown Feather Weed

**Appearance:** Tufts of relatively thin uprights, 0.5-0.8 cm in height, with opposite branches.

**Structure:** Base of small creeping filaments from which the regularly branched uprights arise. Main branches have opposite branches in one plane. They arise from mainly all superior secondary segments. Branches are unbranched, and it appears as if their lower part is embedded in the main branches. Upper part of main branches, 53-74 µm in width, while the lower part only, 40-50 µm in width. Secondary segments are 0.5-1 times as long as wide, with the longest in the lower part of the alga. Secondary segments are divided by radiating longitudinal walls and form a parenchyma without medullary cells. There are no secondary transverse walls except in the very basal part of main branches where a few may occur. Downward-growing rhizoids appear, but they do not form a confluent cortex. Hairs are rare.

**Reproduction:** Propagules develop on the branches. They have a stalk cell and are wedge-shaped with two small lateral horns and a small lens-shaped apical cell.


A: *Sphacelaria plumula*. Main branch with opposite branches. Scale 50 µm. A-C: On Whelk (*Buccinum*), Mellemgrund, Lønstrup, dredge, 10-8 m, 2.8.1904. Leg. & det.: Rosenvinge.


B: *Sphacelaria plumula*. Young club-shaped propagule. Scale 20 µm.


C: *Sphacelaria plumula*. Wedge-shaped propagule with two small horns and a small lens-shaped apical cell.
Scale 20 µm.

They are 115-140 µm in height and 103-131 µm in width. Young propagules are club-shaped. Sporangia are not observed in this species from Danish waters.
**Seasonal variation:** Collected in July and August.
**Habitat:** On Whelk (*Buccinum*) and stone, 8-14 m depth.
**Comment:** Perhaps a feather-shaped form of *S. tribuloides* according to Prud'homme van Reine (1993, p. 152).

Collections from Danish waters are sparse, the most recent in the algal herbarium, Natural History Museum of Denmark is from 1904.
**References:** Lund (1950), Prud'homme van Reine (1982, 1993), Rueness (1977).

## *Sphacelaria reticulata*

**Lyngbye**

Netted Brown Feather Weed

**Appearance:** Filamentous alga, appearing as a net with straight or curved branches in one plane. Thalli are typically 1-3 mm in height, but may be 1 cm.
**Structure:** Basal branches are relatively long and unbranched, while the distal branches are closely repeatedly dichotomously branched. Branches, 40-50 µm in width consist of secondary segments which are divided by longitudinal walls and secondary transverse walls. Apical cells are divided into two uniform cells at branching points, so genuine dichotomous branches develop.
**Reproduction:** Reproductive structures unknown.
**Seasonal variation:** Collected in February and September.
**Habitat:** Loose, matted with other unattached algae between Eelgrass (*Zostera marina*).
**Comment:** The species was described by Lyngbye in Hornemann (1818) and has its type locality at North Funen. Here it was collected by phycologists from Hofmansgave in the 19th century, with the last collection in 1867. It has been looked for in vain at the same locality in April 1970 and August 1977 by Prud'homme van Reine (1982), who suspects that it is extinct. Unfortunately, remnants of the collections from Hofmansgave are no longer present in the algal herbarium, Natural History Museum of Denmark.
The species was originally the type species for the genus *Sphacelaria*, but it was proposed that this should be replaced by *S. cirrosa* (Draisma and Prud'homme van Reine, in Draisma et al., 2010).
**References:** Draisma et al. (2010), Lund (1950, *Disphacella reticulata*), Lyngbye (1818, 1819), Prud'homme van Reine (1982).

# *Sphacelaria solitaria*

**(Pringsheim) Kylin**

Solitary Brown Feather Weed

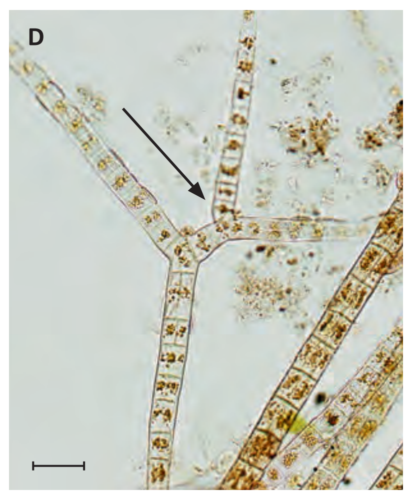
**Appearance:** Small tufts, up to 1.2 cm in height.
**Structure:** Upright main branches, 17-35 µm in width, with scattered sparse branches on all sides. Segments are 1-2 times as long as wide. Secondary segments have 1-2 (-3) radial longitudinal walls. Secondary cross walls not observed in specimens from Danish waters but reported in the alga from Korea. Hairs occur scattered. Base of creeping filaments which may form small discs, the lower part of which may be endophytic in soft host algae.
**Reproduction:** Propagules on stalks have two cylindrical arms and a small apical cell. The arms are symmetrical or of uneven length, and one of them sometimes branched after the second secondary segment, so it appears as if there are two secondary arms.
**Seasonal variation:** Propagules reported in July-August and January. Sporangia not observed in algae from Danish waters.

**Habitat:** Collected on stone, 2-4 m depth, on shell of Whelk (*Buccinum*), stipes of Oar Weed (*Laminaria digitata*) and Forest Kelp (*L. hyperborea*), 9-13 m depth.
**References:** Keum et al. (2001), Lund (1950, *S. furcigera*), Prud'homme van Reine (1982, *S. rigidula*).


A: *Sphacelaria solitaria*. Propagule with two symmetrical arms and a small apical cell. Scale 20 µm. A-D: On small stone. Outside Hygum Church, 2-4 m, 23.8.2000.


B: *Sphacelaria solitaria*. Branches with 2-3 longitudinal walls per segment, no secondary transverse walls. Several consecutive propagules. Scale 50 µm.


C: *Sphacelaria solitaria*. Large apical cell, primary segment, and young hair. Scale 20 µm.




D: *Sphacelaria solitaria*. Old propagule, one of the original arms branched, appearing as if it has two secondary arms (arrow). Scale 50 µm.

# *Sphacelaria tribuloides*

**Meneghini**

Stiff Brown Feather Weed

**Appearance:** Brown tufts of stiff uprights, up to 1-1.5 cm in height.

**Structure:** Base of small irregular discs on short creeping stolons. Uprights are unbranched or irregularly branched, no great difference between main branches and branches as they are approximate uniform in height and (29-) 33-36 (-41) µm in width. The secondary segments have 1-3 longitudinal walls. Secondary transverse walls are rare and only observed in the lower part. Hairs are common.

**Reproduction:** Propagules are wedge-shaped with two lateral horns in the upper end and a small lens-shaped apical cell. They have a stalk cell and are lateral on the upright branches. Propagules are 120-156 µm long and 94-126 µm wide. Young propagules are club-shaped. Sporangia not observed in algae from Danish waters.

**Seasonal variation:** Collected in July.

**Habitat:** On cemented sand.

**Resembles:** The propagules are reminiscent of those found in Plume Brown Feather Weed (*S. plumula*), but this species has uprights which are feather-like and thicker (53-74 µm in width) than the uprights of Stiff Brown Feather Weed (*S. tribuloides*).

**Comment:** Only a single collection from Danish waters, on cemented sand, Hulsig Stene, Aalbæk Bugt, 25.7.1933. According to the notebook of Rosenvinge, No. 11272: *Sphacelaria plumula*, dredge "konkretions of cemented sand 1.5 Kvm [quarter-mile] outside Hulsig" [depth not mentioned].

**References:** Lund (1950), Prud'homme van Reine (1982).


A: *Sphacelaria tribuloides*. Wedge-shaped propagule with two horns and small lens-shaped apical cell. Hulsig Stene, Aalbæk Bugt, 25.7.1933. Leg.: Rosenvinge. Scale 20 µm.

# *Sphacelorbus nanus*

**(Nägeli ex Kützing) Draisma, Prud'homme & H.Kawai**

Dwarf Felt Weed

**Appearance:** Felty or plush-like mats of closely packed filaments, 2-3 mm in height and covers an area of 5-6 cm². Sand grains are commonly retained by the thalli.

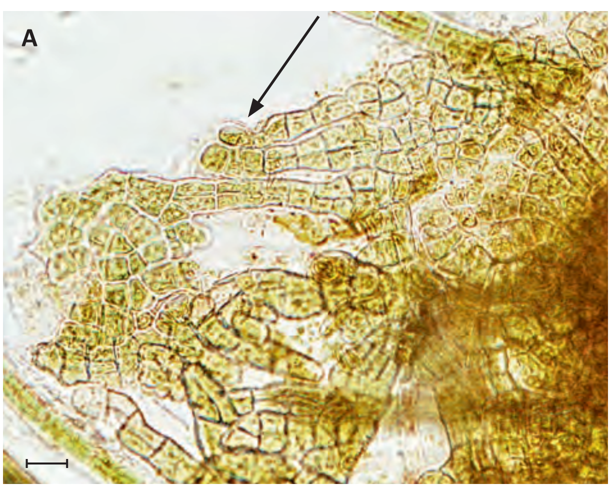
**Structure:** Uprights are typically unbranched or have only sparse and scattered branches. They arise from creeping branches (stolons) or discs. A young disc consists of radiating confluent filaments. Stolons are frequent and run more or less parallel and confluent, and small discs may form from them. Upright branches, (16-) 25-30 (-33) µm in width may have irregular swellings. Segments typically longer than wide with 1-2 (3) longitudinal walls and without medullary cells, secondary transverse walls are rare. There are no pericysts or hairs. Sparse branches develop below the apex and are approximately of the same width as the main branches. In the lower part of thalli, branches may develop into rhizoids or stolons. Rhizoids are slightly thinner and more curved than upright branches. They do not cover the branches as a cortex but entangle branches. Stolons are often slightly thicker than upright branches.

**Reproduction:** Uni- and plurilocular sporangia occur on different individuals. Unilocular sporangia typically occur individually on short stalks of 1-2 cells, occasionally on longer stalks which may be branched. Most unilocular sporangia occur in the lower part of the alga, on the uprights, the basal stolons or the discs. Unilocular sporangia are ellipsoid, ovoid or approximate spherical, 45-66 µm long and 33-45 µm wide. Plurilocular sporangia have a stalk cell and are elongate, approximate cylindrical and frequently slightly curved, 33-125 µm long and 16-25 µm wide. No propagules.

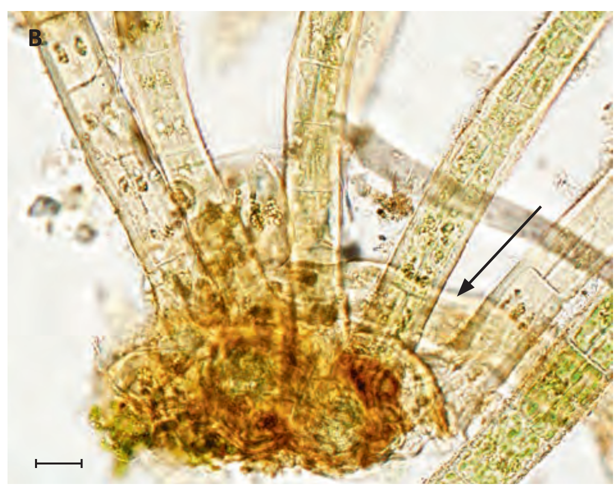
**Seasonal variation:** Perennial, collected in January, March-April and June. Mature unilocular sporangia recorded in January, March and empty unilocular sporangia in April, plurilocular sporangia in January, March, and empty plurilocular sporangia in March.

**Habitat:** On stone, 1 m depth and epiphytic on stipes of Forest Kelp (*Laminaria hyperborea*), 4-10 m depth.

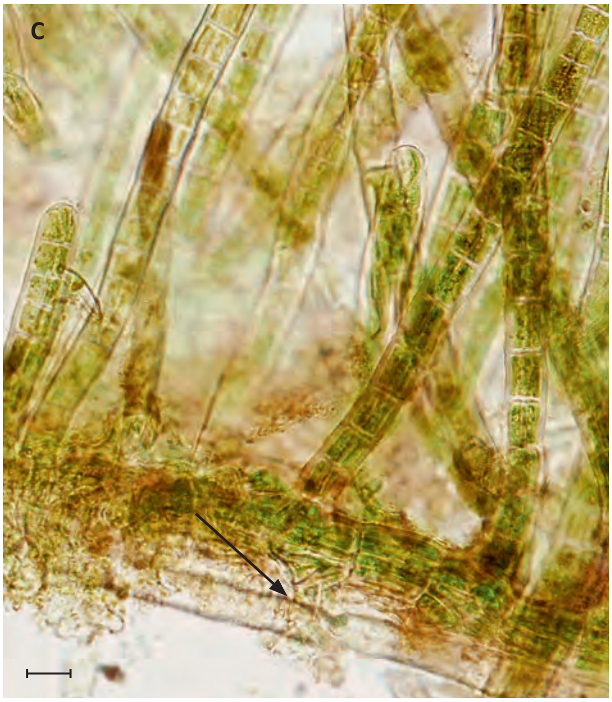
**References:** Draisma et al. (2010), Kylin (1947, *Sphacelaria olivacea)*, Lund (1949, 1950, *S. brittanica*, *S. saxatilis*), Prud'homme van Reine (1982, *S. nana*), Wærn (1952, *S. brittanica)*.



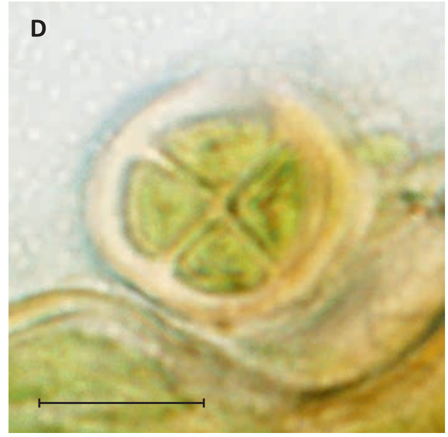

A: *Sphacelorbus nanus.* Basal crust, approximately parallel stolons (arrow). Scale 20 µm. A, D, F: Store Middelgrund, 9.5 m, 14.1.1997.




B: *Sphacelorbus nanus.* Small basal disc with upright branches and a rhizoid (arrow). Scale 20 µm. B, E: Vejrø, 13 m, 27.3.1992.




C: *Sphacelorbus nanus.* Upright and creeping filaments. Rhizoids with attachment pads (arrow). Vejrø, 8 m, 4.3.1997. Scale 20 µm.




D: *Sphacelorbus nanus.* Segment divided by radiating walls, optical transverse section. Scale 10 µm.


E: *Sphacelorbus nanus.* Stalked unilocular sporangia. Scale 20 µm.

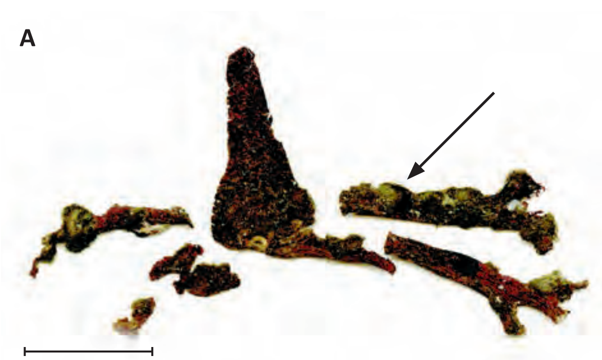

F: *Sphacelorbus nanus.* Stalked plurilocular sporangia from basal system. Scale 20 µm.

## Family: Sphacelodermaceae

# *Sphaceloderma caespitulum*

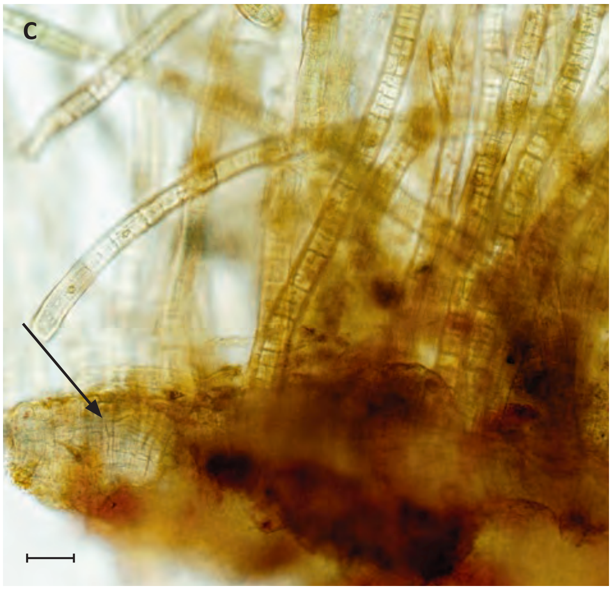
**(Lyngbye) Draisma, Prud'homme & H.Kawai**
Stiff Little Felt Weed

**Appearance:** Stiff, sparsely branched dark brown uprights, often densely packed so they form a mat. Upright branches arise from a robust crust and may consist of several individuals which grow on top of each other. Branches typically c. 2 mm in height but may be up to 8 mm in height.
**Structure:** Crusts are polystromatic and consist of radiating coherent filaments, with marginal growth. Stolons are few and short, no rhizoids. Upright main branches arise from the lowest layer in the crust. They have few branches, not much different from main branches. Branches are uniform in thickness, 21-30 (-33) µm in width. Segments are divided by 1-4 radial longitudinal walls and many secondary transverse walls, but no medullary cells. Pericysts occur, but not many and not very conspicuous.
**Reproduction:** Uni- and plurilocular sporangia on different individuals. Plurilocular sporangia are apical on short stalks which arise from the lower part of upright branches. Unilocular sporangia occur similarly and may be sessile on the crust. Stalks consist of 2-3 segments, with or without longitudinal walls. Unilocular sporangia are ellipsoid to spherical. Plurilocular sporangia are ellipsoid, 86-156 µm long and 62-90 µm wide. Inner walls are thin and dissolve early, so it may be difficult to distinguish them from unilocular sporangia. No propagules.
**Seasonal variation:** Collected in January-October, unilocular sporangia recorded in January and plurilocular sporangia in January-February.
**Habitat:** On stone and epiphytic on the lower part of stipe and haptera of Forest Kelp (*Laminaria hyperborea*). Collected in 4-23 m depth and very common on stone reefs.
**References:** Draisma et al. (2010), Lund (1950, *Sphacelaria caespitula*), Prud'homme van Reine (1982, *S. caespitula*).




A: *Sphaceloderma caespitulum*. Small mats (arrow) on haptera of Forest Kelp (*Laminaria hyperborea*). Dried material. Scale 2 cm. A, D: Stålhage, Hirsholm, 6 m, 3.2.1996.


B: *Sphaceloderma caespitulum*. Basal crust with closely packed upright branches. Per Nilen, 8 m, 16.8.2016. Photo by S. Lundsteen. Scale 1 mm.

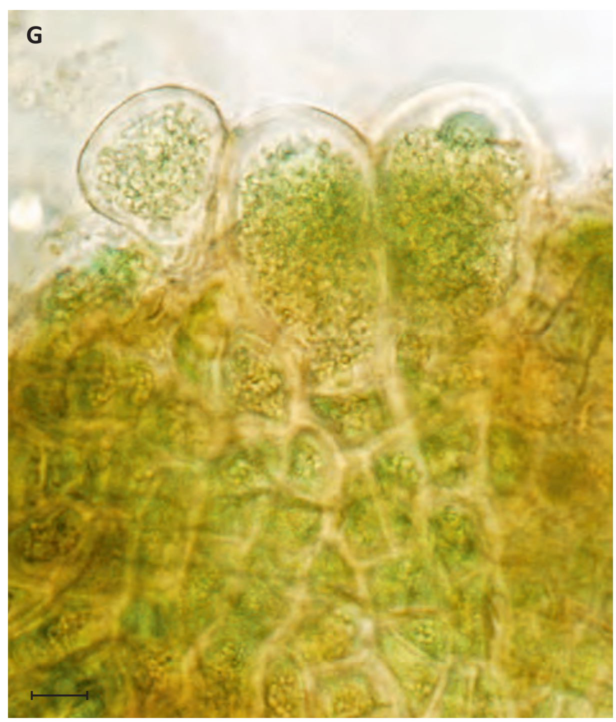



C: *Sphaceloderma caespitulum.* Robust polystromatic crust of upright filaments (arrow), and lower parts of upright branches, (longitudinal section). Kims Top, 14.5 m, 25.8.1993. Scale 50 µm.


D: *Sphaceloderma caespitulum.* Vegetative branch, segments with many secondary transverse walls and a pericyst (arrow). Scale 10 µm.

E: *Sphaceloderma caespitulum.* Plurilocular sporangia on upright branches which arise from the crustose base. Tønneberg Banke, 14.5 m, 16.1.1997. Scale 50 µm.


F: *Sphaceloderma caespitulum.* Plurilocular sporangium. Tønneberg Banke, 11.5 m, 1.2.1996. Scale 10 µm.




G: *Sphaceloderma caespitulum.* Unilocular sporangia, sessile on the crust. Store Middelgrund, 9.5 m, 14.1.1997. Scale 10 µm.

## Family: Stypocaulaceae

# *Halopteris scoparia*

**(Linnaeus) Sauvageau**

**Recent synonym: *Stypocaulon scoparium* (Linnaeus) Kützing**

Sea Flax Weed

**Appearance:** Stiff, richly branched dark brown bushy thalli, 4-10 cm in height.

**Structure:** Upright branches are repeatedly branched with alternating branches close together. Some branches remain short, while others continue growth into new main branches. Branches develop from a small lens-shaped apical cell, from which also one or several true brown algal hairs develop. Thus the hairs arise in clusters in corners of branches. Secondary segments develop into parenchyma with many longitudinal walls and medullary cells. Below the apex, growth of the segments is restricted in length and in width. Loose sterile forms are small and mentioned by Lund (1950) as f. *patentissimum* (Sauvageau) S. Lund and f. *spinulosum* (Lyngbye) Reinke of *Stypocaulon scoparium*. Both of them have protruding branches which are branched in f. *patentissimum* and typically spine-like and unbranched in f. *spinulosum*.

**Reproduction:** Sporangia not observed in the alga from Danish waters.

**Comment:** Typical Sea Flax Weed (*H. scoparia*) probably does not occur in Danish waters. Lund (1950) mentioned a single individual, 9 cm in height, collected by dredge at 15 m depth. This was probably a drift specimen because the species typically grows at 0.5-1 m depth (Kylin, 1947). The drifting forms, f. *patentissimum* and f. *spinulosum* are recorded in the Limfjord, Lillebelt and the district around Samsø, with collections from several localities in the middle of the 19th century, but there are no recent collections in the algal herbarium, Natural History Museum of Denmark.

**References:** Draisma et al. (2010, *Stypocaulon scoparium*), Kylin (1947, *S. scoparium*), Lund (1950, *S. scoparium*), Nielsen (1998, *S. scoparium*), Prud'homme van Reine (1982, figs 16-20, *S. scoparium*).


A: *Halopteris scoparia*. Probably drift individual, mentioned by Lund (1950). Læsø Trindel, 15 m by dredge, 13.7.1892. Leg.: Rosenvinge. Scale 2 cm.

# *Protohalopteris radicans*

**(Dillwyn) Draisma, Prud'homme & H.Kawai**

Mini Mat Weed

**Appearance:** Low extended dark brown mats, approximately 1 cm in height. They consist of closely packed sparsely branched upright branches, which arise from a small basal disc. Individual thalli are often so close together that they become confluent. Algal mats typically retain sand grains and other particles at the base.

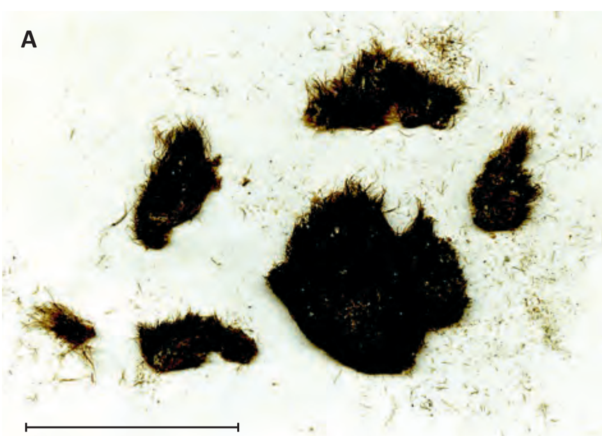
**Structure:** Basal discs of confluent radiating filaments with apical growth. They are monostromatic or become a few cell layers in height by continued upwards growth. Some of the filaments grow beyond the mat margin and become creeping stolons, which may form new discs. Uprights are unbranched or sparsely branched. Branches are uniform in thickness in both main branch and lateral branches, 33-50 µm in width. Most secondary segments are divided by longitudinal and transverse walls, without formation of medullary cells. In surface view, 2-5 longitudinal walls are typically seen. Pericysts are frequent. Protruding rhizoidal filaments are common in the lower part of branches and become entangled with uprights. True brown algal hairs develop pairwise after divisions of a small lens-shaped cell, cut off from the apical cell. Hairs may occur in groups of 4.

**Reproduction:** Unilocular sporangia are sessile or on a unicellular stalk. They are ovoid or spherical, (41-) 53-66 µm long and 45-60 µm wide. They occur on the basal crust or the lower part of upright branches, individually or in pairs. Plurilocular sporangia are cylindrical or ellipsoid on a stalk of 1-4 cells.

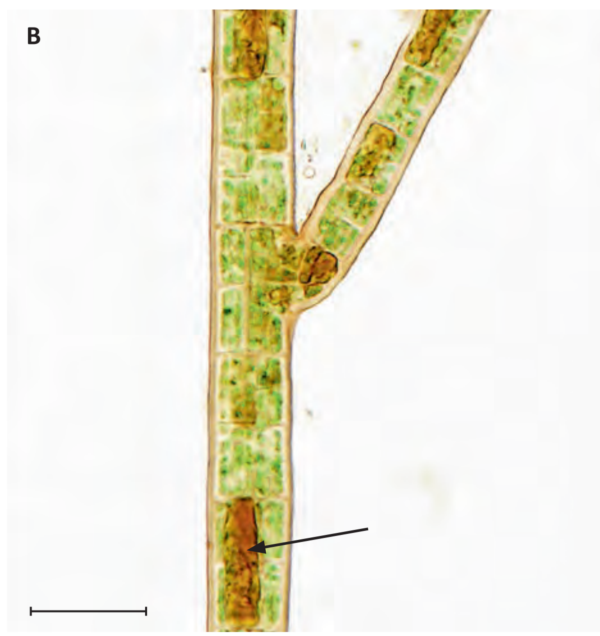
**Seasonal variation:** Collected in January-September, unilocular sporangia recorded in January-February and August, empty unilocular sporangia in July-August and plurilocular sporangia in March.

**Habitat:** On stone and epiphytic on the lower part of Wrack (*Fucus*), common in relatively sheltered localities from the edge of the water to 3-5 (-8) m depth.

**References:** Draisma et al. (2010), Lund (1950, *Sphacelaria radicans*), Prud'homme van Reine (1982, *S. radicans*), Wærn (1945, *S. radicans*).



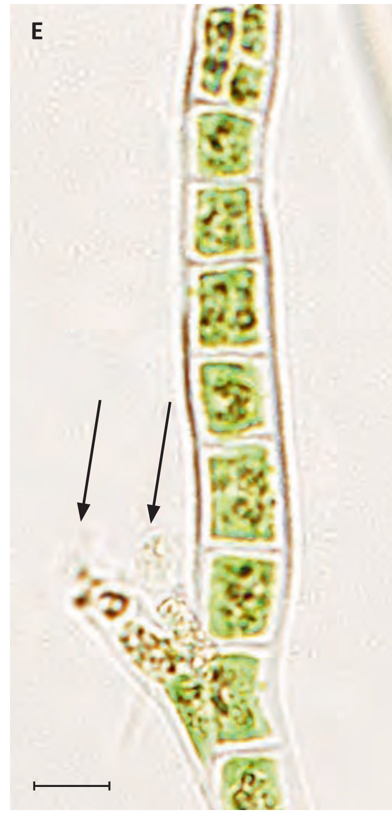

A: *Protohalopteris radicans.* Compact dark brown mats. A sand binding cover on stone, Grenå, 22.8.1891. Leg.: Rosenvinge. Scale 2 cm.



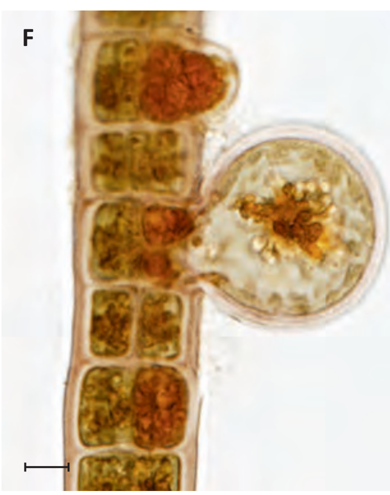

B: *Protohalopteris radicans.* Main branch with a branch and many brown pericysts (arrow). Scale 50 µm. B-D, F-G: Lysegrund, 6 m, 23.8.1996.


C: *Protohalopteris radicans*. Secondary segments divided by many longitudinal and transverse walls. Scale 20 µm.


D: *Protohalopteris radicans*. Apex, a large new apical cell (arrow) and initiation of a young hair. Scale 10 µm.




E: *Protohalopteris radicans*. Branch with 2 hairs, worn down (arrows), they arise from the same cell. Albatros, 5 m, 8.3.1997. Scale 10 µm.




F: *Protohalopteris radicans*. Young unilocular sporangium. Scale 10 µm.


G: *Protohalopteris radicans*. Pair of unilocular sporangia. Scale 10 µm.


H: *Protohalopteris radicans*. Plurilocular sporangium on stipe. Falske Bolsaks, 10.5 m, 5.3.1997. Scale 10 µm.

**Subclass: Fucophycidae · Order: Desmarestiales · Family: Arthrocladiaceae**

## *Arthrocladia villosa*

**(Hudson) Duby**

Fuzzy Branched Weed

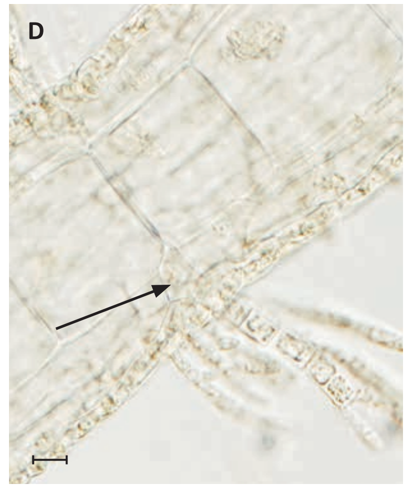
**Appearance:** Alga of terete branches with a distinct main branch and opposite lateral branches, yellow-brown to mid brown, up to 25-35 cm in height. Branches arise regularly, but with long distances between them. Branches are compact and surrounded by whorls of thin, hair-like filaments, 2-4 mm long. Main branch arises from a disc-shaped base. Thallus is soft and flexible, and appears delicate because the thin, hair-like filaments easily fall off after collection.
**Structure:** Uniaxial syntagma with a trichothallic growth zone of short cells at the apex. The trichothallic growth zone forms a short hair-like uniseriate filament with opposite branches outwards, and contributes to the thallus inward. The thallus has a central axis of cylindrical cells, 120-160 µm wide immediately below the apex. Further down in the thallus the axis is surrounded by thin walled colourless elongate cells which decrease in size towards the surface. This consists of slightly elongate angular, relatively thick-walled cells containing several disc-shaped plastids without pyrenoids. Hair-like filaments arise in whorls of 3-4 fascicles around the branches. Young hair-like filaments have opposite branches and cylindrical cells, with several disc-shaped plastids.
**Reproduction:** Series of unilocular sporangia develop in the hair-like filaments. At first, they are in basal cells of opposite branches, but gradually all cells become sporangia. Unilocular sporangia also form in special unbranched filaments where several arise together in proximity of the hair-like filaments.
**Seasonal variation:** Collected in July-October with sporangia.
**Habitat:** On gravel and mollusc shells at considerable water depth. Collected by divers, 10-21 m depth and by dredge, 38 m depth.
**Comment:** The life history was studied in the alga from the Mediterranean Sea by Müller & Meel (1982, as *A. villosa* f. *australis* (Kützing) Hauck) and showed to be heteromorphic with a microthallus, which probably represents monoecious gametophytes, although fertilization was not observed.
**References:** Fletcher (1987), Müller & Meel (1982), Rosenvinge & Lund (1943).

A

A: *Arthrocladia villosa*. Main branch and opposite branches surrounded by hair-like filaments. Scale 2 cm. A, D: Nordøst revet, Hirsholmene, 8 m, 9.8.1977.


B: *Arthrocladia villosa*. Main branch with uniseriate, opposite branched hair-like filaments. Hirsholm, 9 m, 11.8.1973. Scale 50 µm.


C: *Arthrocladia villosa*. Trichothallic growth zone of short cells (arrow). Above this are uniseriate hair-like filaments and below central axial cells surrounded by cortex, and fascicles of hair-like filaments. Scale 50 µm. C, F: Herthas Flak, 8 m, 24.8.1971.




D: *Arthrocladia villosa*. Central axis surrounded by elongate cells covered by small assimilating cells. A fascicle of hair-like filaments arise from the central axis (arrow). Scale 20 µm.


E: *Arthrocladia villosa*. Fascicles of uniseriate unbranched filaments with series of unilocular sporangia (arrow). Gassøjle, Herthas Flak, 20 m, 24.8.2004. Scale 50 µm.


F: *Arthrocladia villosa*. A series of empty unilocular sporangia. Scale 20 µm.

## Family: Desmarestiaceae

### *Desmarestia*

Desmarest's Weeds

Bush-like frond with a distinct main branch. Constructed as a uniaxial syntagma with a conspicuous cortex and a trichothallic growth. Growth zone at the apex forms uniseriate hair-like filaments with opposite branches both outwards and inward. Filaments consist of relatively long cylindrical cells with many disc-shaped plastids. In continuation of the growth zone, a central axis develops covered by cortical tissue which develops from basal cells of hair-like filaments. Further down in the thallus the central axis is surrounded by several layers of colourless, large, irregular cells with thick walls and narrow downward-growing hyphae-like filaments in the centre around the central axis. The surface consists of smaller cells with many disc-shaped plastids. The cells contain sulphuric acid.

The life history comprises microscopic gametophytes and upright sporophytes.

### *Desmarestia aculeata*

**(Linnaeus) J.V.Lamouroux**

Desmarest's Prickly Weed

**Appearance:** Large light brown to dark brown solid, coarse and much branched bushy thalli, up to 1 m in height. Main branch with scattered, and occasionally towards the base, opposite branches, repeatedly branched in one plane. Branches are slightly flattened, oval in transverse section. The margin has characteristic scattered, distichous alternating, 1-2 mm long flat spine-like branchlets. Young shoots are light brown in spring and surrounded by narrow, approximately 0.5 cm long branched hair-like filaments. Later in the year the hair-like filaments are worn off, and branches are dark brown. The main branch is attached by a small, conical base.

**Structure:** Uniaxial syntagma with trichothallic growth, as described for the genus. Some of the hair-like filaments become covered by cortical tissue like the main branches, and become alternating spines



A: *Desmarestia aculeata*. Much branched coarse bushy alga with spiny branches with epiphytic Pompon Brown Feather Weed (*Sphacelaria cirrosa*). Briseis Flak, 5 m, 7.6.1990. Scale 2 cm.

B: *Desmarestia aculeata*. Spring form, young branches surrounded by hair-like filaments. Scale 2 cm. B-C: Herthas Flak, 14 m, 9.4.1991.

when growth is restricted and to long branches when growth continues.

**Reproduction:** Unilocular sporangia develop from vegetative cells and appear as dark brown cells among vegetative surface cells. Upright thalli are sporophytes, which alternate with microscopic filamentous, dioecious male and female gametophytes, according to culture studies by Müller & Lüthe (1981).

**Seasonal variation:** Upright thalli are perennial. New branches with hair-like filaments arise from branch angles of older thalli, in the middle of February. Hair-like filaments remain until May-June and disappear. Sporangia recorded in February.

**Habitat:** On stone and mollusc shells, collected by divers, from a few to 21 m depth (Herthas Flak) and by dredge to 40 m depth (Little Belt).

**References:** Christensen (1980), Fletcher (1987), Müller & Lüthe (1981), Rosenvinge & Lund (1943).



C: *Desmarestia aculeata*. Older alga, only the young branches surrounded by hair-like filaments. Scale 2 cm.

D: *Desmarestia aculeata*. Very young alga. Herthas Flak, 13.5 m, 5.6.1989. Scale 1 cm.



E: *Desmarestia aculeata*. Branches with and without hair-like filaments. Stone reef at Frederikshavn, 3-4 m, 8.3.1973. Scale 1 cm.

F: *Desmarestia aculeata*. Trichothallic growth zone with short cells, hair-like filaments with opposite branches. Below the growth zone, the cortex develops from basal cells of the opposite filaments (arrow). Kims Top, 16 m, 7.6.1995. Scale 20 µm.

# *Desmarestia viridis*

**(O.F.Müller) J.V.Lamouroux**

Desmarest's Green Weed

**Appearance:** Golden-brown to bright reddish brown bush-like thalli with distinct main branch and terete opposite branches. Thallus, up to 45 cm in height, but typically smaller, is smooth and flexible, slightly cartilaginous at base. Branches are in one plane with regularly repeated opposite branches with relatively short distances between branching points. Main axis attached by a disc-shaped or short conical base. Young individuals have branches surrounded by brown, hair-like filaments with opposite branches. Cells contain much sulphuric acid, and the cell sap pH is 1-2. The acid is released when thalli are damaged at collection and cause the alga to become greenish grey and decay easily.

**Structure:** Uniaxial syntagma with trichothallic growth, as described for the genus.

**Reproduction:** Unilocular sporangia develop from vegetative cells and occur among surface cells. Upright sporophytes alternate with monoecious microscopic gametophytes, revealed by culture studies (Fletcher, 1987).

**Seasonal variation:** Upright thalli are annual. Most vigorous growth in May-June, after which the hair-like filaments are lost. Collected in March-October and once in January (older collection). Unilocular sporangia recorded in May-August and October.

**Habitat:** On stone, mollusc shells and poles, common at shallow water, 1-2 m depth. Collected by divers to 22 m depth and by dredge to 30 m depth in Kattegat, and to 38 m depth in the North Sea.

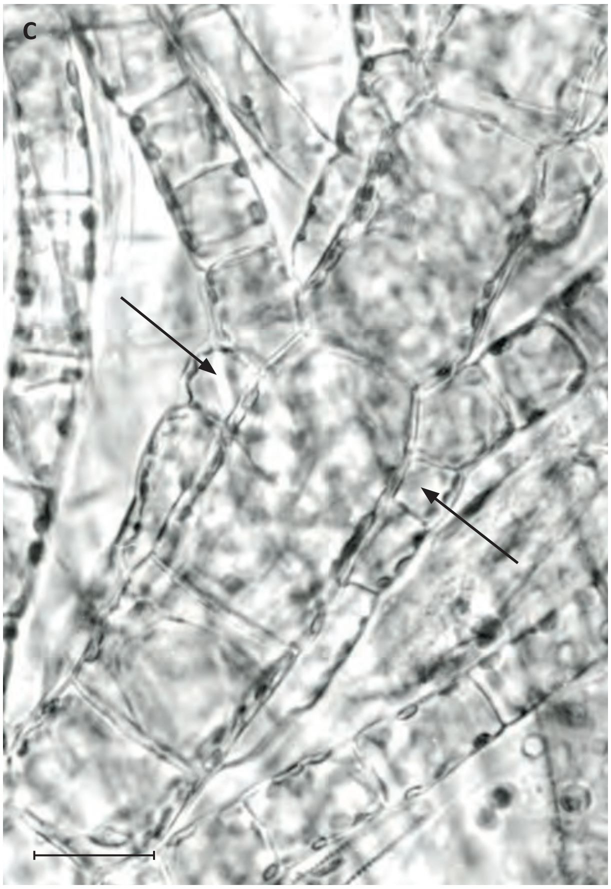
**References:** Christensen (1980), Fletcher (1987), Rosenvinge & Lund (1943).

A

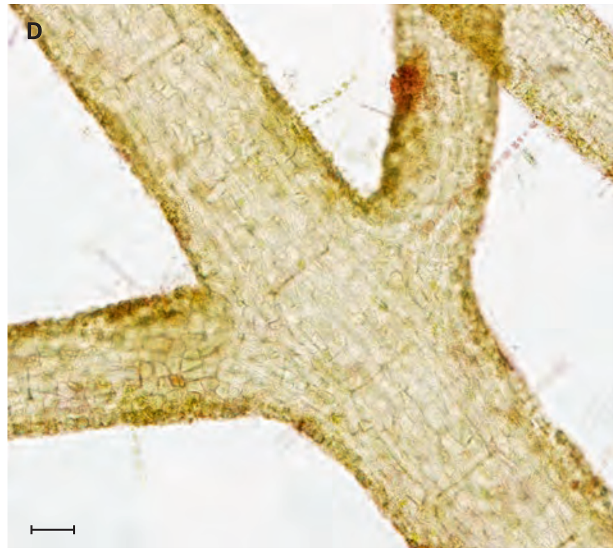
A: *Desmarestia viridis*. Distinct main axis with opposite branches. Briseis Flak, 5 m, 7.6.1990. Scale 2 cm.

B

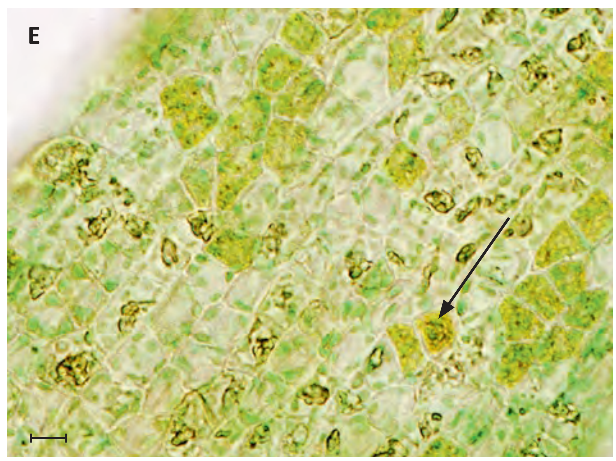
B: *Desmarestia viridis*. Young alga, branches surrounded by hair-like filaments. Schultz's Grund, dredge, 9-13 m, 3.6.1989. Scale 1 cm.




C: *Desmarestia viridis*. Young cortical filaments develop from basal cells of the opposite hair-like filaments (arrows). Schultz's Grund, 4.5 m, 25.3.1992. Scale 20 µm.




D: *Desmarestia viridis*. Opposite branches, central axis visible through the cortex as a series of cross walls in centre of main branch. Optical longitudinal section. Tønneberg Banke, 15 m, 20.8.1991. Scale 50 µm.




E: *Desmarestia viridis*. Surface of vegetative cells with disc-shaped plastids and unilocular sporangia (arrow). Schultz's Grund, 15 m, 10.8.1992. Scale 10 µm.

**Order: Ectocarpales · Family: Acinetosporaceae**

## *Acinetospora crinita*

**(Carmichael) Sauvageau**

Brown Fairy Hair

**Appearance:** Delicate branched bush-like alga, up to 8 cm in height and commonly intertwined with other algae.

**Structure:** Uniseriate filaments, 30-56 µm wide, with few scattered branches which often arise at 90° branch angle. Branches terminate in relatively long narrow cells (false hairs) and below these a growth zone of short cells typically occurs. Diffuse growth also occurs and is typical in old branches. Cells are cylindrical, 1-4 times as long as wide. Upright branches arise from creeping filaments, which are attached by rhizoids or short branches (crampon). Young cells contain many disc-shaped plastids, each with a single pyrenoid. Plastids become slightly elongate to approximately filiform in older cells.

**Reproduction:** In Danish waters monosporangia are the only reproductive structure observed in Brown Fairy Hair (*A. crinita*) in nature. Monosporangia are approximately spherical, 45-53 µm long and 32-42 µm wide, sessile or on a stalk cell. They occur individually or in small groups with 2-3 monosporangia on the same stalk cell. In culture studies of the alga from Danish waters by Pedersen & Kristiansen (2001), germinated monospores developed into filaments on which monosporangia or two different kinds of plurilocular sporangia developed. The development was dependent on physical conditions such as temperature and salinity.

**Seasonal variation:** Collected in July-August with monosporangia.

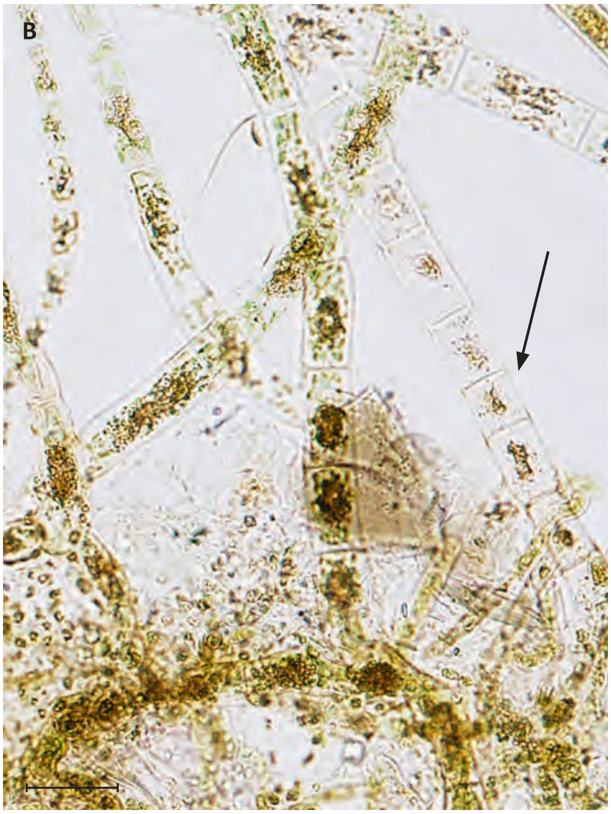
**Habitat:** On Eelgrass (*Zostera marina*) or loose, entangled with other algae such as Black Siphon Weed (*Vertebrata fucoides*), Cotton Wool Weeds (*Ectocarpus* spp.) and Green Branched Weeds (*Cladophora* spp.), 3-9 m depth.

**Comment:** Different reproductive structures are reported from other geographic areas with a large variation in the occurrence of the different kinds. There are various plurilocular sporangia, unilocular sporangia, monosporangia and vegetative reproduction by fragments. A survey is presented by Pedersen & Kristiansen (2001) and Kim (2010) with relevant references. See also *Feldmannia paradoxa*.

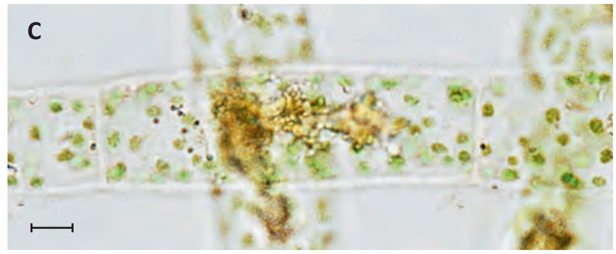
**References:** Kim (2010), Kornmann (1953), Kornmann & Sahling (1977), Pedersen & Kristiansen (2001), Rosenvinge & Lund (1941, *A. pusilla*).

A

A: *Acinetospora crinita*. Delicate branched alga around Black Siphon Weed (*Vertebrata fucoides*). Vageren på Mullerne in East 2.5 Kvm [quarter-mile], Nissum Bredning, 5 m, 26.7.1905. Leg.: Rosenvinge. Scale 2 cm.




B: *Acinetospora crinita.* Creeping and sparsely branched upright filaments with diffuse growth (arrow). Scale 25 µm. B-F: Læsø Trindel, 5 m, 20.8.1991.




C: *Acinetospora crinita.* Relatively long vegetative cell, many disc-shaped plastids, each with 1 pyrenoid. Scale 10 µm.


D: *Acinetospora crinita.* Young monosporangium on stalk cell of older sporangium. Scale 10 µm.



E: *Acinetospora crinita.* Sessile monosporangium. Scale 10 µm.

F: *Acinetospora crinita.* Monosporangium on stalk cell. Scale 10 µm.

# *Feldmannia irregularis*

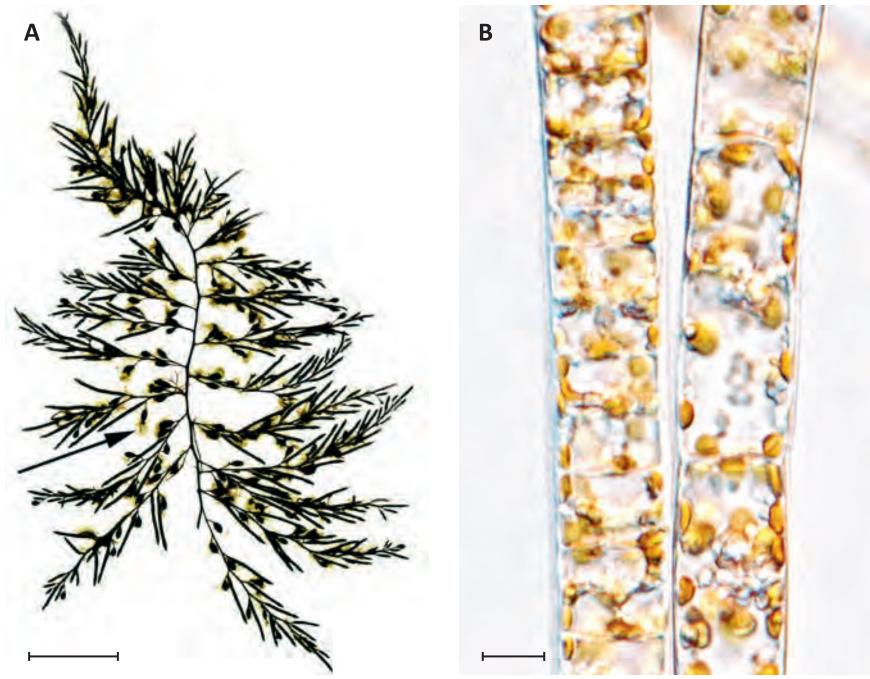
**(Kützing) Hamel**

Feldmann's Irregular Weed

**Appearance:** Delicate, branched brown tufts, 1-3 cm in height.

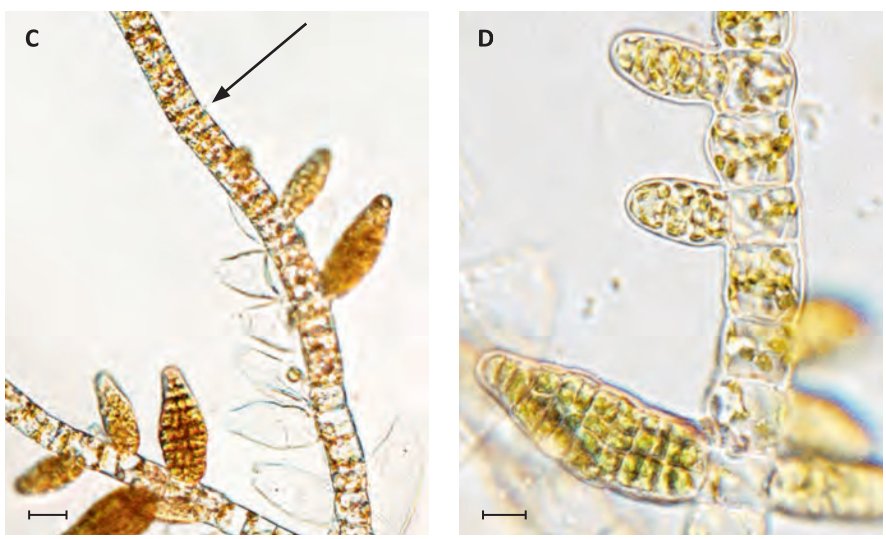
**Structure:** Uniseriate filaments arise from creeping, slightly coalescent filaments. Upright filaments are much branched with scattered branches on all sides. An intercalary growth zone typically occurs below an apical false hair, and other growth zones may occur further down in the alga. Branches are of uniform thickness, but often decrease in width towards the apex. Main branches 30-45.5 µm in width, while the lateral branches are thinner. Cylindrical to barrel-shaped cells are 1-3 (-4) times as long as wide, with shorter cells in the growth zones. Each cell contains many disc-shaped plastids.

**Reproduction:** Plurilocular sporangia are lateral,




A: *Feldmannia irregularis*. Small brown tufts (arrow). Scale 2 cm. A-D: On Wire Weed (*Sargassum muticum*), northern harbour basin, Vesterø Havn, Læsø, 0.5 m, 12.8.2015.

B: *Feldmannia irregularis*. Cylindrical vegetative cells, many disc-shaped plastids. Scale 10 µm.




C: *Feldmannia irregularis*. Branch with plurilocular sporangia below the growth zone (arrow). Scale 20 µm.

D: *Feldmannia irregularis*. Plurilocular sporangia, ovoid or elongate with a conical apex. Scale 10 µm.

scattered or in short unilateral series, rarely opposite, typically sessile, rarely on a stalk-cell and often arise from short intercalary cells of branches. They are elongate ovoid, ellipsoid with an oblique base and a conical top, or approximate cylindrical with a rounded apex, 43-63 µm long and 21-30 µm wide. Unilocular sporangia may occur. They are ellipsoid to obovate, 28-35 µm long and (17.5-) 19-23 µm wide.

**Seasonal variation:** Only few collections from Danish waters, July-August and October. Plurilocular sporangia recorded in July-August and October and unilocular sporangia in July.
**Habitat:** Epiphytic on Wire Weed (S*argassum muticum*) and on other algae, 0.5-5.5 m depth.
**References:** Pedersen & Kristiansen (2001), Rosenvinge & Lund (1941, *Ectocarpus irregularis*), Womersley (1987).

## *Feldmannia paradoxa*

**(Montagne) Hamel**

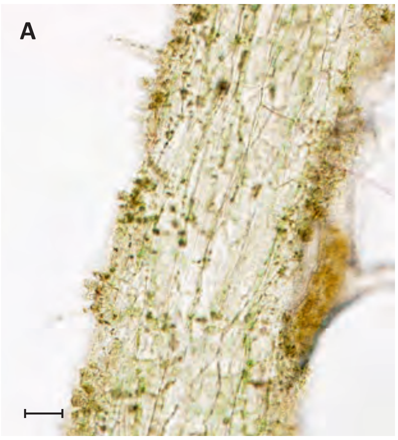
Lund mentioned some algae from the Limfjord and the Northern Kattegat as *F. paradoxa* (Rosenvinge & Lund, 1941), based on notes left by Rosenvinge. These algae are probably different species. The algae from the Limfjord are possibly *Acinetospora crinita,* as Rosenvinge also suspected. They have protruding branches, cells up to 5 times as long as wide and also protruding plurilocular sporangia. The algae from the Northern Kattegat were unbranched or sparsely branched, with intercalary growth zones below false hairs. There were algae with variable thickness of the filaments but none with opposite branches. Plurilocular sporangia were often on a stalk-cell and, in some cases, opposite. Some of the algae were similar to *Hincksia ovata* var. *intermedia*, although filaments are thinner, and other were similar to *F. irregularis*, perhaps a deviating form. None of the algae can with certainty be referred to *F. paradoxa*, which has opposite branches and plurilocular sporangia on stalk-cells, opposite or opposite a branch according to Womersley (1987). It is therefore uncertain if *F. paradoxa* occurs in Danish waters.

## *Herponema desmarestiae*

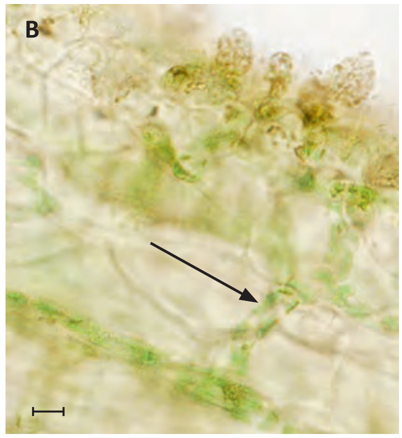
**(H.Gran) Cardinal**

Creepy Brown Weed

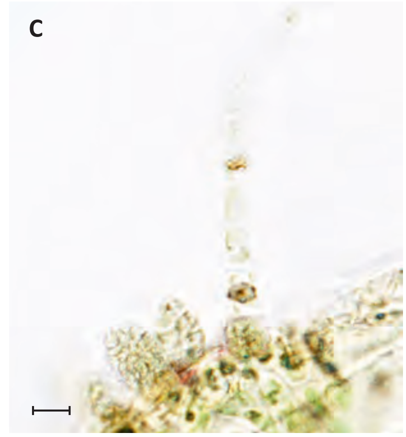
**Appearance:** Microscopic, endophytic filaments with a few filaments outside the host. Visible with a magnifying glass as an uneven cover on the surface in the lower part of the host alga, Desmarest's Green Weed (*Desmarestia viridis*).
**Structure:** Uniseriate, endophytic filaments, 7-8 µm in width, with scattered branches. A few of the filaments grow out of the host, 9-10 µm wide at the base and terminate in false hairs of long slender cells. Cylindrical vegetative cells contain several disc-shaped plastids.
**Reproduction:** Unilocular sporangia are ovoid, 17-25.5 µm in height and 11.5-18 µm in width. They are sessile or have a few-celled stalk and are scattered on the filaments. The sporangia grow out of the host from endophytic filaments or sessile on the free filaments, which terminate in false hairs.
**Seasonal variation:** Collected in August-September, with sporangia.
**Habitat:** Endophytic in Desmarest's Green Weed (*Desmarestia viridis*). On stone reefs, 6-18 m depth.
**References:** Cardinal (1964), Kylin (1947, *Feldmannia desmarestiae*).




A: *Herponema desmarestiae*. Endophytic filaments with unilocular sporangia and false hairs outside the host alga. Scale 50 µm. A-C: In *Desmarestia viridis*, Tønneberg Banke, 13 m, 20.8.1991.




B: *Herponema desmarestiae*. Endophytic filaments (arrow) in optical longitudinal section, with unilocular sporangia outside the host alga. Scale 10 µm.




C: *Herponema desmarestiae*. Unilocular sporangia and a false hair outside the host alga. Scale 10 µm.

## *Hincksia*

Hincksia's Weeds

**Appearance:** Delicate yellow-brown or dark brown bushy algae.
**Structure:** Upright thalli consist of uniseriate filaments with scattered and opposite branches. Cells are cylindrical to barrel-shaped and relatively short, in the basal part often 0.5-1.5 times as long as wide. Growth is diffuse. Each cell contains many disc-shaped plastids with pyrenoids. Upright branches arise from creeping filaments which are typically closely packed.
**Reproduction:** Uni- and plurilocular sporangia are mainly sessile.
**Resembles:** Pylaie's Brown Filaments (*Pylaiella littoralis*) reminiscent of Hincksia's Weeds (*Hincksia* spp.) but has intercalary uni- and plurilocular sporangia and the filaments are typically slightly twisted together. Feldmannia's Weeds (*Feldmannia* spp.) also appears similar but has intercalary growth zones.

**Identification key to species of *Hincksia***

| | | |
|---|---|---|
| 1a. | Delicate thalli, main branches, 15-35 µm wide. Sporangia ovoid, often opposite or opposite a branch | *H. ovata* |
| 1b. | Slightly coarser thalli with relatively thick main branches | 2 |
| 2a. | Unilateral branches, plurilocular sporangia in series on the adaxial side of branches and close to each other | *H. hincksiae* |
| 2b. | Scattered and opposite branches. Sporangia mutually free | 3 |
| 3a. | Main branches ≥ 60-80 µm in width, opposite branches common. Sporangia individual and wide ovoid | *H. granulosa* |
| 3b. | Main branches 25-56 µm in width, branches scattered, occasional unilateral or opposite. Sporangia elongate in unilateral series | *H. sandriana* |

# *Hincksia granulosa*

**(Smith) P.C.Silva**

Hincksia's Granular Weed

**Appearance:** Delicate, branched dark brown bushy alga, 8-15 cm in height.

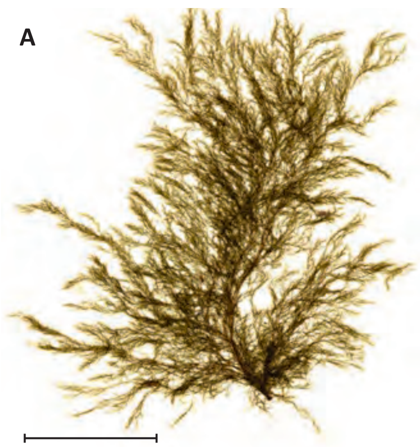
**Structure:** Thalli are much branched with distinct main branches, 60-80 (-116) µm wide, with opposite, scattered and unilateral lateral branches. Branches arise with open angles, they decrease in width towards the apex, and cells become elongate, 6-8 times as long as wide (false hairs). In the lower part of the alga rhizoidal filaments are common, forming a cortex around the lower part of main branches. Cells are barrel-shaped and relatively short, 0.5-1.5 times as long as wide, and contain many disc-shaped plastids.

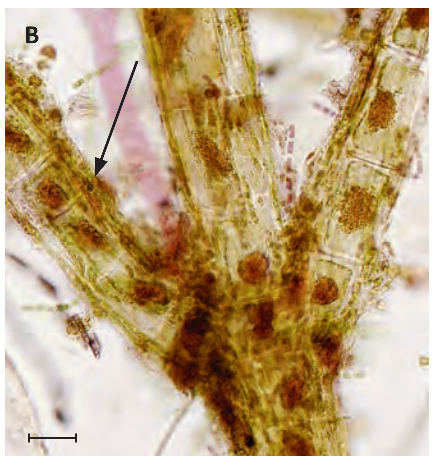
**Reproduction:** Plurilocular sporangia are typically individual, sessile on the adaxial side of branches, and in rare cases on a stalk cell. Sporangia are broad ovoid with a wide base, 60-90 (-120) µm long and 38-53 (-65) µm wide, and often slightly curved towards the branch on which they occur. Unilocular sporangia not observed in specimens from Danish waters.

**Seasonal variation:** Collected in May-August and October. Plurilocular sporangia recorded in July-August.

**Habitat:** Epiphytic on larger algae, the bryozoan Hornwrack (*Flustra foliacea*) and the mollusc Common Pelican's Foot (*Aporrhais pespelecani*). Collected at 0.5 m depth and by dredge to 31 m depth in the North Sea.

**References:** Rosenvinge & Lund (1941, *Ectocarpus granulosus*), Rueness (1977, *Giffordia granulosa*).




A: *Hincksia granulosa*. Dark brown bushy alga, branches on all sides. Stone reef at Frederikshavn, 2 m, 9.7.1973. Scale 2 cm.

B: *Hincksia granulosa*. Main branch with opposite branches covered by narrow rhizoidal filaments (arrow). Herthas Flak, 13 m, 28.8.1993. Scale 50 µm.



C: *Hincksia granulosa*. Vegetative cells with many disc-shaped plastids, cells of uneven length, diffuse growth. Scale 10 µm.
C-D: Tile works, Helligsø, 3.5 m, 22.8.2000.

D: *Hincksia granulosa*. Wide plurilocular sporangium. Scale 20 µm.

## *Hincksia hincksiae*

**(Harvey) P.C.Silva**

Hincksia's Retro Weed

**Appearance:** Dark brown bushy alga, up to 3.5 cm in height with branches close together.

**Structure:** Much branched with unilateral branches typically curved backwards and main branches, 40-60 µm wide. Cells are short and barrel-shaped with many disc-shaped plastids. Lower part of main branches covered by a cortex of rhizoids.

**Reproduction:** Plurilocular sporangia in unilateral, closely packed series on the adaxial side of branches. They are conical, and wider in the lower part, so that they touch each other, giving the branches a serrated outline. Approximately spherical unilocular sporangia occur in specimens at Helgoland but not recorded in those from Danish waters.

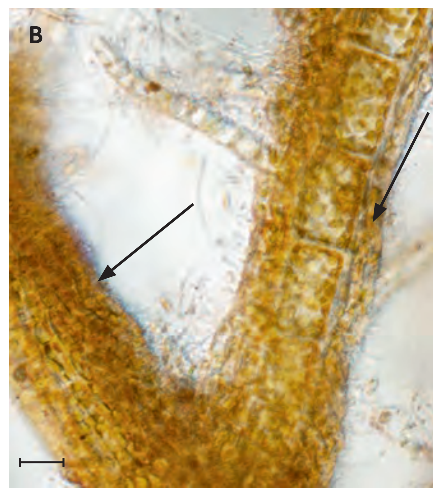
**Seasonal variation:** Collected in April, August-September and November. Plurilocular sporangia recorded in July-August.

**Habitat:** On stone and larger algae, 1 m depth.

**References:** Kornmann & Sahling (1977, *Giffordia hincksiae*), Parodi & Müller (1994), Rueness (1977, *G. hincksiae*).

A: *Hincksia hincksiae*. Dark brown bushy algae with dense branching. Epiphytic on Laver (*Porphyra* sp.). On boulder on shore below the lighthouse, Hirtshals, shallow water, 4.8.1974. Leg.: Aa. Kristiansen. Scale 2 cm.

B: *Hincksia hincksiae*. Lower part of branches with conspicuous rhizoidal cortex (arrows). Scale 20 µm. B, D-E: Below the lighthouse, Hirtshals, drift, 31.7.2017.


C: *Hincksia hincksiae*. Small alga on Oar Weed (*Laminaria digitata*). On boulder below the lighthouse, Hirtshals, shallow water, 28.8.1972. Scale 2 cm.

D: *Hincksia hincksiae*. Backwards curved branch with closely packed plurilocular sporangia. Scale 20 µm.

E: *Hincksia hincksiae*. Branch which is curved backwards. Scale 20 µm.



## *Hincksia ovata*

**(Kjellman) P.C.Silva**

Hincksia's Northern Weed

**Appearance:** Small tufts or delicate branched brown bushy alga, 1-2 cm in height.

**Structure:** Upright main branches have scattered and many opposite branches. Branches may arise from 2-3 consecutive cells, and thus appear in short series. Some individuals have pointed branches, whereas others terminate in false hairs. Main branches, 15-35 µm wide, consist of cylindrical cells, 1-2 (-3) times as long as wide. Cells contain many disc-shaped plastids. Branches terminate in false hairs in var. *intermedia* with an intercalary growth zone just below the hairs. Such specimens were previously referred to a separate species, *H. intermedia* (Rosenvinge) P.C.Silva.

**Reproduction:** Uni- or plurilocular sporangia are ovoid, sessile or seldom on a stalk cell, typically opposite or opposite a branch. Plurilocular sporangia are common and typically on 2-3 consecutive cells. Sporangia in var. *intermedia* are typically scattered and occasional unilateral.

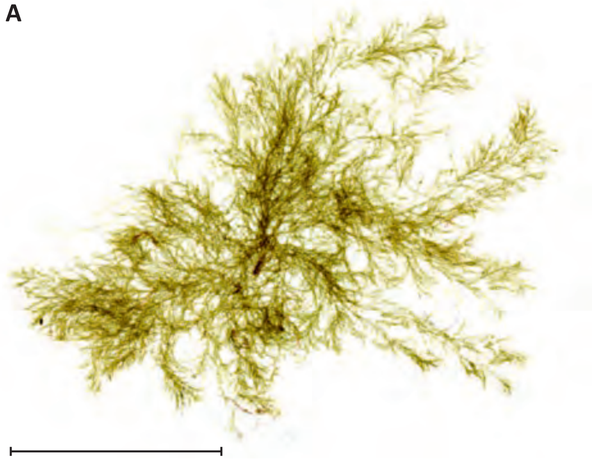
**Seasonal variation:** Collected in February-October. Plurilocular sporangia recorded in May-June and August and unilocular sporangia in June.

**Habitat:** On stone, larger algae, Eelgrass (*Zostera marina*), hydroids and mollusc shells, 0.5-21 m depth. The variety *intermedia* recorded on a mollusc shell.

**Comment:** Pedersen (1979) studied *H. ovata* from Greenland in culture. He found a direct life history in which swarmers from plurilocular sporangia germinated and developed a microthallus, from which uprights arose. Large morphological variation was observed in relation to different physical conditions. He found an intercalary growth zone below false hairs in this material, which grew in dense cultures, and thus showed that the variation of *H. ovata* encompasses specimens previously known as *H. intermedia*.

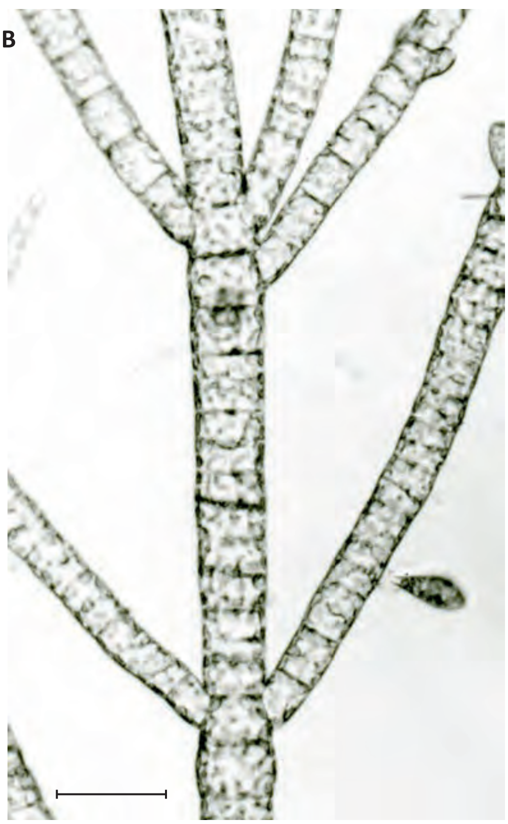
**References:** Kornmann & Sahling (1977, *Giffordia fuscata*), Pedersen (1979a, *G. ovata*, 2011), Rosenvinge & Lund (1941, *Ectocarpus ovatus*, *E. ovatus* var. *intermedia*).

A

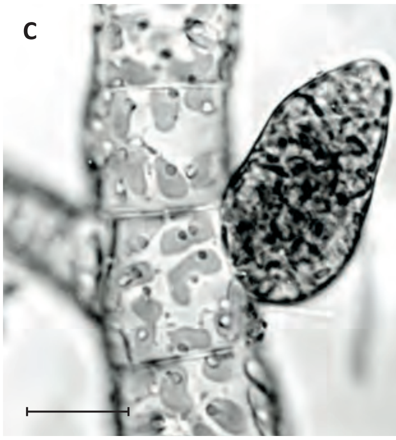


A: *Hincksia ovata*. Delicate branched bushy alga. Borfeld, Nordre Rønner, Læsø, 6.5 m, 22.5.1988. Scale 1 cm.

B



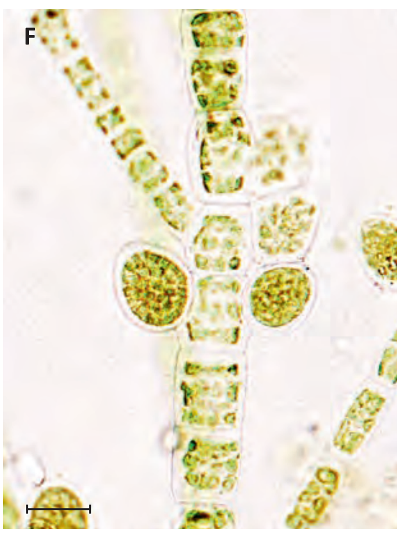
B: *Hincksia ovata*. Opposite branches. Diffuse growth. Scale 50 µm. B-C: Vejrø, 9 m, 26.3.1992.

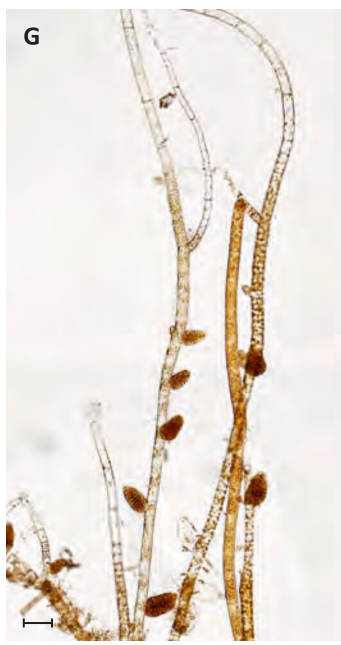


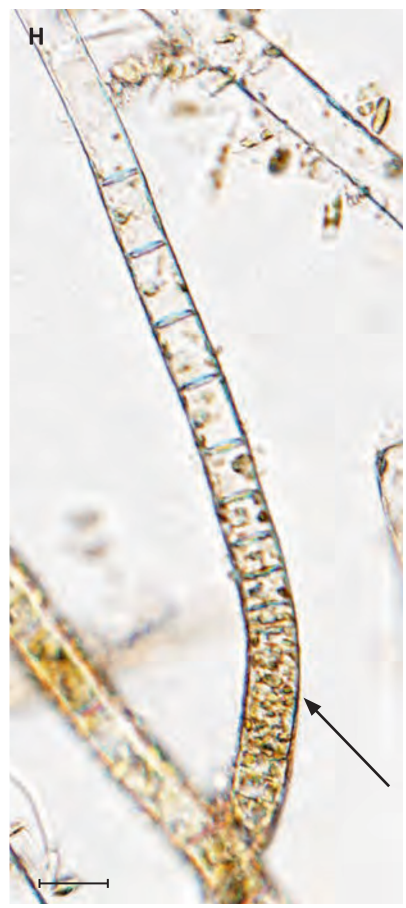

C: *Hincksia ovata*. Vegetative cells, many disc-shaped plastids with pyrenoids and a plurilocular sporangium. Scale 10 µm.


D: *Hincksia ovata*. Empty plurilocular sporangium with apical aperture. Scale 10 µm. D-E: Kims Top, 18 m, 5.6.1993.


E: *Hincksia ovata*. Plurilocular sporangia, opposite or opposite a branch with pointed apex. Scale 20 µm.




F: *Hincksia ovata*. Unilocular sporangia. Kims Top, 16 m, 7.6.1995. Scale 20 µm.

G: *Hincksia ovata*. Upright sparsely branched filaments with terminal false hairs and scattered plurilocular sporangia. Scale 50 µm. G-H: On shell of Baltic Tellin (*Limecola* (*Macoma*) *balthica*), Beach south of Vesterø Havn, Læsø, drift, 27.8.2014.

H: *Hincksia ovata*. False hair above an intercalary growth zone (arrow). Scale 20 µm.

# *Hincksia sandriana*

**(Zanardini) P.C.Silva**

Hincksia's Yellow-brown Weed

**Appearance:** Delicate branched yellow-brown bushy alga, up to 12 cm in height.

**Structure:** Main branches with several orders of scattered branches with a tendency to be unilateral on the adaxial side of branches. Main branch, 25-56 µm wide, with slender branches decreasing in width towards the apex. Cells in lower part of the alga are 0.5-1.5 times as long as wide. They contain many discshaped plastids. Downward-growing rhizoids may occur at the base, but never forming a closely coherent layer.

**Reproduction:** Plurilocular sporangia are elongate ovoid, 28-47 (-60) µm long and 10.5-21 µm wide. They are typically slightly curved, and sessile in unilateral series between the youngest branches.

**Seasonal variation:** Collected in May-October. Plurilocular sporangia recorded in June-August.

**Habitat:** Epiphytic on larger algae, hydroids and tunicates (Ascidiaceae). In shallow water and collected by divers to 18 m depth and by dredge to 37.5 m depth.

**References:** Kornmann & Sahling (1977, *Giffordia sandriana*), Rosenvinge & Lund (1941, *Ectocarpus sandrianus*).


A: *Hincksia sandriana.* Delicate yellow-brown bushy alga. The small basin near the outer end at the sheltered side of the northern harbour jetty, Frederikshavn, 1 m, 13.7.1971. Leg.: T. Christensen. Scale 2 cm.


B: *Hincksia sandriana.* Unilateral, scattered branches and plurilocular sporangia. Kims Top, 18 m, 5.6.1993. Scale 50 µm.

C: *Hincksia sandriana*. Vegetative cells with many disc-shaped plastids (arrow). Sessile, slightly curved plurilocular sporangia. Kims Top, 18 m, 1.6.1992. Scale 20 µm.

## *Pogotrichum*

Brown Beard Weeds

Terete unbranched filiform algae, which are uniseriate or in part a parenchyma, with an apical cell. Vegetative cells with many disc-shaped plastids. No hairs.

**Identification key to species of *Pogotrichum***

| | | |
|---|---|---|
| 1a. | Thin uniseriate or parenchymatous threads, up to 45 µm in width and 1 cm in height | *P. filiforme* |
| 1b. | Club-shaped thalli, 250 µm in width and 4-5 cm in height | *P. setiforme* |

# *Pogotrichum filiforme*

**Reinke**

Fine Brown Beard Weed

**Appearance:** Thin threads which occur in distinct tufts and arise from a disc-shaped base. They may be so numerous that they form a hairy cover up to 1 cm in height.

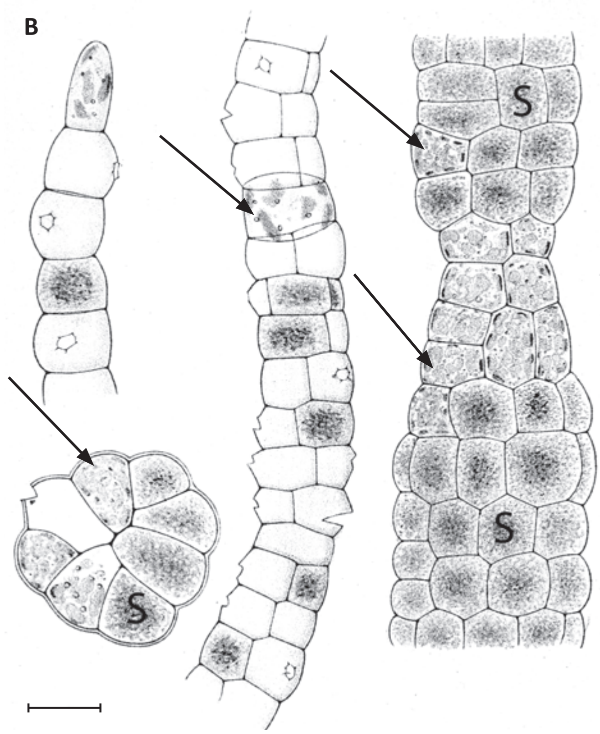
**Structure:** Base of uniseriate, creeping filaments, confluent to a monostromatic disc. Young upright threads are uniseriate with an apical cell, but have diffuse growth. Cells in older thalli are longitudinally divided one or several times and the parenchymatous threads appear segmented. Inner cells are colourless and only slightly different in size from outer cells which contain many disc-shaped plastids with pyrenoids. Threads are 37-45 µm in width. Many rhizoids arise from the basal part. There are no hairs.

**Reproduction:** Plurilocular sporangia develop from vegetative cells in both upright and creeping filaments. Vegetative cells divide to become plurilocular sporangia. It is typical that all cells of a segment and those in many consecutive segments become sporangia, without a noticeable increase in width of the thread. Unilocular sporangia not recorded in the alga from Danish waters, but observed in other localities (Fletcher, 1987).

**Seasonal variation:** Only a few collections in Danish waters, June-July with sporangia.

**Habitat:** Epiphytic on Serrated Wrack (*Fucus serratus*)


A: *Pogotrichum filiforme.* A hairy cover on a torn off upper part of Sugar Kelp (*Saccharina latissima*). Vejrø, 5 m, 8.6.1989. Scale 2 cm.




B: *Pogotrichum filiforme.* Uniseriate apex, transverse section of a thread and fertile filaments. Vegetative cells (arrows), sporangia (S), both mature and empty. After Kuckuck (1899). Scale 20 µm.

and Sugar Kelp (*Saccharina latissima*), 0.5-25 m depth.
**Resembles:** Fine Bundle Weed (*Leptonematella fasciculata*) is another unbranched epiphytic brown algal thread. It differs from Fine Brown Beard Weed (*P. filiforme*) by the sporangia, which develop from vegetative cells divided by both longitudinal and transverse walls, and the fertile area of threads becomes broader than vegetative parts.
**Comment**: Culture studies of Fine Brown Beard Weed (*P. filiforme*) from Greenland by Pedersen (1978b) showed a direct life history. The swarmers from plurilocular sporangia germinated and developed creeping filaments from which new upright filaments arose. Intercalary sporangia developed from both creeping and upright filaments.
**References:** Fletcher (1987), Kuckuck (1899), Pedersen (1978b), Rosenvinge & Lund (1947, fig. 4, *Litosiphon filiformis*).

## *Pogotrichum setiforme*

**(Rosenvinge) P.M.Pedersen**
Bristle Brown Beard Weed

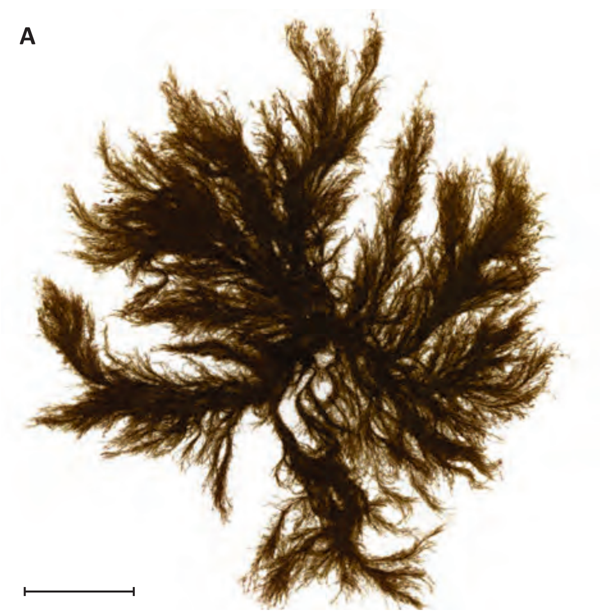
**Appearance:** Thread-like thalli are slightly club-shaped, 4-5 cm in height. The upper part is approximately 250 µm in width, but narrower at the base.
**Structure:** In the central part of the thallus there is a medulla of relatively large, pale cells and a cortex of irregularly angular cells. Towards the base the cells are elongate with many rhizoids.
**Reproduction:** Unilocular sporangia form from surface cells. Sporangia are 51-60 µm in length and 34-42 µm in width.
**Seasonal variation:** Collected in May with unilocular sporangia.
**Habitat:** There is only a single collection from Danish waters, obtained at the harbour jetty, Aggersund, 6.5.1895.
**Comment:** Differs from *P. filiformis* by being larger, but whether it is a separate species is questionable, according to Pedersen (1978b).
**References:** Pedersen (1978b), Rosenvinge & Lund (1947, *Litosiphon setiformis*).

## *Pylaiella littoralis*

**(Linnaeus) Kjellman**

Pylaie's Brown Filaments

**Appearance:** Finely branched yellow-brown or dark brown tufts or bushy algae, 7-15 cm in height. Filaments have a tendency to be twisted together.
**Structure:** Uniseriate, much branched filaments with scattered and opposite branches on all sides. Branches terminate in a vegetative cell or in false hairs. Thickness of the filaments varies, typically, 20-50 µm in width, with diffuse growth. Cells contain many disc-shaped plastids, each with a drop-shaped pyrenoid. Occasionally cells are divided by a longitudinal wall. The base consists of creeping, more or less entangled branched filaments.
**Reproduction:** Uni- and plurilocular sporangia develop in series of transformed vegetative cells within the filaments (intercalary sporangia), rarely individually or apical. Unilocular sporangia are approximately spherical, 37-50 µm in diameter, and reminiscent of a necklace. Plurilocular sporangia are approximately 25-54 µm in width, developed from a few consecutive vegetative cells, and divided into many small compartments. They appear as dark slightly thickened areas, intercalary in the filaments. The two kinds of sporangia occur on the same or different individuals.
**Seasonal variation:** Occurs all year, best developed in spring.
**Habitat:** Common in shallow water on boulders and other solid substrata and epiphytic on larger algae such as Egg Wrack (*Ascophyllum nodosum*), species of Wrack (*Fucus*) and on Eelgrass (*Zostera marina*). Also unattached as cotton-like drifting masses together with Cotton Wool Weeds (*Ectocarpus* sp.). Common



A: *Pylaiella littoralis*. Dark brown bushy alga, slightly entangled branches. Vesterø Havn, Læsø, 0.2 m, 21.5.2005. Scale 2 cm.

B: *Pylaiella littoralis*. False hairs and intercalary sporangia. Scale 100 µm. B, F, H: Beach north of Vesterø Havn, Læsø, drift at the water's edge, 9.5.2014.

in the littoral and upper sublittoral and scattered at greater depth. Collected by divers to 13 m depth and by dredge at Bornholm to 24 m depth.

**Resembles:** Easiest to distinguish from Cotton Wool Weeds (*Ectocarpus* sp.) by the opposite branches and intercalary sporangia, in addition to the disc-shaped plastids as opposed to ribbon-shaped plastids in Cotton Wool Weeds (*Ectocarpus* sp.).

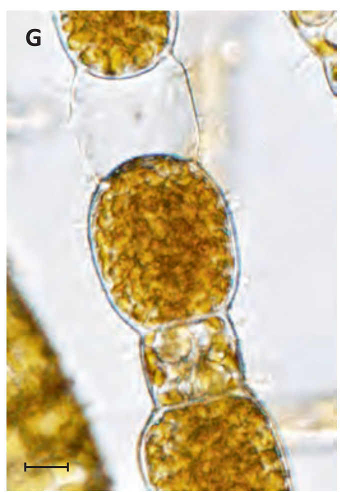
**References:** Kornmann & Sahling (1977, *Pilayella*), Kristiansen (1972, *Pilayella*), Pedersen (1984, *Pilayella*), 2011, Rosenvinge & Lund (1941, *Pylaiella littoralis* and *P. rupincola*), Russel (1994, *Pilayella*).


C: *Pylaiella littoralis.* Vegetative cells, many disc-shaped plastids. Scale 10 µm. C-D: Southern part of Teglværkshavnen, Copenhagen, 0.5 m, 27.11.2007.


D: *Pylaiella littoralis.* Vegetative cells, parietal plastids, optical longitudinal section. Scale 10 µm.


E: *Pylaiella littoralis.* Filament with longitudinal cell wall (arrow). Wooden pole just south of the harbour, Vesterø Havn, Læsø, 0.5 m, 5.6.2017. Scale 10 µm.


F: *Pylaiella littoralis.* Opposite branches, intercalary unilocular sporangia. Scale 20 µm.




G: *Pylaiella littoralis.* Mature and an empty unilocular sporangia. Gilleleje, 0.5 m, 29.5.2014. Scale 10 µm.


H: *Pylaiella littoralis.* Series of intercalary plurilocular sporangia. Scale 10 µm.

## Family: Chordariaceae

# *Acrothrix gracilis*

**Kylin**

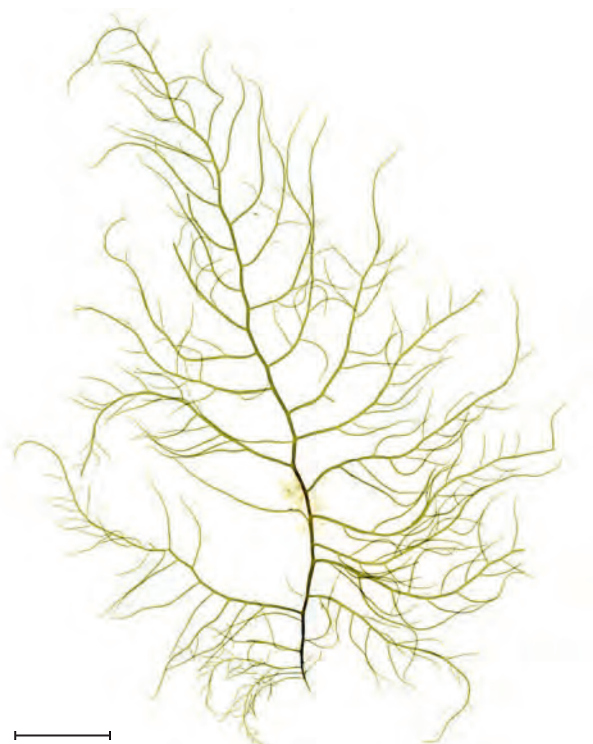
Pointed Hair Weed

**Appearance:** Sparsely branched, very smooth, yellow-brown frond, up to 30 (-36) cm in height, terete branches with a main axis, 0.5-1 mm in width at the base. There are 1-3 orders of scattered branches on all sides, and they gradually become narrower towards a pointed apex. Most thalli characteristically appear approximately triangular in outline when taken out of the water, put down and spread out. Older parts of branches are hollow.

**Structure:** Uniaxial syntagma with trichothallic growth, in which the apex terminates in a true brown algal hair. Primary assimilating filaments arise from all cells of the central axis near the apex. They consist of 6-10 cylindrical cells, curve and overtop the growth zone of the central axis. Further down in the thallus there is a medulla of longitudinal elongate cells which become shorter and more rounded towards the surface. Secondary assimilating filaments and true brown algal hairs arise from each of the outermost medullary cells. Secondary assimilating filaments consist of 4-7 cells, of which the lowest are cylindrical, while the upper ones are rounded and swollen to one side.

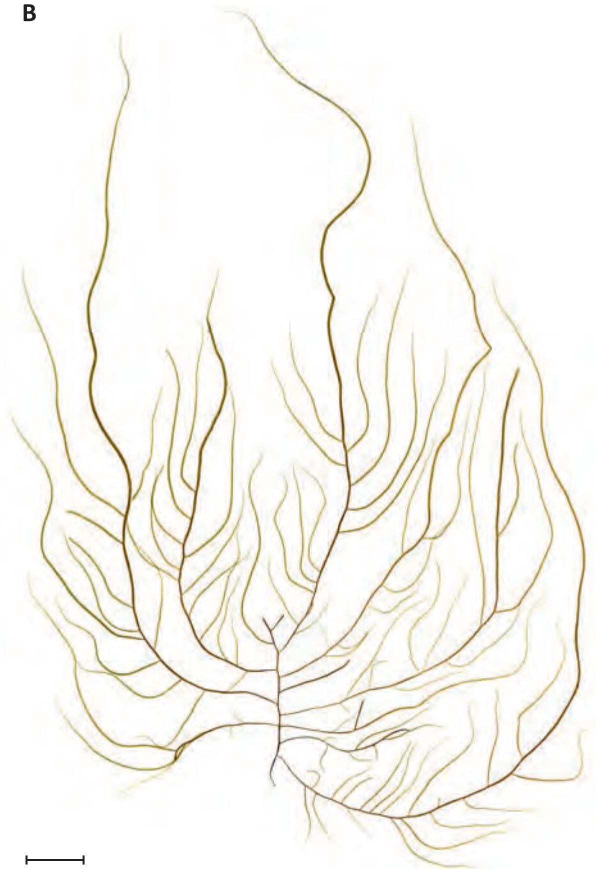
**Reproduction:** Unilocular sporangia form from the

A



A: *Acrothrix gracilis.* Young yellow-brown alga with terete branches, turned greenish after drying. Bredsund, Hirsholm, 4 m, 29.6.1992. Scale 2 cm.

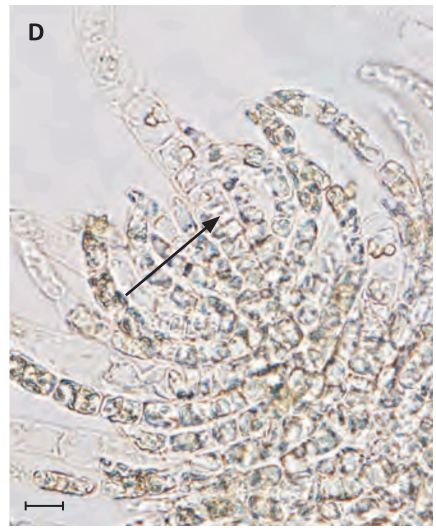
B



B: *Acrothrix gracilis.* Older alga. Both this and the young alga in fig. A have pointed branches. Hirsholm, drift, 18.7.1996. Scale 2 cm.

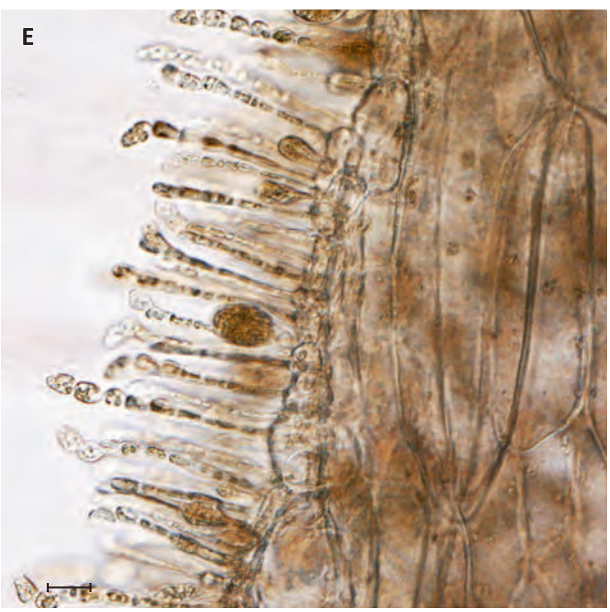
basal cell of the secondary assimilating filaments. Sporangia are ovoid, 30-40 µm wide and 49 µm long. Culture studies from Canada by Forward & South (1985) showed that swarmers from unilocular sporangia germinated and developed into a microscopic pseudoparenchyma reminiscent of *Microsyphar* sp. Plurilocular intercalary sporangia were formed but sexual reproduction was not documented. In addition, upright thalli arose from the microscopic phase.

**Seasonal variation:** Collected in June-September. Unilocular sporangia recorded in July and September.
**Habitat:** On small stone and mollusc shells, epiphytic on coarser algae and Eelgrass (*Zostera marina*), 0.5-12 m depth. A single collection by dredge, 16 m depth.
**Resembles:** Recognizable from other smooth brown algae in Danish waters by the pointed branches.
**References:** Forward & South (1985), Kylin (1947), Rosenvinge & Lund (1943).


C: *Acrothrix gracilis*. Apical true brown algal hair and curved primary assimilating filaments. Scale 20 µm. C-H: Beach south of Vesterø Havn, Læsø, drift, 16.7.2017.

D: *Acrothrix gracilis*. Trichothallic growth zone (arrow), squash preparation. Scale 10 µm.




E: *Acrothrix gracilis*. Older branch, medullary cells and surface of secondary assimilating filaments and unilocular sporangia. Scale 20 µm.


F: *Acrothrix gracilis*. Secondary assimilating filaments with cylindrical cells in lower part and 3-4 oblique swollen cells in the upper end. Scale 10 µm.

G: *Acrothrix gracilis*. True brown algal hair (arrow). Scale 10 µm.

H: *Acrothrix gracilis*. Unilocular sporangia and secondary assimilating filaments. Scale 10 µm.

## *Asperococcus*

Sausage Weed

Upright unbranched thalli are constructed as hollow parenchyma. Medulla consists of large pale cells surrounded by a cortex of small cells, each of which contain several plastids with pyrenoids. Scattered brown algal hairs with sheath arise from surface cells.
Uni- and plurilocular sporangia develop from cortical cells and form dark brown spots (sori) on the thalli together with short multicellular filaments (paraphyses) and hairs with sheath. Culture studies showed that the life history comprises a microthallus of creeping filaments. It has vegetative cells with many disc-shaped plastids, and brown algal hairs with sheath, such as Hundred Thread Weed (*Hecatonema* sp.). There is a direct development of upright thalli from the creeping microthallus which may also have plurilocular sporangia. Sexual reproduction is not recorded.
**References:** Fletcher (1987), Pedersen (1984), Rosenvinge & Lund (1947), Rueness (1977).

**Identification key to species of *Asperococcus***

| | | |
|---|---|---|
| 1a. | Ribbon-shaped upright thalli | *A. ensiformis* |
| 1b. | Approximately cylindrical upright thalli | 2 |
| 2a. | Inflated finger-stall-looking, sharply attenuated at base, 0.5-2 cm in width. Paraphyses up to 4 cells in height | *A. bullosus* |
| 2b. | Tube-like, cylindrical, gradually attenuated at base, 1-3 mm in width. Paraphyses up to 7 cells in height | *A. fistulosus* |

## *Asperococcus bullosus*

**J.V.Lamouroux**

Fat Sausage Weed

**Appearance:** Hollow unbranched thalli, inflated with a rounded apex, resembling a finger-stall, up to 5-17 cm in height and 0.5-2 cm in width slightly constricted at irregular intervals. The base is sharply attenuated into a terete stipe. Thalli are yellow-brown or olive-brown, slightly darker in late summer. Dark brown spots occur occasionally. Thalli are very fragile and easily rupture when taken out of the water. They do not attach very well to paper when dried as herbarium sheets.
**Structure:** Surface of small cells with many plastids with pyrenoids. Medulla consists of 1-2 layer of large, rounded, pale cells. Brown algal hairs with sheath are scattered or in groups typically together with sporangia.
**Reproduction:** Uni- and plurilocular sporangia occur on the same or different individuals. Sporangia together with paraphyses and hairs with sheath form spots (sori). Paraphyses have few and up to 4 cells but are not always present.
**Seasonal variation:** Collected in June-September with plurilocular sporangia. Unilocular sporangia probably present at the same time.
**Habitat:** On stone, larger algae and tunicates (Ascidiaceae).
**References:** Fletcher (1987, *A. turneri*), Pedersen (1984, *A. turneri*), Rosenvinge & Lund (1947).


A: *Asperococcus bullosus*. Finger-stall-looking thalli. Kølpen, Hirsholmene, 5.8.2003. Scale 2 cm.

## *Asperococcus ensiformis*

**(Delle Chiaie) M.J.Wynne**

Flattened Sausage Weed


A: *Asperococcus ensiformis*. Ribbon-shaped thallus with dark points. The only specimen collected in Danish waters. Nordøst revet, Hirsholmene, 8 m, 4.8.1922. Leg.: Rosenvinge. Scale 2 cm.

**Appearance:** Thalli narrow ribbon-shaped but hollow, 2 mm in width and > 10 cm in height. They gradually decrease into a stipe at the base. They are olive-green or light brown with dark spots.
**Structure:** Surface of small cells with many disc-shaped plastids. Medulla of large colourless cells. Hairs with sheath occur.
**Reproduction:** Unilocular sporangia develop in sori with multicellular paraphyses and hairs with sheath.
**Seasonal variation:** Collected in August.
**Comment:** Only a single individual has been collected in Danish waters, obtained by dredge and may have been unattached or drift. It is uncertain whether the species occurs in Danish waters.
**References:** Fletcher (1987, *A. compressus*), Rosenvinge & Lund (1947, *A. compressus*), Wynne (2003).

# *Asperococcus fistulosus*

**(Hudson) W.J.Hooker**

Thin Sausage Weed

**Appearance:** Terete cylindrical, dark brown, unbranched, hollow thalli, gradually decreasing in width towards the base. They are typically 5-10 (-13) cm in height and 1-3 (-6) mm in width, but narrower and shorter thalli occur at deeper water.

**Structure:** Surface of small cells which contain many disc-shaped plastids with pyrenoids. Inside the surface are 1-2 layers of large, rounded cells with a few or no plastids. Scattered brown algal hairs with sheath arise from the surface cells.

**Reproduction:** Unilocular sporangia are approximately spherical, and form sori with paraphyses and brown algal hairs with sheaths. Paraphyses are up to 7 cells long. Plurilocular sporangia are rarely reported and have not been for certain observed in specimens from Danish waters.

**Seasonal variation:** Collected in April-September with unilocular sporangia.

**Habitat:** On Serrated Wrack (*Fucus serratus*), Bladder Wrack (*F. vesiculosus*), other large algae, Eelgrass (*Zostera marina*) and stone. In shallow water and a few collections by dredge at greater depth, to 18 m depth within Skagen and to 25 m depth in the North Sea.

**Comment:** Culture studies of Thin Sausage Weed (*A. fistulosus*) from Danish waters showed that swarmers from unilocular sporangia germinated and developed into a filamentous microthallus, which resembled Hundred Thread Weed (*Hecatonema* sp.).

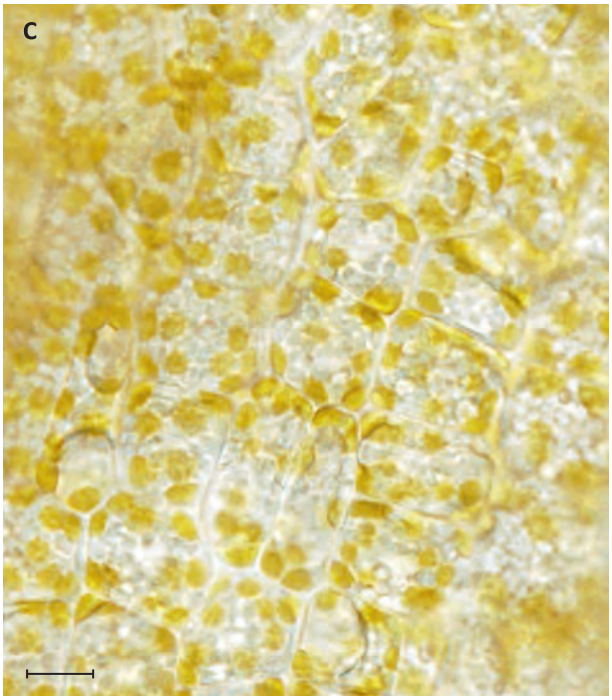
**References:** Fletcher (1987), Pedersen (1984), Rosenvinge & Lund (1947, *A. echinatus*).

A

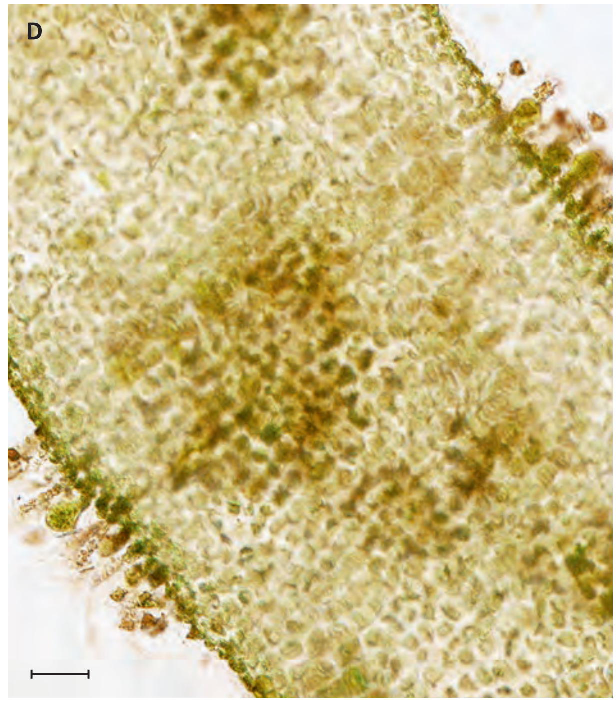
A: *Asperococcus fistulosus*. Terete unbranched thalli on Serrated Wrack (*Fucus serratus*). Deget, Frederikshavn, 1 m, 5.7.1975. Scale 2 cm.

B

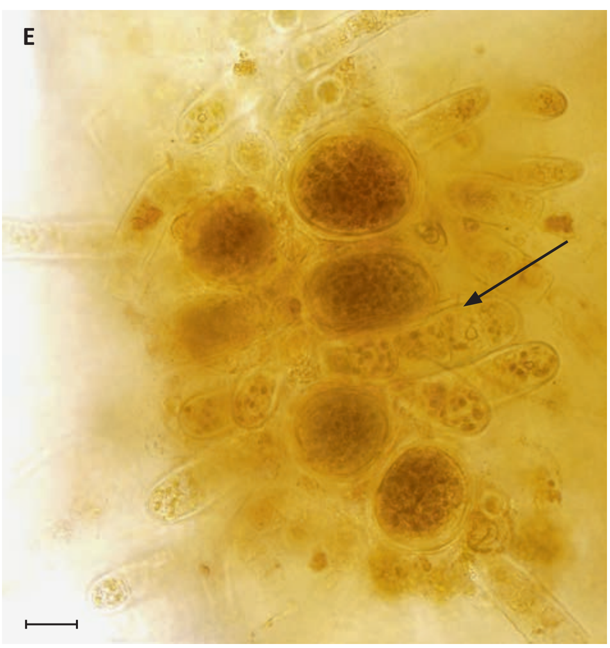
B: *Asperococcus fistulosus*. Several upright thalli from the same base. On stone. Bay at westside of Deget, Frederikshavn, 1 m, 9.7.1972. Scale 2 cm.




C: *Asperococcus fistulosus.* Surface cells with many disc-shaped plastids. Scale 10 µm. C, E-F: Beach south of Vesterø Havn, Læsø, drift, 29.7.2014.




D: *Asperococcus fistulosus.* Surface with sori of unilocular sporangia, multicellular paraphyses, and brown algal hairs with sheath. Rygård Strand, 4.5 m, 23.6.1992.
Scale 50 µm.




E: *Asperococcus fistulosus.* Sorus of unilocular sporangia and multicellular paraphyses (arrow). Scale 10 µm.


F: *Asperococcus fistulosus.* Part of sorus, brown algal hair with sheath (arrow). Scale 10 µm.

# *Botrytella micromora*

**Bory**

Mini Brown Mulberry Weed

**Appearance:** Delicate branched tufts, up to 4.5 cm in height.

**Structure:** Upright uniseriate filaments have scattered branches and arise from a basal system of creeping filaments. Upright filaments have cylindrical cells, 21-35 µm in width, with the lower cells up to 6 times as long as wide, upper cells are only slightly longer than wide. Filaments terminate in true brown algal hairs, which are pushed aside by continued growth (sympodial growth). Cells contain many disc-shaped plastids.

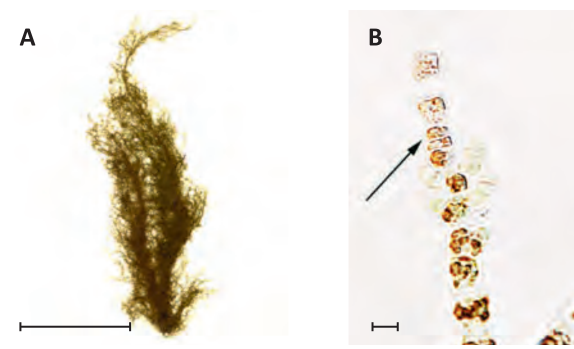
**Reproduction:** Plurilocular sporangia are elongate ovoid, 18-25 µm long and 10.5-12 µm in width. They are typically closely connected in a conical sorus at the base of a terminal hair. Sporangia are lateral, sessile on the branch or on a short stalk. Each sporangium evacuates through an apical pore. Culture studies of Mini Brown Mulberry Weed (*B. micromora*) from Danish waters by Pedersen (1974a) showed that swarmers from plurilocular sporangia germinated and developed a filamentous microthallus from which new uprights with plurilocular sporangia arose.

**Seasonal variation:** Collected in April-May and July-August.

**Habitat:** On stone at shallow water, 0.5-2 m depth.

**Resembles:** See remarks for Club Thread Weed (*Polytretus reinboldii*).

**References:** Kim (2010), Kornmann & Sahling (1984, *Sorocarpus micromorus*, 1988), Pedersen (1974a, 1977, 1989, *S. micromorus*, 2011), Rosenvinge & Lund (1941, *S. uvaeformis*), Taskin & Pedersen (2012).



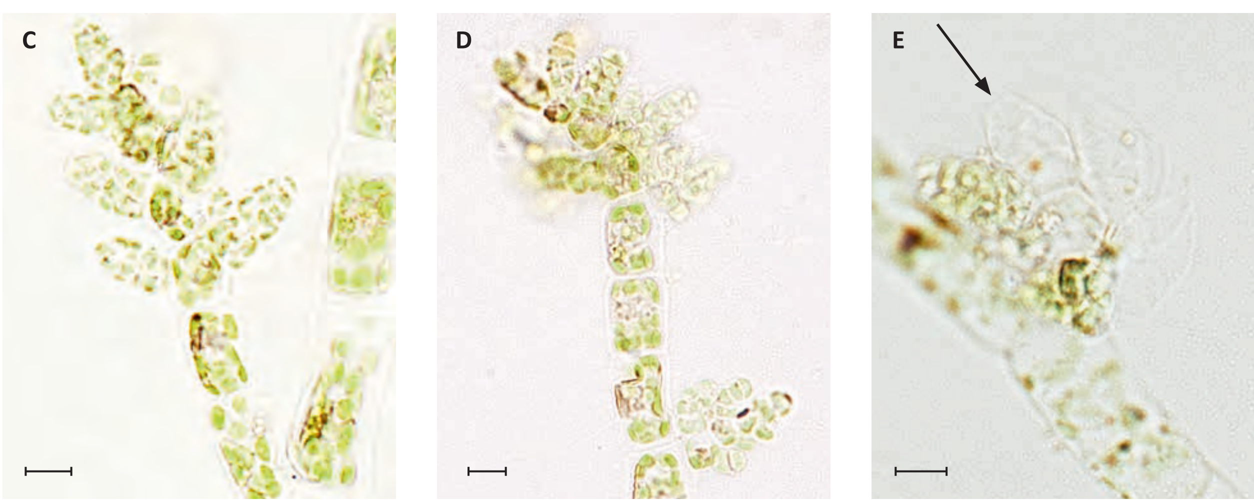

A: *Botrytella micromora*. Branched tuft a few centimetres in height. Vejrø, 1.5 m, 9.4.1989. Scale 1 cm.

B: *Botrytella micromora*. Branch with apical true brown algal hair, below the growth zone (arrow) are initials for sporangia. Scale 10 µm. B, D-E: Venegrund, 3 m, 26.9.1992.

C: *Botrytella micromora*. Nearly mature, elongate ovoid plurilocular sporangia; vegetative cells with many disc-shaped plastids. Vejrø, 4.5 m, 26.3.1992. Scale 10 µm.

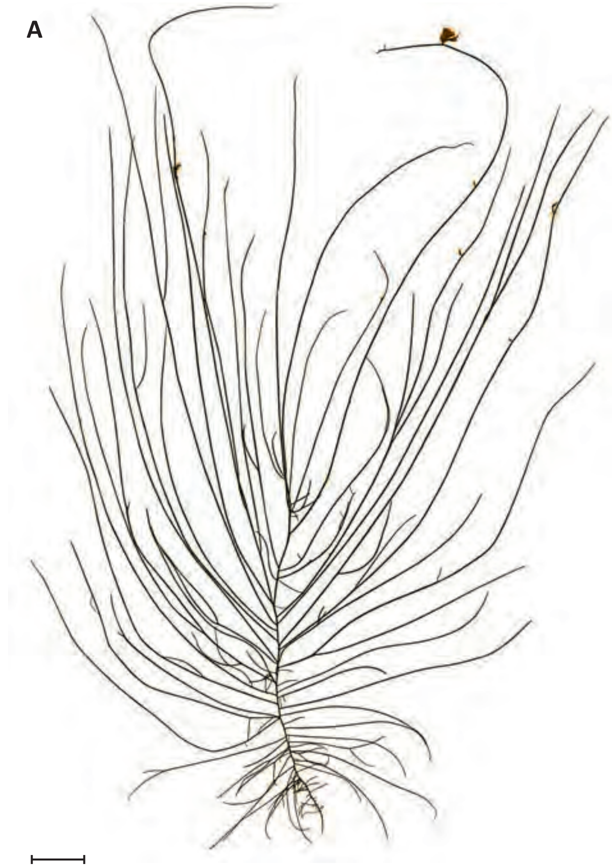
D: *Botrytella micromora*. Conical sorus formed of plurilocular sporangia which are close together. Scale 10 µm.

E: *Botrytella micromora*. Sporangium emptied through an apical pore (arrow). Scale 10 µm.



# *Chordaria flagelliformis*
## (O.F.Müller) C.Agardh
Slimy Whip Weed

**Appearance:** Dark brown, almost black thalli of terete branches, typically, 10-30 cm, occasionally more than 50 (-80) cm, in height. The main branch has one order of scattered branches on all sides. Occasionally, a few of them may have a short branch near the apex. Upper branches overtop the main branch, while the lower ones are relatively short. Branches are uniform in thickness, 0.5-1.5 mm in width, with a blunt apex. The thallus is smooth and of a solid consistency.
**Structure:** Multiaxial syntagma, medulla of longitudinal elongate ellipsoid cells entangled by thin hyphae-like filaments. Surface of assimilating filaments close together, each consisting of 6-8 cells, slightly increasing in width towards the surface, with inner cylindrical cells and outer cells ellipsoid to spherical. Several assimilating filaments arise from a basal cell together with scattered true brown algal hairs. Hairs are frequent in vigorously growing individuals. Young, individuals up to a few centimetres long have loosely connected assimilating filaments and appear more fluffy than older individuals.
**Reproduction:** Unilocular sporangia are ellipsoid or obovate and develop from the basal cell of the assimilating filaments. Zoospores from unilocular sporangia germinate and grow into microscopic uniseriate filaments with scattered branches. Plurilocular sporangia develop on the microthalli and swarmers from these plurilocular sporangia may form similar microthalli or develop disc-shaped thalli, from which new upright thalli arise. Upright and microscopic thalli probably represent sporophyte- and gametophyte generations.
**Seasonal variation:** Collected all year, best developed in summer. Mature unilocular sporangia recorded in January-March, July-September and November-December.
**Habitat:** Mainly on stone but occasionally epiphytic on coarse algae, shells of Edible Periwinkle (*Littorina littorea*), in posts and other solid substrata. Forming close stands in upper sublittoral in wave exposed localities, such as the outside of harbour jetties, and observed scattered on stone reefs, to 11 m depth.

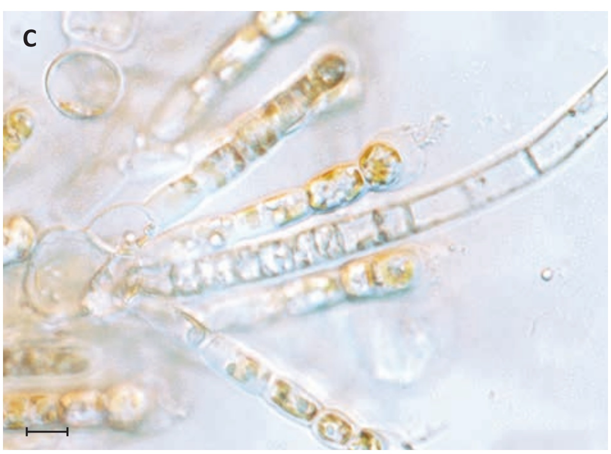



A: *Chordaria flagelliformis*. Dark brown terete alga with scattered long branches. Southern harbour jetty, Hirsholm, 0.5 m, 23.6.1988. Scale 2 cm.

**Comment:** Microthalli are reminiscent of *Streblonema chordariae* (Wolney) A.D.Cotton ex L.Newton according to Pedersen (2011), and this name is recorded as a synonym of *C. flagelliformis* in Algaebase (Guiry in Guiry & Guiry, 2021). *Streblonema chordariae* has creeping endophytic filaments with short upright uniseriate dichotomous branched filaments. Cells contain several disc-shaped plastids. Brown algal hairs with sheath occur (Kuckuck 1954). Plurilocular sporangia are apical on the upright filaments and typically in pairs. *Streblonema chordariae* is endophytic in Slimy Whip Weed (*C. flagelliformis*), but not recorded in Danish waters. The occurrence of brown algal hairs with sheath in *S. chordariae* and brown algal hairs without a sheath in Slimy Whip Weed (*C. flagelliformis*) might indicate that they are different species.

**References:** Caram (1955), Guiry in Guiry & Guiry (2021), Jaasund (1963), Kornmann (1962c), Kuckuck (1954, *Streblonema chordariae*), Kylin (1947), Pedersen (2011, *S. chordariae*), Rosenvinge & Lund (1943).


B: *Chordaria flagelliformis*. Surface of assimilating filaments and scattered true brown algal hairs (arrow). Squash preparation of transverse section. Scale 20 µm. B-C: Beach north of Vesterø Havn, Læsø, drift, 23.6.2013.




C: *Chordaria flagelliformis*. True brown algal hair and assimilating filaments. Scale 10 µm.

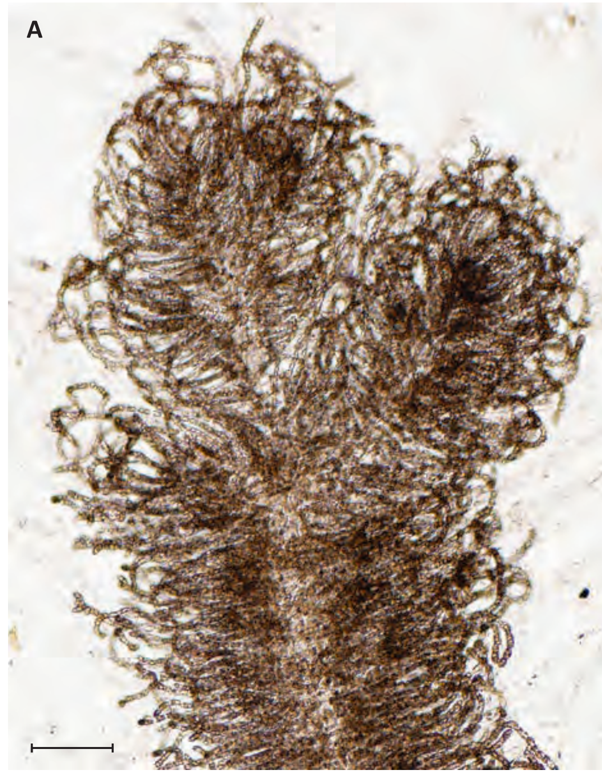

D: *Chordaria flagelliformis*. Unilocular sporangium. Briseis Flak, 6 m, 18.1.1997. Scale 10 µm.


E: *Chordaria flagelliformis*. Apex of young alga, assimilating filaments loosely connected (lower arrow), and many brown algal hairs (upper arrow). Beach north of Vesterø Havn, Læsø, drift, 29.4.2016. Scale 20 µm.

## *Cladosiphon*

Slimy String Weeds

**Appearance:** Terete, gelatinous smooth, very soft algae with scattered branches or unbranched. Branches typically hollow slightly below the apex.
**Structure:** Multiaxial syntagma, the medulla is like a central string of several pale filaments close together, each consisting of relatively long ellipsoid cells. The surface consists of assimilating filaments, which arise as branches on a subcortex or directly from medullary cells. The subcortex consists of short filaments of colourless ellipsoid cells and are approximate perpendicular to the central medullary filaments. Assimilating filaments consist of many cells and are loosely connected in a mutual gelatinous wall substance. They are sparsely branched at the base and their cells contain disc-shaped plastids. From their lower cells brown algal hairs arise which may have a sheath in Branched Slimy String Weed (*C. contortus*) according to Sansón et al. (2006). Filaments of the central axis commonly terminate in a true brown algal hair, which is pushed aside with the upper part of the filament and longitudinal growth continuing from an assimilating filament below. Intercalary growth also contributes to longitudinal growth of the central string.
**Reproduction:** Plurilocular sporangia develop from the outermost cells of assimilating filaments and unilocular sporangia from the base of the filaments.
**Comment:** Culture studies, referred to by Rosenvinge & Lund (1943) showed that germinating zoospores develop into *Myrionema*- or *Streblonema*-like stages with plurilocular sporangia. Crustose *Myrionema magnusii* with several upright filaments, each with an apical brown algal hair resembling medullary filaments of *Cladosiphon*, was observed by Sanson et al. (2006).
**References:** Kylin (1940, 1947), Rosenvinge & Lund (1943), Sansón et al. (2006).




A: *Cladosiphon zosterae*. Medulla, like a central string with loosely connected assimilating filaments. Beach north of Vesterø Havn, Læsø, drift, 16.7.2017. Scale 100 µm.

**Identification key to species of *Cladosiphon***

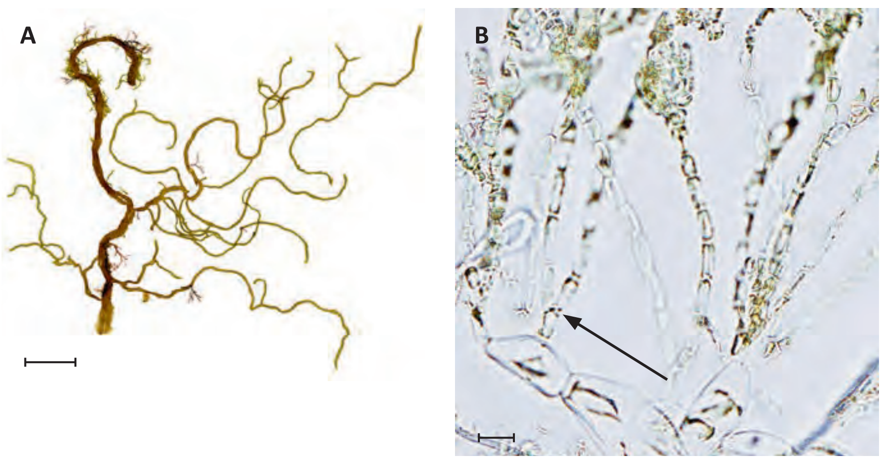
| | | |
|---|---|---|
| 1a. | Thalli up to 12 cm in height and typically branched. Assimilating filaments with plurilocular sporangia on short branches in apical part | *C. contortus* |
| 1b. | Thalli up to 2-6 cm in height, unbranched or with short branches. Assimilating filaments without branches at the apex. Plurilocular sporangia in uniseriate rows | *C. zosterae* |

# *Cladosiphon contortus*

**(Thuret) Kylin**

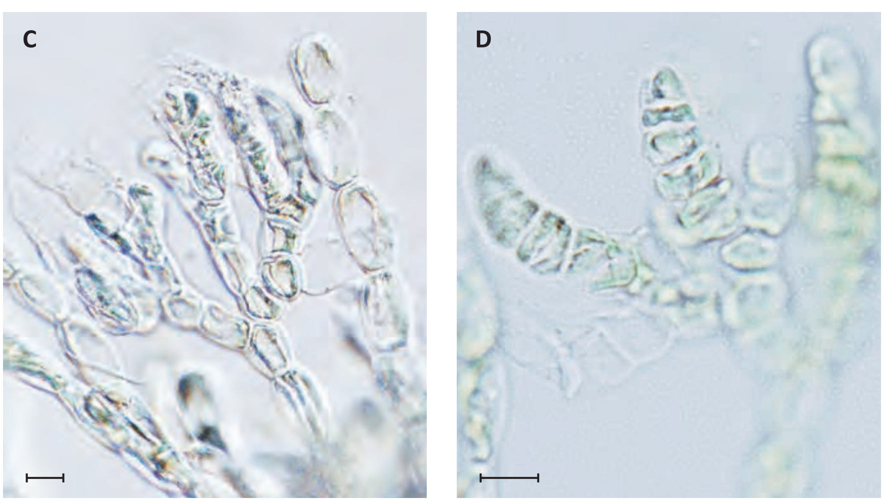
Branched Slimy String Weed

**Appearance:** Terete, hollow, upright thalli, which are unbranched or have scattered branches, brown or dark brown, up to 12 cm in height and 2 mm in width.
**Structure:** Assimilating cortical filaments arise as branches from a subcortex of short filaments which arise as branches from central medullary filaments and consist of ellipsoid cells. Downward-growing thin filaments also arise from the medullary cells and entangle the central filaments. Assimilating filaments are sparsely branched at the base and typically more branched at the apex but may be unbranched. Their lower cells are cylindrical, while the upper cells are elongate ellipsoid.
**Reproduction:** Uni- and plurilocular sporangia are recorded on the same individual in Danish waters. Unilocular sporangia occur at the base of the assimilating filaments, are obovate sessile or on a stalk cell, 60-80 µm long and 40-45 µm in width. Plurilocular sporangia develop in the upper part of the assimilating filaments. They form from upper cells in short branches, typically uniseriate, seldom with single longitudinal walls.
**Seasonal variation:** Collected in July-August. Unilocular sporangia recorded in August and plurilocular sporangia in July-August.
**Habitat:** Epiphytic on Eelgrass (*Zostera marina*), 0.5-7.5 m depth.
**References:** Kylin (1940, 1947), Rosenvinge & Lund (1943), Sansón et al. (2006).




A: *Cladosiphon contortus*. Terete branched soft alga. Scale 2 cm. A-D: Kølpen, Hirsholmene, 2.5 m, 31.7.2000. Leg. et det.: P.M. Pedersen & Aa. Kristiansen.

B: *Cladosiphon contortus*. Subcortex of pale ellipsoid cells with assimilators, which have scattered branches at the base (arrow). Scale 20 µm. B-D: Rehydrated herbarium material.




C: *Cladosiphon contortus*. Distal part of branched assimilator, with apical plurilocular sporangia, some empty. Scale 10 µm.

D: *Cladosiphon contortus*. Apical, uniseriate plurilocular sporangia. Scale 10 µm.

# *Cladosiphon zosterae*

**(J.Agardh) Kylin**

Eelgrass Slimy String Weed

**Appearance:** Upright terete, hollow thalli, unbranched or have short, occasional numerous branches. They are brown, 2-6 cm in height and 0.5 mm in width.

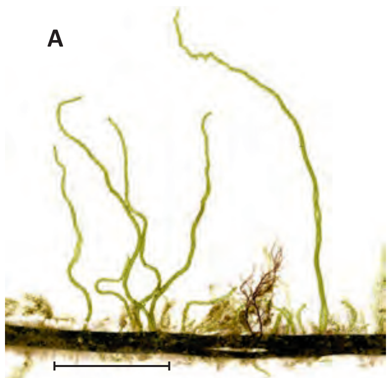
**Structure:** Assimilating filaments are branches of the medullary filaments or of a monostromatic subcortex. They arise individually or in clusters of a few filaments and are curved, sparsely branched at the base, unbranched in the distal end. Basal cells are cylindrical while upper ones are rounded, slightly swollen and to one side.

**Reproduction:** Uni- and plurilocular sporangia are recorded on different individuals in Danish waters. Unilocular sporangia occur at the base of the assimilating filaments. Plurilocular sporangia are in series and develop from cells in the upper end of assimilating filaments after longitudinal and transverse divisions of the cells, typically as uniseriate papilla close together, resembling a cock's comb.

**Seasonal variation:** Collected in April-August. Unilocular sporangia recorded in May-June in the Sund and the western and middle part of the Baltic Sea. Plurilocular sporangia recorded in July, in the northern part of Kattegat and the western part of the Limfjord.

**Habitat:** Epiphytic on Eelgrass (*Zostera marina*), on stone in a single collection from the Limfjord, shallow water by hand and by dredge, 8-11.5 m depth.

**References:** Kylin (1940, 1947), Rosenvinge & Lund (1943), Sansón et al. (2006).





A: *Cladosiphon zosterae.* Short terete unbranched thalli on Eelgrass (*Zostera marina*). Kølpen, Hirsholmene, 3.5 m, 25.7.2002. Scale 2 cm.

B: *Cladosiphon zosterae.* Central string surrounded by assimilating filaments and true brown algal hairs (arrow). Læsø Trindel, 5 m, 31.5.1992. Scale 50 µm.



C: *Cladosiphon zosterae.* Unbranched assimilating filaments, true brown algal hair with basal growth zone (arrow). Scale 20 µm. C-D: Kølpen, Hirsholmene, 7 m, 28.7.1997.

D: *Cladosiphon zosterae.* Plurilocular sporangia in uniseriate series from the apical cells of an assimilating filament. Empty sporangium. Scale 10 µm.

## *Coelocladia arctica*

### Rosenvinge

**Appearance:** Unbranched yellow-brown terete thalli, slightly > 7 cm in height and 0.25 mm in width. Thalli occasionally branched and hollow, but this is not observed in the alga from Danish waters.

**Structure:** Constructed as a parenchyma, the medulla consists of large, rounded cells of which there are more than four when seen in transverse section. These cells are surrounded by a monostromatic layer of small cortical cells. True brown algal hairs are frequent, and relatively coarse, 29-38 µm in width. Young individuals are uniseriate with an apical true brown algal hair.

**Reproduction:** Plurilocular sporangia are unique. They develop from surface cells which produce small outgrowths which grow into short unbranched or branched filaments. The cells of these filaments form sporangia, typically occurring four together on a stalk cell. In the youngest part of the thallus the sporangia are clearly separated in sori, while they are more or less confluent in older algae. Culture studies of the alga from Greenland showed a direct life history, swarmers from plurilocular sporangia germinated into creeping filaments from which one or several upright thalli arose (Pedersen 1976, 2011).

**Seasonal variation:** Collected in May-June with sporangia.

**Habitat:** On egg mass of Common Whelk (*Buccinum undatum*) and entangled with Fluffy Cotton Wool Weed (*Ectocarpus siliculosus*), 11-12 m depth.

**Resembles:** Thallus structure is similar to species of *Stictyosiphon* but they only have four medullary cells when seen in transverse section. Best identified on the distinctive sporangia.

**Comment:** Only few collections from Danish waters, one from 1893 and one from 2017.

**References:** Lund (1959, *Litosiphon subcontinuus*), Pedersen (1976, 2011), Pedersen et al. (2000), Rosenvinge & Lund (1947, *L. subcontinuus*).

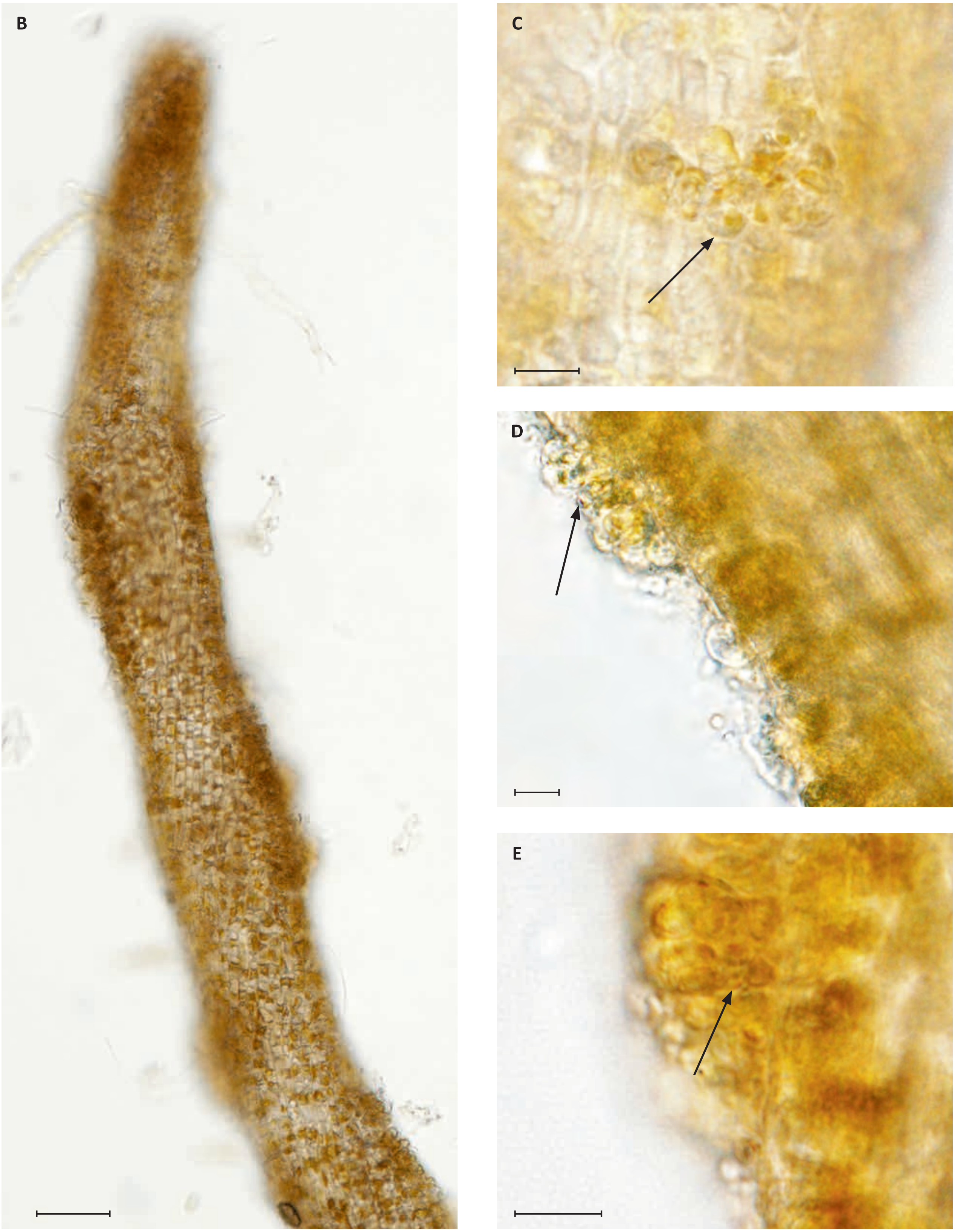

A: *Coelocladia arctica*. Terete unbranched upright thalli entangled with finer, bushy Fluffy Cotton Wool Weed (*Ectocarpus siliculosus*). Fladen, 11-12 m, 12.5.1893. Leg.: L. K. Rosenvinge. Scale 2 cm.

B: *Coelocladia arctica*. Parenchyma with swellings of plurilocular sporangia. Scale 50 µm. B-E: On egg mass of Common Whelk (*Buccinum undatum*), Storedal, Læsø, drift, 3.6.2017.

C: *Coelocladia arctica*. Small branch system, developed from surface cell and the initiation for plurilocular sporangia. Scale 10 µm.

D: *Coelocladia arctica*. Sporangial sori (arrow) in optical longitudinal section. Scale 10 µm.

E: *Coelocladia arctica*. Plurilocular sporangia on stalk cell (arrow). Scale 10 µm.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C
D
E

## *Delamarea attenuata*

### (Kjellman) Rosenvinge

**Appearance:** Tufts of terete yellow brown or dark brown slightly club-shaped thalli with a rounded apex. Filamentous at the base and up to 1 mm in width in the upper part, 5-7.5 cm in height. Young thalli are compact, while older thalli are hollow.

**Structure:** Parenchyma which develop from a uniseriate filament with an apical brown algal hair with sheath. Young thalli are compact, they consist of large irregularly rounded pale medullary cells surrounded by smaller cells with many disc-shaped plastids. The cavity in older specimens is surrounded by 3-4 layers of irregularly rounded cells with the largest in the innermost layer. The surface of the upper part of the thallus is covered by elongated unicellular club- or sac-shaped paraphyses, 133-156 µm in height and 35 µm in width, with many disc-shaped plastids in the distal end. Brown algal hairs with sheath are scattered between the paraphyses.

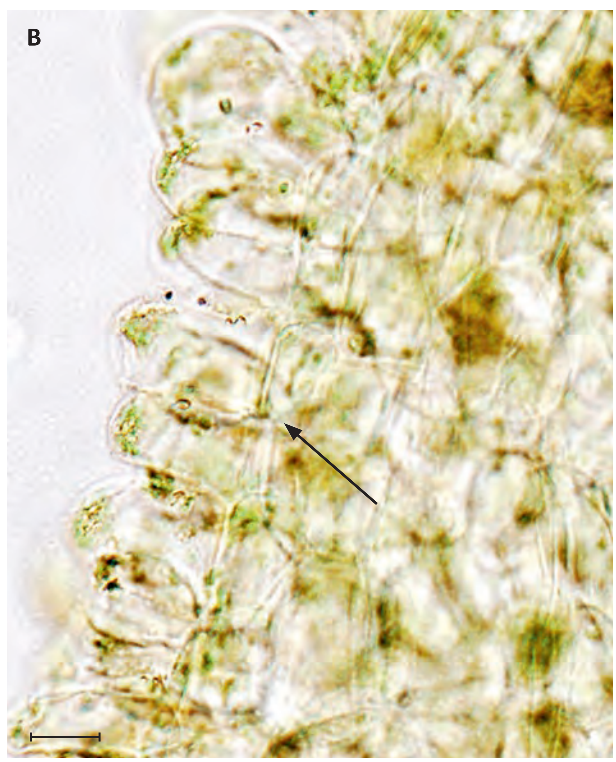
**Reproduction:** Uni- and plurilocular sporangia occur in different individuals with the sporangia at the base of the paraphyses. Unilocular sporangia are broad egg- or club-shaped or approximately spherical, 61-86 µm in height and 43-55 (-63) µm in width. Plurilocular sporangia observed on a single occasion, were elongate, rounded to conical at the apex, 91-123 µm in height and 19-21 µm in width. Pedersen (1974b, 2011) in culture studies documented an alternation between upright thalli and a filamentous microthallus with brown algal hairs with sheath and plurilocular sporangia, similar to Hundred Thread Weed (*Hecatonema*).

**Seasonal variation:** Collected in May-July, unilocular sporangia recorded in May and plurilocular sporangia in May-July.

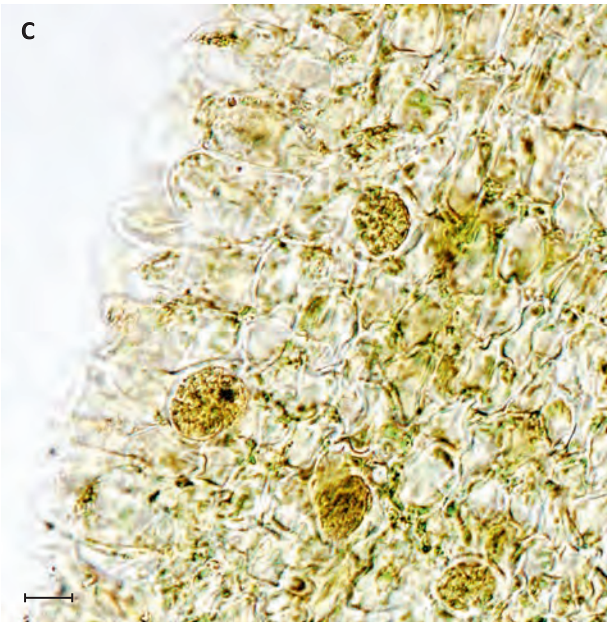
**Habitat:** On stone and wooden poles, 0-8 m depth.

**References:** Kawai & Kurogi (1980), Pedersen (1974b, 2011), Rosenvinge & Lund (1947).

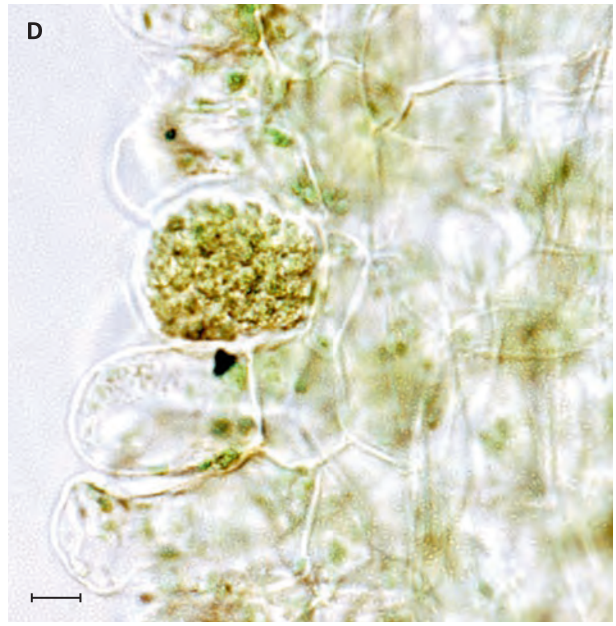

A: *Delamarea attenuata.* Club-shaped upright thalli. Exposed side of southern harbour jetty, Hirsholm, at water edge, 5.5.1978. Scale 1 cm.




B: *Delamarea attenuata.* Medulla of large, rounded cells, cortex of angular cells (arrow), covered by club- or sac-shaped paraphyses (optical longitudinal section). Scale 20 µm.



C: *Delamarea attenuata*. Surface of large cells and unilocular sporangia, seen from outside. Scale 20 µm. B-D: Læsø Trindel, 5 m, 31.5.1992.



D: *Delamarea attenuata*. Unilocular sporangium between paraphyses. Scale 10 µm.

## *Dictyosiphon*

Net Weeds

Terete algae, much branched on all sides with scattered branches of a light brown colour. The thalli are compact but soft.

Thalli constructed as parenchyma, with a small apical cell, but the largest increase in growth is by intercalary cell divisions (diffuse growth). The medulla is of relatively large pale cells surrounded by small cortical cells with many disc-shaped plastids with pyrenoids. True brown algal hairs arise from surface cells.

Unilocular dark brown sporangia are embedded among the surface cells.

**Identification key to species of *Dictyosiphon***

| | | |
|---|---|---|
| 1a. | Much branched with several orders of branches without constrictions at base | *D. foeniculaceus* |
| 1b. | Most branches are of first order with a constricted base, typically without second order branches | *D. chordaria* |

## *Dictyosiphon chordaria*

**Areschoug**

Golden Net Weed

**Appearance:** Golden-brown slightly shiny upright thalli with a distinct main axis and typically with only a single order of branches. Thalli up to 23 cm in height with branches 1-2 mm in width. Main branch occasionally up to 3 mm in width. Branches scattered on all sides, slightly constricted at the base and gradually narrowed towards the apex, are hollow with a jelly-like consistency.

**Structure:** Parenchymatous with an apical cell and intercalary cell divisions. Medulla of large irregularly rounded cells which decrease in size towards the surface. The cortex consists of 1-2 layers of small cells which are closely connected in young thalli. In older thalli, the cortex typically has a slightly loose surface, because mutually free filaments, 2-3 cells long, develop from the original surface cells. The cortical cells contain several disc-shaped plastids. True brown algal hairs arise from scattered surface cells.

**Reproduction**: Unilocular sporangia are embedded between surface cells and protrude. Culture studies of Golden Net Weed (*D. chordaria*) from Denmark by Pedersen (1984) showed that swarmers from unilocular sporangia germinated and developed filamentous syntagmatic microthalli. They developed branches with plurilocular sporangia, and depending on day-length and temperature, also upright macrothalli.

**Seasonal variation:** Collected in May-August. Unilocular sporangia recorded in May-July.

**Habitat:** On small stone at shallow water and may occur epiphytically on larger algae, 0-1 m depth.

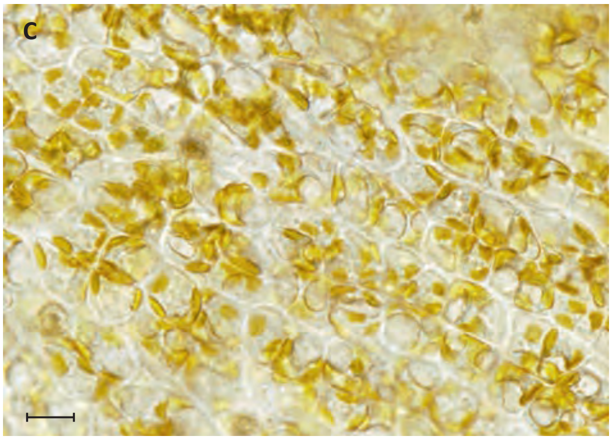
**References:** Kylin (1947), Levring (1940), Pedersen (1984), Rosenvinge & Lund (1947).

A

A: *Dictyosiphon chordaria*. Several upright thalli from the same point of attachment. Only first order branches, slightly constricted at the base. Rågø, 0.5 m, 7.6.1980. Scale 2 cm.

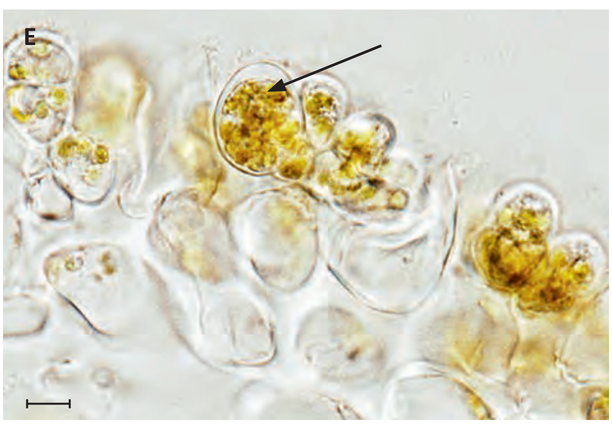
B

B: *Dictyosiphon chordaria*. Atypical much branched thallus. On small stone just west of the harbour, Hirsholm, 0.2 m, 21.6.1989. Scale 2 cm.

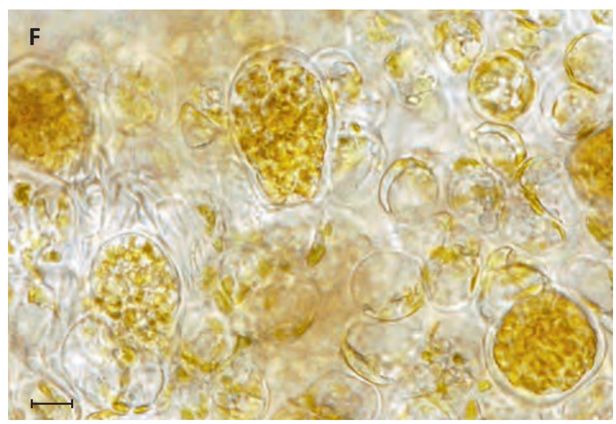



C: *Dictyosiphon chordaria*. Surface cells with many disc-shaped plastids. Scale 10 µm. C-F: Beach south of Vesterø Havn, Læsø, drift, 3.6.2017.


D: *Dictyosiphon chordaria*. Elongated medullary cells, decreasing in size towards the surface of small, loosely connected, rounded cells (arrow). Optical longitudinal section. Scale 20 µm.




E: *Dictysiphon chordaria*. Surface of radiating, loosely connected filaments, 1-3 cells long and a unilocular sporangium (arrow). Transverse section. Scale 10 µm.




F: *Dictyosiphon chordaria*. Unilocular sporangia, slightly protruding among surface cells. Scale 10 µm.

## *Dictyosiphon foeniculaceus*

**(Hudson) Greville**

Tubular Net Weed

**Appearance:** Much branched yellow-brown or dark brown bush-like thalli, up to 40 (-53) cm in height, with scattered branches, up to 0.5 mm in width on all sides. Main branch slightly thicker but does not deviate from branches in other ways. Thalli attached to the substratum by a disc-shaped base. Branches gradually decrease in width towards the apex. Thalli are soft and flexible but with a firm consistency. Older thalli occasionally become hollow at base. Appearance varies according to locality. Coarse and dark thalli occur at wave-exposed localities, much branched and large thalli occur at sheltered localities and may form large, entangled masses.

**Structure:** Parenchymatous and terminating in a single apical cell, although diffuse growth results in the most increase in size. The cortex consists of 1-2 (-3) layers of angular to rounded cells, with many disc-shaped plastids, each with a pyrenoid. The medulla consists of large elongate colourless cells. In the lower part, thin downward-growing, hyphae-like filaments develop from the central cells. True brown algal hairs arise from scattered surface cells.

**Reproduction:** Unilocular sporangia occur between surface cells appearing as dark brown spots. Culture studies, e.g. from the Swedish west coast (Peters & Müller, 1985) showed, that the life history comprised a microthallus of filamentous dioecious gametophytes. Male and female gametes of a uniform appearance developed from plurilocular sporangia. Female gametes settled first and attracted male gametes by sending chemotactic signals. Upright thalli represent the sporophyte generation.

**Seasonal variation:** Collected in March-November. Unilocular sporangia recorded in April-November.

**Habitat:** On stones and epiphytic, common on Slimy Whip Weed (*Chordaria flagelliformis*). Typically in shallow water and collected by divers to 6.5 m depth and a few collections by dredge from greater depth.

**Resembles:** Winding Broom Weed (*Stictyosiphon tortilis*) is also a much-branched terete brown alga, but its apical true brown algal hairs distinguishes it from Tubular Net Weed (*D. foeniculaceus*).

**References:** Pedersen (1984, 2011), Peters & Müller (1985), Rosenvinge & Lund (1947).


A: *Dictyosiphon foeniculaceus.* Well-developed alga, many scattered branches. Hirsholm, 0.5 m, 9.7.1992. Scale 2 cm.

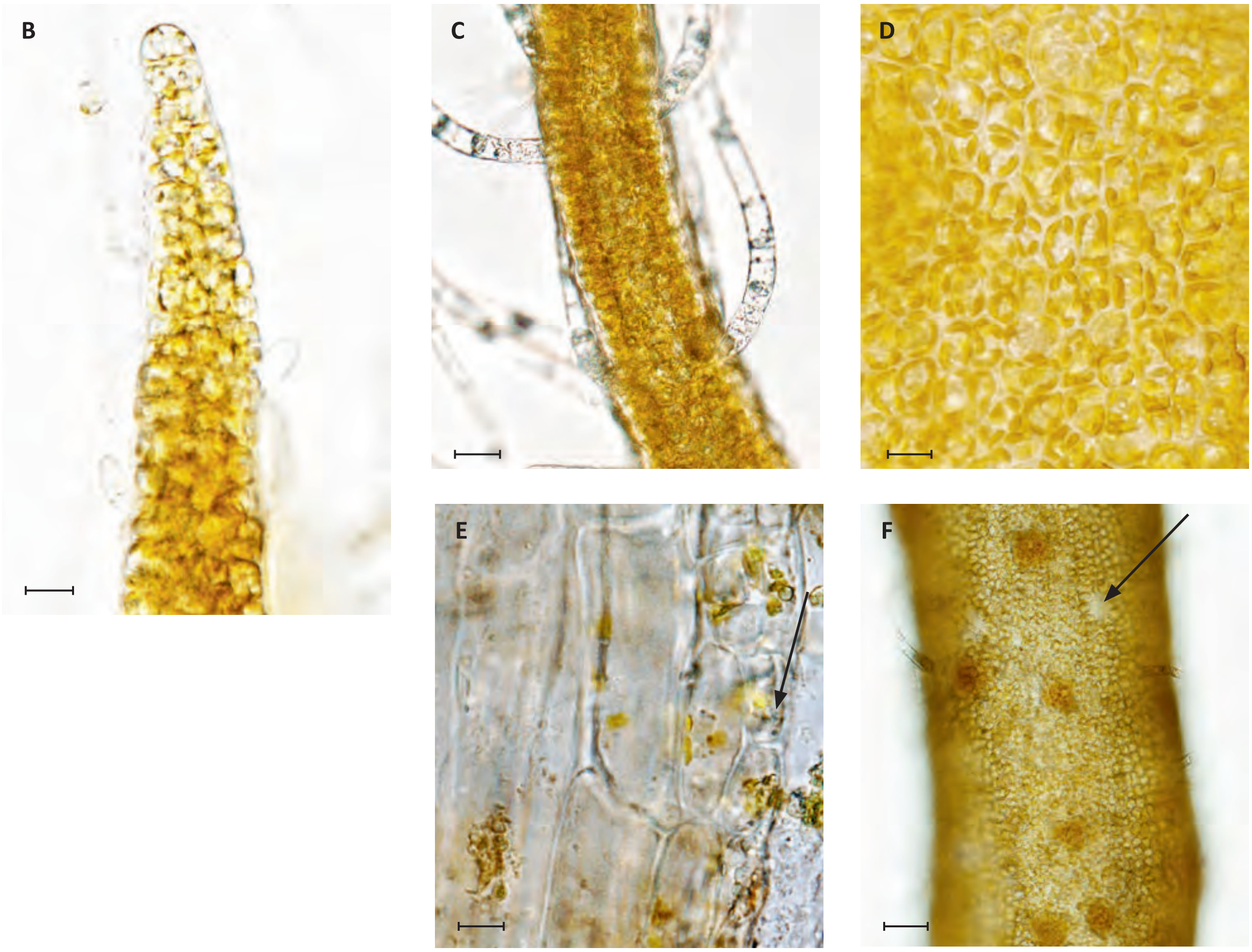
B: *Dictyosiphon foeniculaceus.* Apex with a single apical cell. Scale 10 µm. B, F: Beach north of Vesterø Havn, Læsø, drift, 23.6.2013.

C: *Dictyosiphon foeniculaceus.* Young branch with true brown algal hairs, basal growth zones. Scale 20 µm. C-D: Beach south of Vesterø Havn, Læsø, drift, 9.7.2013.

D: *Dictyosiphon foeniculaceus.* Parenchyma, surface of small cells each with several disc-shaped plastids. Scale 10 µm.

E: *Dictyosiphon foeniculaceus.* Elongated medullary cells and angular surface cells close together. Optical longitudinal section. Beach south of Vesterø Havn, Læsø, drift, 3.6.2017. Scale 10 µm.

F: *Dictyosiphon foeniculaceus.* Older branch with dark brown unilocular sporangia and an empty sporangium (arrow). Scale 50 µm.




# *Elachista*

Wrack Bush

**Appearance:** Small hemispherical tufts of tiny unbranched filaments, 0.5 cm to slightly more than 1 cm in height.

**Structure:** Tufts consist of uniseriate unbranched filaments with thick walls. Filaments (assimilators) have cylindrical cells with many disc-shaped plastids without pyrenoids. Assimilating filaments arise from a basal system of closely packed filaments which form a small knot in older individuals. Growth by cell divisions in a zone slightly above the base. Paraphyses are short, uniseriate filaments, which arise from the distal cells of the basal system and are visible between the lower parts of the assimilators. There are no brown algal hairs.

**Identification key to species of *Elachista***

| | | |
|---|---|---|
| 1a. | Paraphyses club-shaped. Unilocular sporangia from the basal system, common on *Fucus* | *E. fucicola* |
| 1b. | Paraphyses cylindrical and occur scattered. Uni- and plurilocular sporangia both on the basal system and lateral on the assimilating filaments, not on *Fucus* | *E. stellaris* |

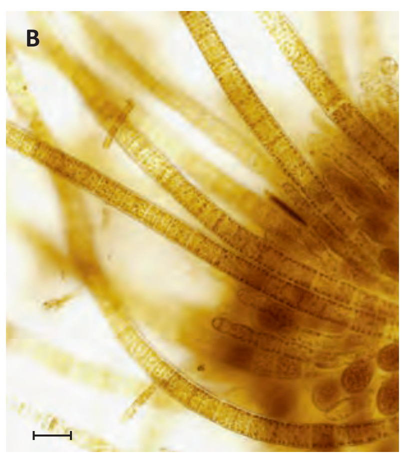
# *Elachista fucicola*

**(Velley) Areschoug**

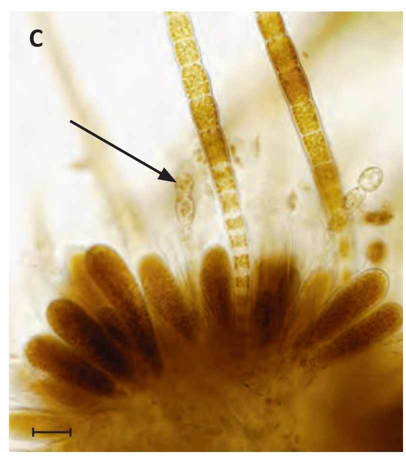
Tiny Wrack Bush

**Appearance:** Small tufts of unbranched assimilating filaments, 0.5-1.3 cm in height, arising from a small knot.
**Structure:** Basal system of creeping filaments from which the upright filaments arise. Assimilators consist of cylindrical cells with many disc-shaped plastids. They become 25-35 (-46) µm in width in the upper part, with cells as long as wide or longer than wide. Growth occurs in the lower part in which the filaments are narrow and the cells short, with most of them approximately 0.5 times as long as wide. Paraphyses, which also arise from the basal system, are uniseriate, club-shaped and typically slightly curved.
**Reproduction:** Unilocular sporangia are obovate, sessile on upper cells of the basal system together with paraphyses.
**Seasonal variation:** Present all year. Well-developed thalli occur in summer and autumn while the assimilators decay in the last month of the year and the thalli appear as small bulb-like thalli on the host algae and a few of them survive the winter. Unilocular sporangia recorded all year.
**Habitat:** Epiphytic on Wrack (*Fucus*), rare on other species. Collected from shallow water and by divers to 9 m depth, and by dredge at Bornholm, 20 m depth.
**Comment:** Culture studies showed that the upright thalli alternated with microthalli of creeping filaments. Upright thalli are diploid sporophytes. Meiosis probably takes place in the unilocular sporangia. Swarmers germinate and develop into microscopic filaments which are haploid and develop plurilocular sporangia. Swarmers from the plurilocular sporangia develop into new creeping filaments. Upright assimilating filaments arise from the microthalli and are the beginning of new tufts. The diploid phase is probably established by vegetative diploidisation. The change between the different phases is caused by external conditions such as temperature and daylength.
**References:** Fletcher (1987), Koeman & Cortel-Breeman (1976), Kornmann (1962d), Kornmann & Sahling (1977), Kylin (1947), Pedersen (1979b), Rosenvinge (1935).


A: *Elachista fucicola*. Tufts (arrow) on Two-headed Wrack (*Fucus distichus*). Northern part of Fiskerihavnen, Copenhagen, 0.5 m, 21.9.2007. Scale 2 cm.




B: *Elachista fucicola*. Assimilating filaments of cylindrical cells with many disc-shaped plastids. Unilocular sporangia. Scale 50 µm. B-C: Northern part of Teglværkshavnen, Copenhagen, 1 m, 27.11.2007.




C: *Elachista fucicola*. Mature and empty unilocular sporangia and paraphyses (arrow). Scale 50 µm.

# *Elachista stellaris*

**Areschoug**

Starry Wrack Bush

**Appearance:** Small tufts of unbranched assimilating filaments.

**Structure:** The base consists of radiating filaments which in older thalli form a small bulb-like thallus of rounded cells, from which uniseriate assimilating filaments arise. These are narrow at the base but soon become 18-50 µm in width. Cells at first approximately barrel-shaped, as long as wide, and elongate upwards in the filaments and become cylindrical, 2-4 times as long as wide or even longer and narrower. Between the assimilating filaments are scattered short thin filaments, which can be interpreted as paraphyses.

**Reproduction:** Uni- or plurilocular sporangia occur at the base of the assimilating filaments. Unilocular sporangia are obovate, 23-34 µm in width and 67-84 µm in height. Plurilocular sporangia are uniseriate and 5-7 µm in width. Sporangia in small sori also occur on the assimilating filaments where they form at different heights and uni- or plurilocular sporangia occur. Unilocular sporangia are ovoid or spherical, 19-26 µm in height and 16-19 µm in width, occasionally on a unicellular stalk. Plurilocular sporangia are cylindrical or conical, uniseriate or with longitudinal cell walls.

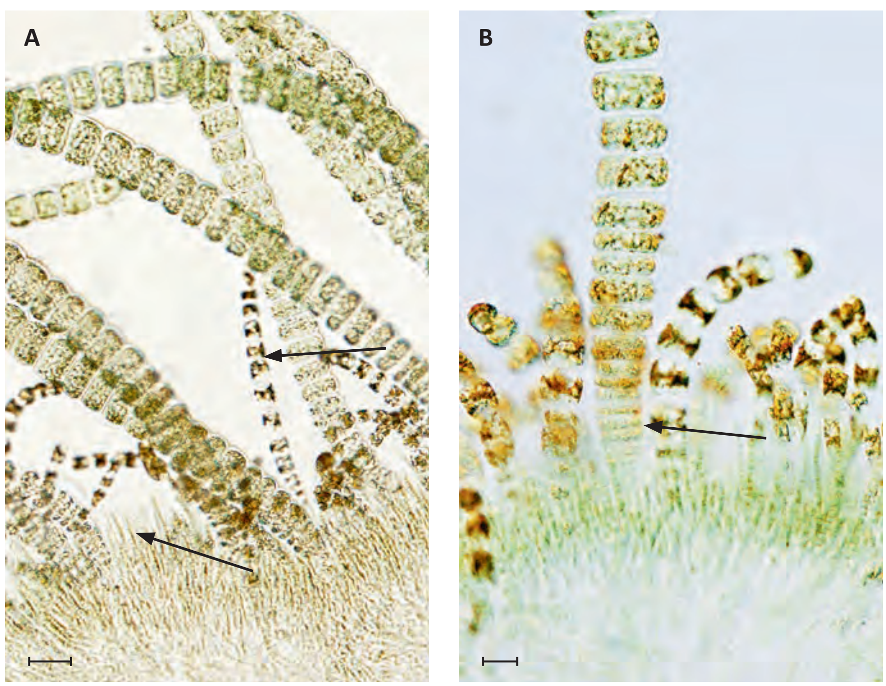
**Seasonal variation:** Collected in July-September, with uni- and plurilocular sporangia.

**Habitat:** Epiphytic on various algae, on bryozoans and ascidians, collected by dredge, 8-24.5 m depth.

**Resembles:** Reminiscent of *Myriactula* sp. but differs by lacking brown algal hairs.

**Comment:** Culture studies of specimens from the Mediterranean Sea showed a regular alternation between diploid macrothalli and haploid microthalli. Vegetative reproduction from plurilocular sporangia occurred in both generations. Meiosis took place in unilocular sporangia on the macrothalli. Swarmers from both uni- and plurilocular sporangia developed into haploid filamentous microthalli. New macrothalli arose from the microthalli and became diploid in cells of the growth zones in the filaments (Müller & Schmidt, 1988).

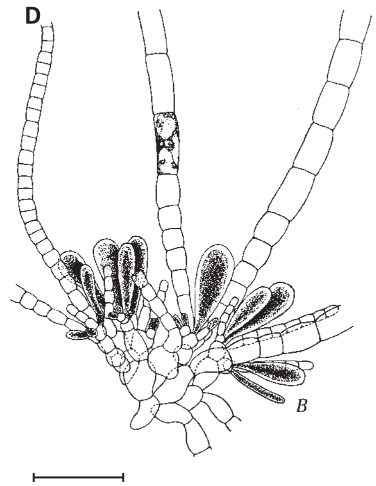
**References:** Fletcher (1987), Müller & Schmidt (1988), Rosenvinge (1935).



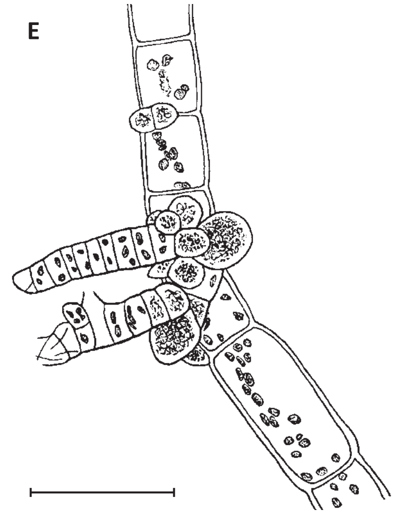

A: *Elachista stellaris.* Part of bulbous base with upright assimilating filaments, short, slender, slightly curved paraphyses (right arrow) and narrow, plurilocular sporangia (left arrow). Scale 50 µm. A-C: On Wire Weed (*Sargassum muticum*), tile works, Helligsø, 3.5 m, 22.8.2000.

B: *Elachista stellaris.* Assimilating filament with growth zone of short cells (arrow) and curved paraphyses. Vegetative barrel-shaped cells with disc-shaped plastids. Scale 50 µm.

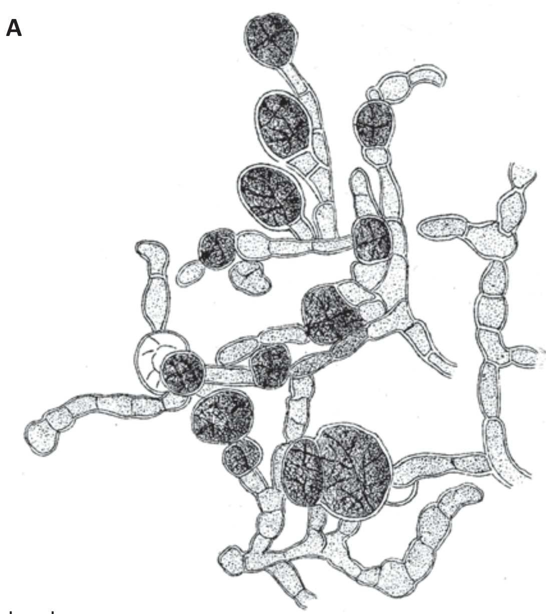

C: *Elachista stellaris.* Lower part of assimilating filament with a branch which is repeatedly dichotomously divided and have apical plurilocular sporangia. Scale 10 µm.




D: *Elachista stellaris.* Unilocular sporangia and paraphyses at the base of assimilating filaments. Scale 50 µm. D, E: After Rosenvinge (1935).




E: *Elachista stellaris.* Sorus of uni- and plurilocular sporangia on assimilating filament. Scale 50 µm.




A: *Endodictyon infestans.* Branched uniseriate filaments with plurilocular sporangia. After Gran (1897). Scale 10 µm.

## *Endodictyon infestans*

### Gran

**Appearance:** Microscopic, brown filaments in the theca of bryozoans.
**Structure:** Uniseriate filaments with scattered branches. Cells with a few plate- or ribbon-shaped plastids. No upright filaments but occasional true brown algal hairs according to Kylin (1947).
**Reproduction**: Plurilocular sporangia, which develop from vegetative cells that become irregularly rounded in shape, are apical or intercalary in the filaments.
**Habitat:** In theca of bryozoans.
**Comment:** Only a single collection from Danish waters, the North Sea, 12.5 m depth, 8.8.1905.
**References:** Gran (1897), Kylin (1947), Rosenvinge & Lund (1941, *Streblonema infestans*).

# *Eudesme virescens*

**(Carmichael ex Berkeley) J.Agardh**

Brown Jelly Weed

**Appearance:** Terete, jelly-like smooth and very soft thalli with scattered branches. Yellow-brown colour which may change to olive-green when dried as herbarium specimen. Thalli become 8-30 (-37) cm in height with branches up to 2 mm in width. Branches of first order may develop small, second order branches, but third order branches seldom occur.

**Structure:** Syntagma in which the central part consists of several branched filaments with relatively long cylindrical cells, loosely connected in a soft wall structure and terminating in a true brown algal hair. Growth of the central filaments is sympodial, upper part of central filaments curve outwards and the longitudinal growth continues from a basal cell in a short branch. Surface of branches consist of bunches of assimilating filaments, sessile on short branches, which curve out from the central filaments. Assimilating filaments are unbranched or sparsely branched in the basal end. They have a uniform thickness or are slightly club-shaped. Basal cells are cylindrical while the upper cells may be slightly swollen. True brown algal hairs arise from a basal cell of the assimilating filaments.

**Reproduction:** Unilocular sporangia are ellipsoid or obovate, 44-88 µm in height and 30-60 µm in width, and develop at the base of the assimilating filaments. Plurilocular sporangia observed once in Danish waters (Rosenvinge & Lund, 1943). They appeared as small papillae with a couple of transverse walls in the apical end of assimilating filaments with short cells.

Culture studies of Japanese specimens showed a direct life history (Kawai, 1986) in which a creeping phase developed, with upright thalli at right conditions of temperature and daylength.

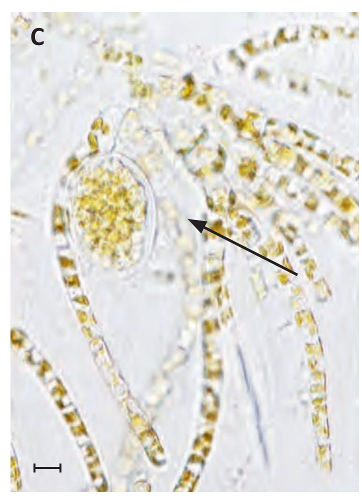
**Seasonal variation:** Collected in April-August, best developed in spring and early summer. Unilocular sporangia recorded in April-August and plurilocular sporangia in August, Adler Grund, at Bornholm, 10.5 m depth, 1894.

**Habitat:** On stone and epiphytic, common on leaves of Eelgrass (*Zostera marina*), but also on large algae, 0-13 m depth.

**References:** Kawai (1986), Kylin (1940), Rosenvinge & Lund (1943).


A: *Eudesme virescens*. Very soft and smooth alga, branches on all sides. Nordre Rønner, Læsø, 0.5 m, 24.5.2005. Scale 2 cm.


B: *Eudesme virescens*. Apex with central filament (arrow). Scale 20 µm. B-C: Beach south of Vesterø Havn, Læsø, drift, 3.6.2017.

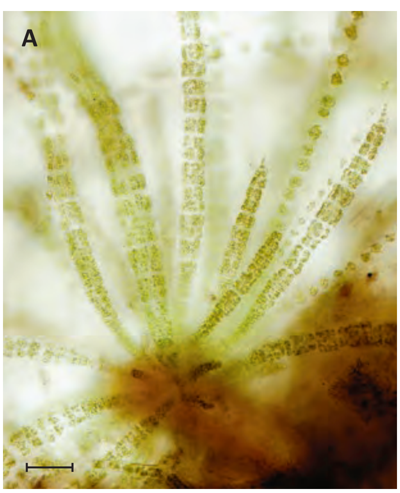



C: *Eudesme virescens*. Unilocular sporangium between uniformly thick assimilating filaments, base of true brown algal hair (arrow). Scale 10 µm.

# *Giraudya sphacelarioides*

### Derbès & Solier in Castagne

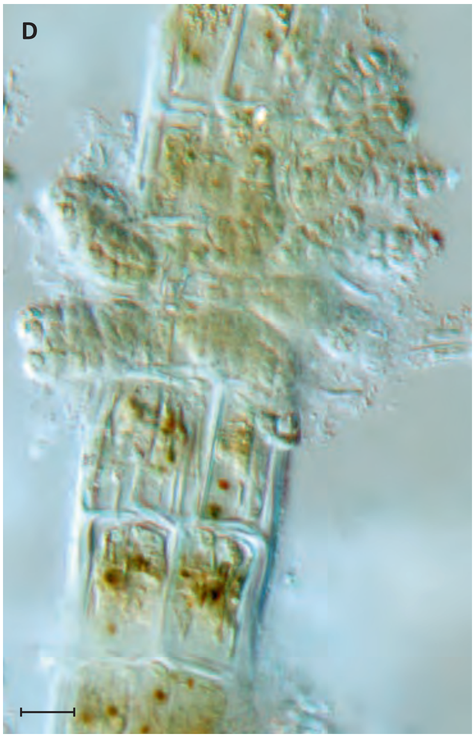
**Appearance:** Brown tufts, a few millimetres in height. **Structure:** Unbranched uprights are uniseriate at the base, where there is a growth zone of short cells. Branches above this area, become wider with longitudinally divided cells, and they appear as if segmented, and segments are of uniform height. Apex of young uprights terminates in a true brown algal hair, reported to have a sheath by some authors. A tuft of several true brown algal hairs later develops from the upper cells. True brown algal hairs also occur scattered further down in the thalli. Uprights arise from creeping filaments and in older thalli from other uprights below the growth zone as well. Vegetative cells contain many disc-shaped plastids, each with a pyrenoid. **Reproduction:** Plurilocular sporangia may be ellipsoid to cone-shaped and occur as sori, which completely or in part surround the uprights as a mantle-like cover. Other plurilocular sporangia are rounded-ellipsoid and form small low cushions on the segmented part of the thalli. Plurilocular sporangia may also occur in fascicles on short branches from the lower part of the uprights. Unilocular sporangia not known. Life history is direct, swarmers from the sporangia germinate and develop into a filament or disc-shaped phase from which uprights arise.
**Seasonal variation:** Collected in May, July-September, plurilocular sporangia recorded in May and August.
**Habitat:** On Eelgrass (*Zostera marina*), various macroalgae and animals. Collected by divers, 10.5 m depth and by dredge, 2-18 m depth.
**References:** Coppejans (1983), Kylin (1947, *Giraudia*), Rosenvinge & Lund (1947, *Giraudia*), Womersley (1987).



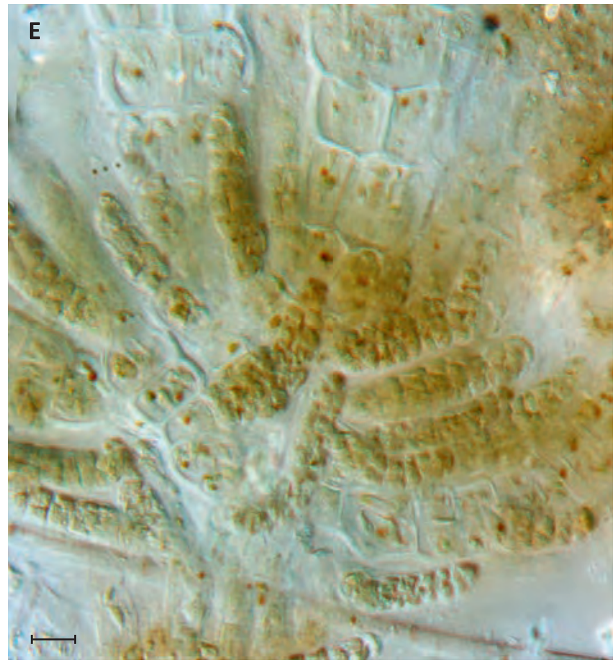

A: *Giraudya sphacelarioides.* Tuft of uprights. Scale 50 µm. A-C: On Eelgrass (*Zostera marina*). Kølpen, Hirsholmene, 3-5 m (dredge), 20.5.1998.


B: *Giraudya sphacelarioides.* Multiseriate upright, segments with cells of uniform height. At base uniseriate growth zone of short cells (arrow). Scale 10 µm.


C: *Giraudya sphacelarioides.* Apex with tuft of true brown algal hairs. Scale 10 µm.




D: *Giraudya sphacelarioides.* Sorus of plurilocular sporangia on segments. Scale 10 µm. D-E: Per Nilen, 10.5 m, 17.8.2015. Photo by S. Lundsteen.




E: *Giraudya sphacelarioides.* Fascicle of plurilocular sporangia at the base of thalli. Scale 10 µm.

## *Halonema subsimplex*

### Jaasund

**Appearance:** Terete soft sparsely branched thalli with a distinct main branch and scattered short branches on all sides. Thalli up to 13 cm in height and 1-1.5 mm in width with branches, 1-2 cm in height according to Jaasund (1951).

**Structure:** Syntagma with a single central filament visible at the apex. Central part of the thallus has a medulla which consists of the central filament surrounded by uniseriate branches. Cells are cylindrical and become wider outward. The surface consists of short, close together, assimilating filaments, which arise approximately perpendicular to the medulla. They are 4-5 cells in length according to Nicolaisen in Moestrup et al. (1975), and each has a slightly swollen apical cell. Brown algal hairs have a special elongate cell just below the growth zone.

**Reproduction:** Plurilocular sporangia develop from the outer cells of assimilating filaments. They have an uneven, rounded shape.

**Seasonal variation:** Collected in June with plurilocular sporangia.

**Habitat:** Epiphytic and on the rocks between Slimy Whip Weed (*Chordaria flagelliformis*).

**Comment:** Described from northern Norway and only collected once in Danish waters, where it occurred between young Slimy Whip Weed (*C. flagelliformis*), Deget, Frederikshavn, 0.10 m, 20.6.1971.

The special hairs with a long basal cell are similar to those of Long Cell Pustule (*Phaeostroma pustulosum*).

**References:** Jaasund (1951), Nicolaisen in Moestrup et al. (1975).

## *Halorhiza* and *Stilophora*

It is difficult to distinguish between *Halorhiza vaga*, *Stilophora nodulosa* and Knobbly Branched Weed (*S. tenella*) and it is uncertain as to whether they are separate taxonomic entities. They are therefore treated together in this book.

**Appearance:** Terete, repeatedly dichotomously divided thalli, compact apart from older individuals which may be hollow in the basal part. Branches typically decrease in width towards the apex, where the youngest may be filiform.

**Structure:** Multiaxial syntagma in which the branches have 4-5 (-6) central filaments, each terminating in an apical cell. Growth apical and one or a few primary assimilating filaments arise from the new cells. These curve upwards and overtop the apical cells of the central filaments together with true brown algal hairs, which develop from the basal cells of the assimilating filaments. A cortex of downward-growing filaments develops from the basal cells of the primary assimilating filaments. Simultaneously, longitudinal elongation of the cells occurs in the central filaments. The cortex becomes polystromatic, with large colourless cells towards the central filaments, and surface of small, rounded cells with several disc-shaped plastids. Secondary assimilating filaments arise from the surface cells. They are unbranched or sparsely branched and typically have slightly swollen apical cells, termed paraphyses when they carry or occur together with sporangia.

**Reproduction:** Uni- and plurilocular sporangia develop from the paraphyses. Unilocular sporangia are sessile, ellipsoid or obovate. Plurilocular sporangia are uniseriate, filamentous and occasionally occur close together in fascicles.

**References:** Kylin (1947), Rosenvinge & Lund (1943).

**Identification key to species of *Halorhiza* and *Stilophora***

| | | |
|---|---|---|
| 1a. | Paraphyses in separate sori with naked cortex in between | *S. tenella* |
| 1b. | Secondary assimilating filaments (or paraphyses) from all cortical cells, no naked cortex | 2 |
| 2a. | Paraphyses longer than secondary assimilating filaments and form wart-like more or less confluent sori together with sporangia | *S. nodulosa* |
| 2b. | Paraphyses and secondary assimilating filaments of approximately uniform height, consisting mainly of cylindrical cells. Sporangia distributed over the surface. Plurilocular sporangia typically in fascicles in the upper end of paraphyses | *H. vaga* |

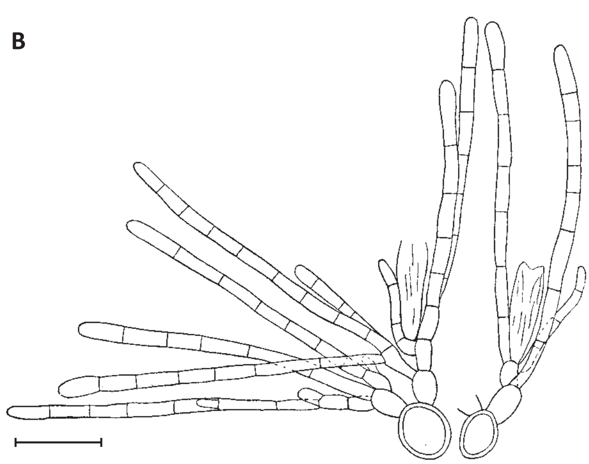
# *Halorhiza vaga*

## Kützing

**Appearance:** Dark brown bush-like thalli, 3-8 (-18) cm in height, dichotomously branched or branches irregularly scattered up to 1 mm in width. Terete branches are cylindrical or gradually tapering and are cartilaginous in texture. Thalli become very dark to almost black after drying.
**Structure:** At the apex are 4-6 central filaments with mutually free primary assimilating filaments. Further down in the thalli secondary assimilating filaments or paraphyses arise from all cortical surface cells. These filaments are approximately uniform in height and evenly distributed to give a smooth surface. Lower cells of the assimilating filaments are cylindrical, 3-5.4 µm in width and 2.5-3 times as long as wide. Upper cells are shorter and rounded or approximately cylindrical, 9.5-12 µm in width and 1-1.5 times as long as wide.
**Reproduction:** Unilocular sporangia occur at the base of the paraphyses and more or less cover the thallus. They are obovate, 32-37 µm long and 15 µm in width. Plurilocular sporangia are individual or in fascicles as branches in the upper part of the paraphyses. Uni- and plurilocular sporangia occur on different individuals.
**Seasonal variation:** Collected in January, April and July-October. Unilocular sporangia recorded in January, July and September, and plurilocular sporangia in April and September.
**Habitat:** Epiphytic on Wrack (*Fucus*) in shallow water.
**References:** Rosenvinge & Lund (1943).

A

B



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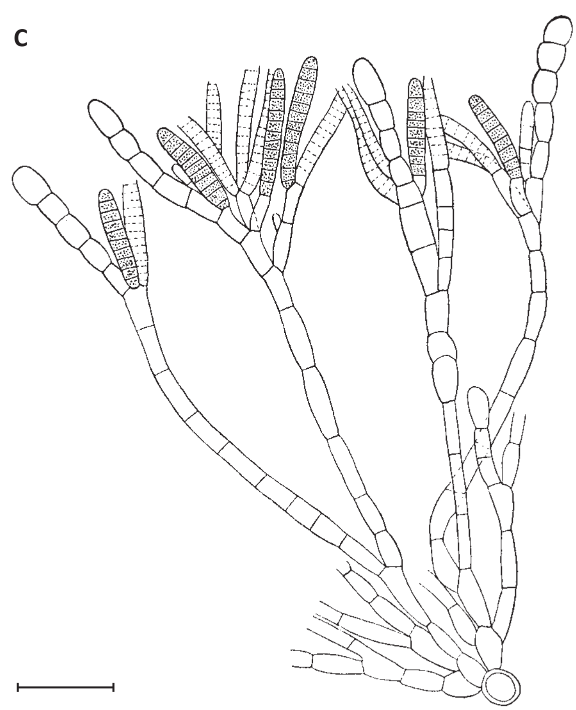


A: *Halorhiza vaga.* Terete, dark brown pseudodichotomous divided branches of approximately uniform thickness. On Bladder Wrack (*Fucus vesiculosus*), Sølager Strand, drift, 26.9.1963. Leg. & det.: H. Nielsen. Scale 2 cm.

B: *Halorhiza vaga.* Paraphyses with empty unilocular sporangia. Avernak Hage close to Nyborg, 24.1.1894. Scale 50 µm. B-C: After Rosenvinge & Lund (1943).

C: *Halorhiza vaga.* Paraphyses with plurilocular sporangia, over-wintering alga. Kalø Rev, 23.4.1894. Scale 50 µm.

## *Stilophora nodulosa*
### (C.Agardh) P.C.Silva

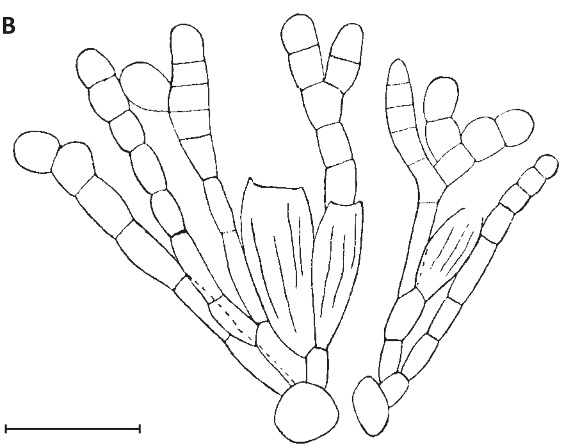
**Appearance:** Dark brown bush-like thalli of terete repeatedly dichotomously divided branches, up to 16 cm in height and 1.5 mm in width. Branches cylindrical, or gradually attenuating towards the apex.
**Structure:** Thallus of 4-5 central filaments. Mutually free primary assimilating filaments at the apex. Secondary assimilating filaments develop from almost all the cortical cells, to completely cover the cortex. Assimilating filaments may have a few short branches.
**Reproduction:** Sporangia form sori with true brown algal hairs and paraphyses, which growth more vigorously than the secondary assimilating filaments. Sori are elongate in outline but are more or less confluent in older part of the thallus, where they cover most of the surface. Uni- and plurilocular sporangia observed on different thalli. Unilocular sporangia are obovate and occur at the base of the paraphyses. Plurilocular sporangia are uniseriate, also occur at the base of the paraphyses, and may also be lateral on the upper part of the paraphyses.
**Seasonal variation:** Collected in June-November and a few wintering individuals in April-May. Unilocular sporangia recorded in August-September and November, plurilocular sporangia in August-September and May.
**Habitat:** Epiphytic on Wrack (*Fucus*) in shallow water, 0.5-5.5 m depth.
**References:** Rosenvinge & Lund (1943, *S. tuberculosa*).

A


A: *Stilophora nodulosa*. Terete, dark brown dichotomously divided smooth branches. Birkholm, 18.9.1890. Leg. & det.: Rosenvinge. Scale 2 cm.

B: *Stilophora nodulosa*. Paraphyses with unilocular empty sporangia. Hou, 18.10.1893. Scale 50 µm. B-C: After Rosenvinge & Lund (1943).

C: *Stilophora nodulosa*. Paraphyses with plurilocular sporangia. Rønnen in Begtrup Vig, 17.5.1893. Scale 50 µm.

B


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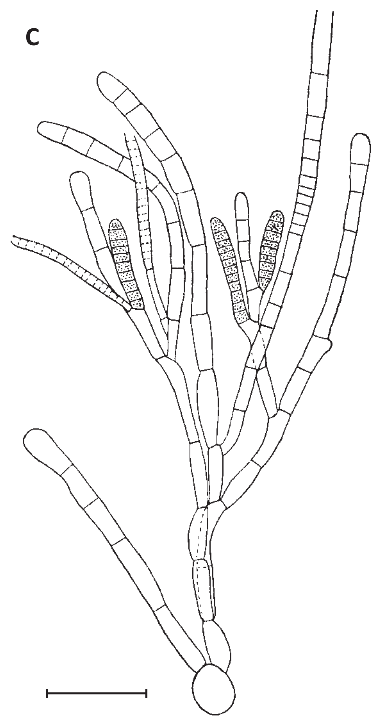


# *Stilophora tenella*

**(Esper) P.C.Silva**

Knobbly Branched Weed

**Appearance:** Terete repeatedly dichotomously branched yellow-brown bush-like thalli, up to 20 cm in height. Branches up to 1 mm in in width at the base and gradually become slender towards the apex. Branches with small approximately semiglobular warts which make them rough to touch.

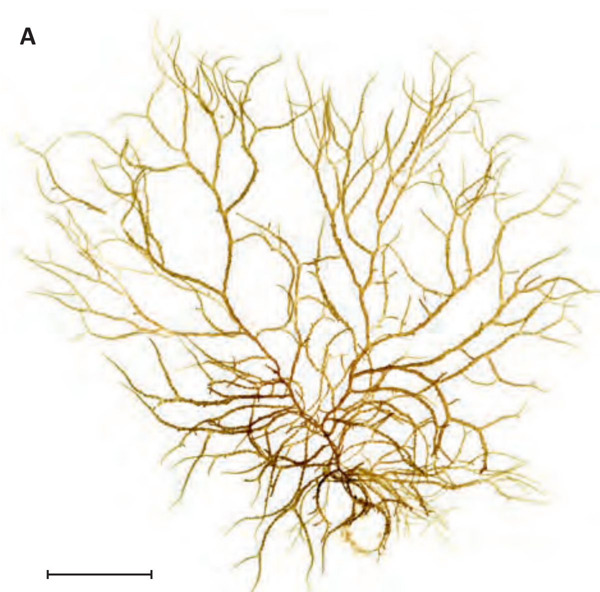
**Structure:** Thalli with 4-5 central filaments. Secondary assimilating filaments (paraphyses) arise from some of the cortical surface cells, and these filaments, together with true brown algal hairs and sporangia, form wart-like sori. Young sori are approximately circular in outline, but paraphyses develop from neighbour cortical cells, so older sori become irregular and more or less confluent in the basal part of the thalli. Paraphyses are club-shaped with cylindrical cells at the base and slightly swollen to approximately spherical cells at the top and might branch a little in the upper part. Large club-shaped cells with a homogenous brown content (ascocysts) may occur between the paraphyses.

**Reproduction:** Uni- or plurilocular sporangia occur at the base of the paraphyses. Unilocular sporangia are obovate. Plurilocular sporangia are uniseriate and may occasionally occur laterally at the upper end of the paraphyses. Two kinds of sporangia can be observed on the same or different individuals. Culture studies of Knobbly Branched Weed (*S. tenella*), some of which were from the Swedish west coast and Canada, showed that the life history comprised a microthallus, with development dependent on temperature (Novaczek et al., 1986, Peters & Müller, 1986). Sexual reproduction was observed with isogametes formed on microthalli at low temperatures. Zygotes germinated into filaments from which macrothalli arose, similar to those known in nature.

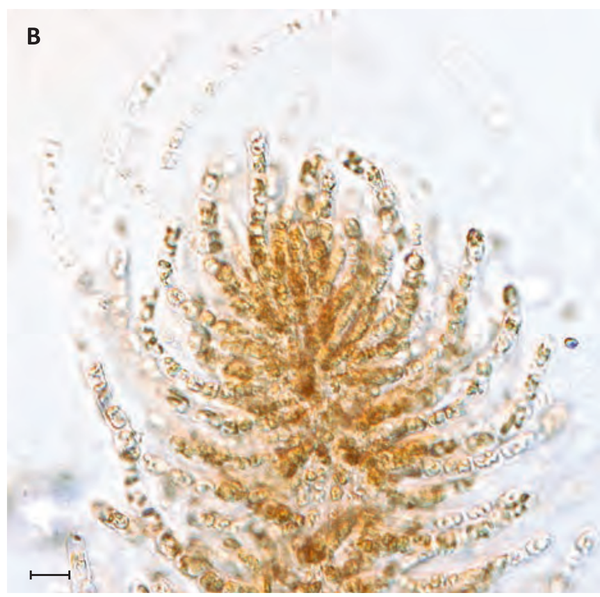
**Seasonal variation:** Collected in July-December with uni- and plurilocular sporangia.

**Habitat:** Epiphytic on Bladder Wrack (*Fucus vesiculosus*) and Serrated Wrack (*F. serratus*), occasional on stone. Typical in shallow water, 0.5-2 m depth, but a few collections by dredge from greater depth.

**References:** Novaczek et al. (1986, *Stilophora rhizodes*), Peters & Müller (1986, *S. rhizodes*), Rosenvinge & Lund (1943, *S. rhizodes*).

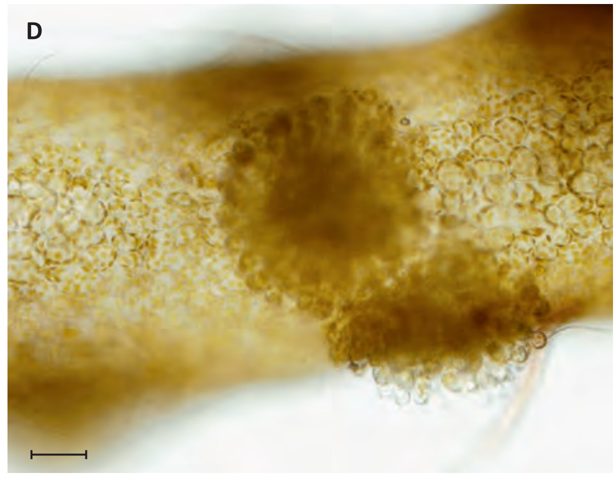



A: *Stilophora tenella.* Terete, yellow-brown dichotomous branches with small wart-like sori. Bredsund, Hirsholm, 4 m, 29.6.1992. Scale 2 cm.

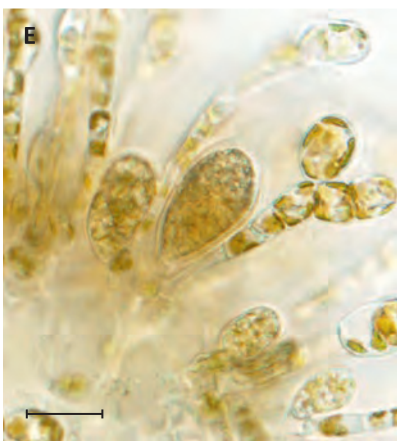



B: *Stilophora tenella.* Apex, primary assimilating filaments, curved and overtopping the apical cells together with true brown algal hairs. Nordre Rønner, Læsø, 0.5 m, 5.9.1972. Scale 20 µm.


C: *Stilophora tenella*. Branch with 4 central filaments (c). Cortex of large pale cells surrounded by surface layer of small cells, each with several disc-shaped plastids. Transverse section. Scale 20 µm. C-E: East of Holtemmen, Læsø, drift, 23.7.2013.




D: *Stilophora tenella*. Surface of small cortical cells with several disc-shaped plastids and wart-like circular sori. Scale 50 µm.




E: *Stilophora tenella*. Unilocular sporangium at the base of branched paraphysis. Scale 20 µm.


F: *Stilophora tenella*. Sorus of club-shaped paraphyses and plurilocular sporangium (arrow). Scale 10 µm. F, G: Beach south of Vesterø Havn, Læsø, drift, 29.7.2014.


G: *Stilophora tenella*. Plurilocular sporangium (arrow), same as in fig. F. Scale 10 µm.

# *Halothrix lumbricalis*

**(Kützing) Reinke**

Woolly Wristlet

**Appearance:** Small tufts of tiny unbranched filaments, 0.5-2 cm in height.

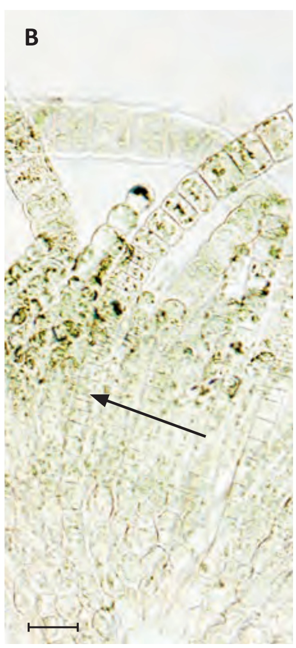
**Structure:** Upright assimilating filaments are uniseriate and unbranched. They consist of cylindrical or barrel-shaped cells, 20-40 µm in width and 0.5-1.5 times as long as wide. Base of filaments typically slender with a basal growth zone, diffuse growth also occurs further up in the filaments. Cells in the apical part are thin and relatively long and contain many disc-shaped plastids without pyrenoids. Upright filaments arise from a basal system of closely packed filaments with rhizoids. From the lower part of upright filaments thin uniseriate filaments with restricted growth arise, typically club-shaped with cylindrical cells at the base and terminate in swollen cells. They are similar to the paraphyses found in Tiny Wrack Bush (*Elachista fucicola*). No brown algal hairs.

**Reproduction:** Plurilocular sporangia occur in sori and surround the filaments at intervals, with sporangia radiating from the filaments. After some initial longitudinal divisions of the surface cells, sporangia develop from these and each one becomes uniseriate with 3-6 small compartments. Culture studies by Pedersen (1979b) documented a direct life history. Swarmers from the plurilocular sporangia germinated and developed into creeping filaments, from which new upright thalli arose, similar to the previous generation.

**Seasonal variation:** Collected in April-October with plurilocular sporangia.

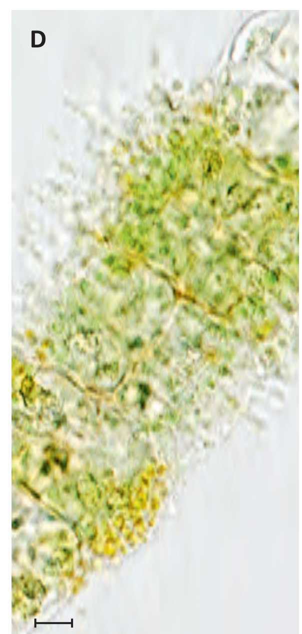
**Habitat:** Epiphytic on leaves of Eelgrass (*Zostera marina*), 0.5-13 m depth.

**References:** Fletcher (1987), Pedersen (1979b), Rosenvinge (1935).


A: *Halothrix lumbricalis*. Tiny brown filaments on Eelgrass (*Zostera marina*). Deget, Frederikshavn, 2 m, 20.5.1989. Scale 2 cm.

B: *Halothrix lumbricalis*. Base of alga, upright filaments with growth zone (arrow). Scale 50 µm. B-D: On Eelgrass (*Zostera marina*), Kølpen, Hirsholmene, 4 m, 14.6.2001.


C: *Halothrix lumbricalis*. Sori of plurilocular sporangia, which surround a filament with divided cell (arrow). Scale 10 µm.

D: *Halothrix lumbricalis*. Sporangia sorus of radiating, plurilocular sporangia. Scale 10 µm.

# *Hecatonema terminale*

**(Kützing) Kylin**

**Recent synonym:** ***Hecatonema maculans*** **(Collins) Sauvageau**

Fluffy Hundred Thread Weed

**Appearance:** Microscopic alga with creeping filaments, from which arise upright filaments up to c. 1 mm in height.

**Structure:** Basal system of radiating filaments, which are mutually free or confluent to pseudoparenchyma, occasionally disc-shaped with forked marginal cells. Upright filaments are mutually free, uniseriate, unbranched or have scattered branches. Branches approximately perpendicular to main branch but turn upwards in same direction. Cells contain several disc-shaped plastids with pyrenoids. Brown algal hairs with sheath are terminal on the upright branches.

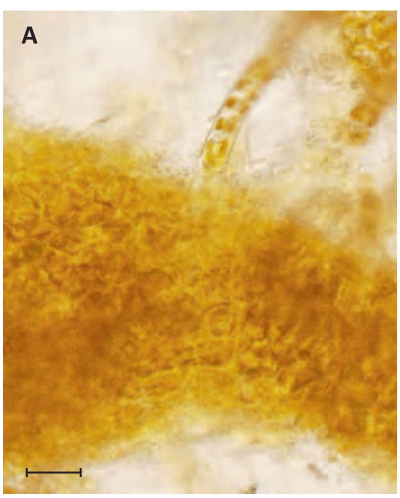
**Reproduction:** Plurilocular sporangia are biseriate, elongate ellipsoid to lanceolate and may be forked. They arise from the upright filaments, and are sessile or terminal, rarely occurring from the basal filaments.

**Seasonal variation:** Recorded in January, March, June-September and December. Plurilocular sporangia recorded in March.

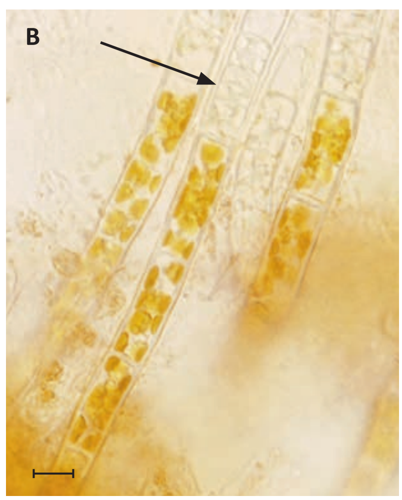
**Habitat:** Epiphytic on other algae, on mollusc shells, stone and other solid substratum, 0.5-13 m depth.

**Comment:** Many uncertain taxonomic problems remain within the genus Hundred Thread Weed (*Hecatonem*a), which can only be solved by future experiments including culture studies and molecular biological investigations. Species determination is difficult, and culture studies showed that *Hecatonema*-looking algae were part of the life history in various larger algae such as Sausage Weed (*Asperococcus*) and Brown Tongue (*Punctaria*) (Pedersen (1981a, 1984). However, a macrothallus did not develop in culture studies of Hundred Thread Weed (*Hecatonema*) from Danish waters (Pedersen 1984).

**References:** Fletcher (1987), Kuckuck (1953), Mathieson & Dawes (2017), Pedersen (1981a, 1984, *H. maculans*), Sauvageau (1897).

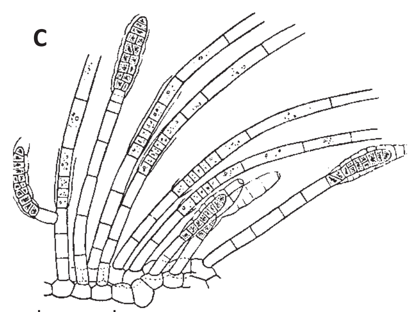



A: *Hecatonema terminale*. Pseudoparenchymatous basal layer with upright filaments. Scale 20 µm. A-B: On egg mass of Common Whelk (*Buccinum undatum*), Storedal, Læsø, drift, 3.6.2017.




B: *Hecatonema terminale*. Upright filaments, terminal brown algal hairs with sheath (arrow), cells with several disc-shaped plastids. Scale 10 µm.

C



C: *Hecatonema terminale*. Creeping and upright filaments with terminal brown algal hairs with sheath and plurilocular sporangia. Helgoland. Scale 50 µm. After Kuckuck (1953).

# *Isthmoplea sphaerophora*

**(Carmichael) Gobi**

Globethread

**Appearance:** Small delicate, branched light brown bushy alga, up to 1 cm in height.

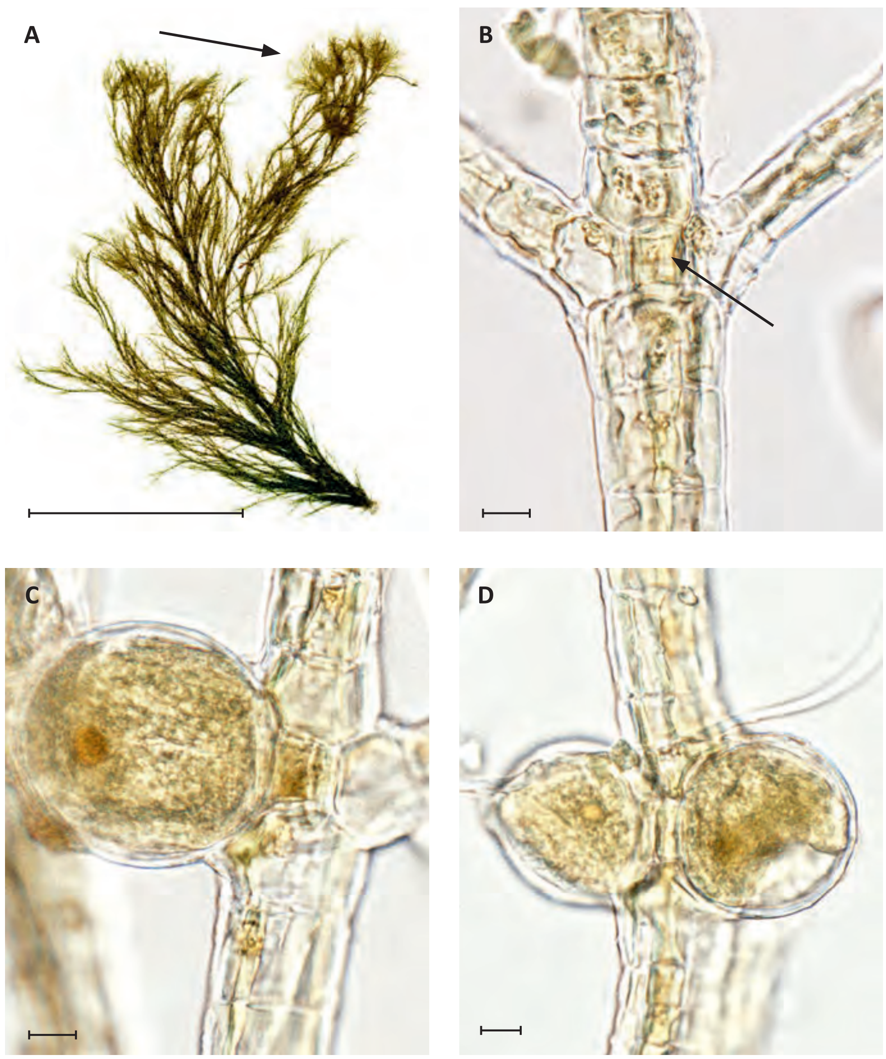
**Structure:** Mainly uniseriate branches but with longitudinal walls at the base of the thallus and at branching points. Diffuse growth. Branching opposite and a few scattered branches. At branching points the cell of the main branch is divided by two longitudinal walls so a central cell appears. Branches attenuate towards the tip. Cells contain many disc-shaped plastids. No hairs.

**Reproduction:** Unilocular sporangia are approximately spherical, 39-54 µm in width. They are lateral, sessile on a central cell of the branch and opposite or opposite a branch. Culture studies of the alga from the area of Oslo, Norway showed a direct life history, in which upright thalli with unilocular sporangia arose from creeping filaments (Rueness, 1974).

**Seasonal variation:** Collected in April-May and July. Unilocular sporangia recorded in April-May.

**Habitat:** Epiphytic on Common Green Branched Weed (*Cladophora rupestris*) and Pitcher Siphon Weed (*Polysiphonia stricta*), 0.5-1 m depth.

**References:** Kornmann & Sahling (1977), Kylin (1947), Pedersen (1975, 2011), Rosenvinge & Lund (1947), Rueness (1974).




A: *Isthmoplea sphaerophora*. Small delicate bushy algae (arrow). Scale 2 cm. A-D: On Common Green Branched Weed (*Cladophora rupestris*), southern harbour jetty, exposed side, Hirsholm, 0.5 m, 15.5.1981.

B: *Isthmoplea sphaerophora*. Opposite branches and central cell (arrow). Scale 10 µm. B-D: Rehydrated herbarium material.

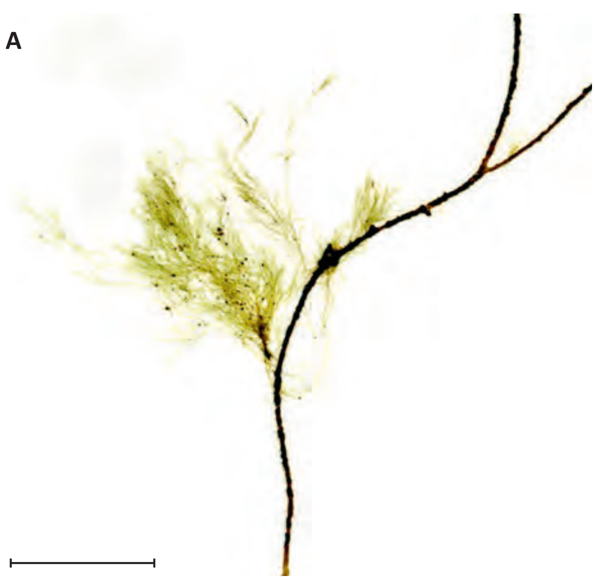
C: *Isthmoplea sphaerophora*. Unilocular sporangium opposite a branch. Scale 10 µm.

D: *Isthmoplea sphaerophora*. Opposite sporangia. Scale 10 µm.

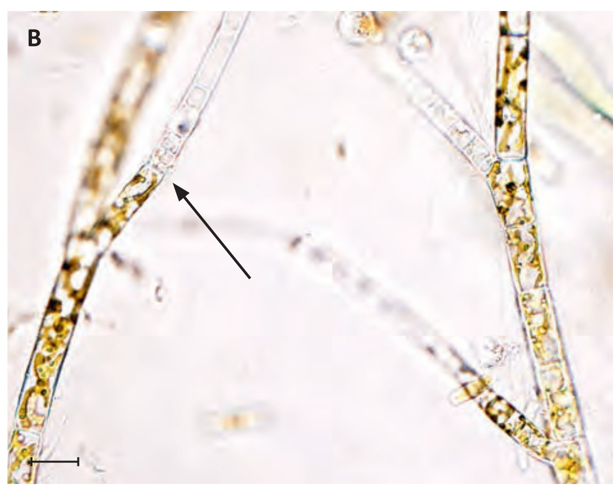
## *Kuckuckia spinosa*

### (Kützing) Kornmann in Kuckuck

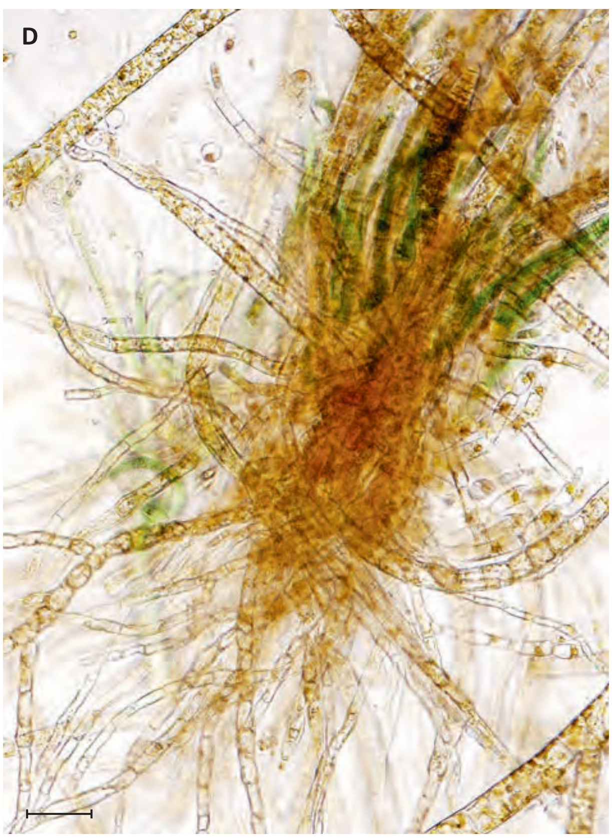
**Appearance:** Small brown bush-like alga, up to 6 cm in height and reminiscent of Cotton Wool Weeds (*Ectocarpus*).
**Structure:** Unbranched or sparsely branched uniseriate filaments with diffuse growth. Filaments terminate in brown algal hairs with a sheath. Hairs are pushed aside by continued growth from the cell below the hair (sympodial growth). Hairs therefore also appear lateral on the branches. Cylindrical cells, 25-30 µm in width and older cells up to 3 times as long as wide, while newly divided cells are approximately as long as wide. Cells contain several ribbon-shaped plastids with pyrenoids.
**Reproduction:** Plurilocular sporangia are elongate conical or approximately cylindrical. They either develop from lateral branches which are completely transformed into sporangia, or they have a stalk of 1-2 cells. Terminal sporangia also occur, that are pushed aside by continued sympodial growth. In culture by Pedersen (2006) swarmers were released from the upper part of the sporangia after the inner walls decayed. Swarmers settled, germinated and grew into creeping filaments from which new upright thalli arose.
**Seasonal variation:** Collected in June and September.
**Habitat:** Epiphytic on Sea Noodle Worm Weed (*Nemalion multifidum*), Knobbly Branched Weed (*Stilophora tenella*) and leaves of Eelgrass (*Zostera marina*), 0.5-4 m depth.
**Comment:** Taxonomic relationships of *Kuckuckia* are uncertain. Pedersen (1984, 1989) compared *K. spinosa, Botrytella* (as *Sorocarpus*) and *Polytretus* and referred them to the same family (Sorocarpaceae) because of the sympodial growth and the true brown algal hairs. Kim (2010) referred *Kuckuckia* to Ectocarpaceae based on molecular studies and considered the true brown algal hairs of minor importance. Silberfeld et al. (2014) referred *Botrytella* (with *Polytretus* in synonymy) in Chordariaceae. The genera Pedersen (1984, 1989) compared are not included in the molecular studies, but the structures Pedersen (1984, 1989) mentioned are so convincing that we refer *K. spinosa* to the Chordariaceae, which *Botrytella* and *Polytretus* are also referred to.
**References:** Kim (2010), Kuckuck (1958), Pedersen (1984, 1989, 2006), Silberfeld et al. (2014), Stache-Crain et al. (1997).




A: *Kuckuckia spinosa* Delicate bush-like algae. Scale 1 cm.
A-E: On Knobbly Branched Weed (*Stilophora tenella*), beach north of Vesterø Havn, Læsø, 0.5 m, 2.9.2017.




B: *Kuckuckia spinosa.* Filaments with terminal and lateral brown algal hairs with sheath (arrow). Scale 20 µm.


C: *Kuckuckia spinosa*. Cells with ribbon-shaped plastids with pyrenoids. Scale 10 µm.

D: *Kuckuckia spinosa*. Base of main branch with many downward-growing rhizoids. Scale 50 µm.

E: *Kuckuckia spinosa*. Plurilocular sporangium. Scale 10 µm.

## *Laminariocolax aecidioides*

**(Rosenvinge) A.F.Peters**

Kelp Dweller

**Appearance:** Microscopic, endophytic filaments, producing dark spots in the host alga. When sporangia form, they break through the surface of the host alga and appear as volcano-like, pinhead spots.
**Structure:** Uniseriate filaments with scattered branches between the cells of the host alga. Diffuse growth. True brown algal hairs are lateral on the filaments together with plurilocular sporangia. These structures break through the surface of the host at irregular intervals. The cells contain 2-3 disc-shaped plastids.
**Reproduction:** Uniseriate plurilocular sporangia in sori together with true brown algal hairs. Unilocular sporangia are reported from the Swedish west coast, but not recorded from Danish waters.
**Seasonal variation:** Collected in April-July and September-October, plurilocular sporangia recorded in May, June and September.
**Habitat:** Endophytic in blades of Oar Weed (*Laminaria digitata*), Forest Kelp (*L. hyperborea*) and Sugar Kelp (*Saccharina latissima*), 0.5-9 m depth.
**Comment**: Referred to *Laminariocolax* following molecular studies which included algae from Danish waters (Burkhardt & Peters, 1998). The species was referred to *Gononema* by Pedersen (1981c, 2011) based on the presence of true brown algal hairs and development of upright thalli in culture. Pedersen (1981c) found a direct life history in culture of thalli from Greenland, where swarmers from plurilocular sporangia germinated and grew into uniseriate filaments in which plurilocular sporangia developed as in the parent generation. Pedersen reported ascocysts, which occurred individually or together with plurilocular sporangia (Pedersen 1981c, 2011).
**References:** Burkhardt & Peters (1998), Kylin (1947, *Entonema aecidioides*), Pedersen (1981c, 2011, *Gononema aecidioides*), Rueness (1977, *Myrionema aecidioides*).


A: *Laminariocolax aecidioides.* Endophytic uniseriate filaments (lower arrow). Plurilocular uniseriate sporangia and true brown algal hair (upper arrow) broken through the surface of the host as a small volcano. Transverse section of Sugar Kelp (*Saccharina latissima*). Tangen, 9 m, 15.9.1996. Scale 10 µm.

A: *Laminariocolax tomentosoides.* Mat of tiny closely packed upright filaments. Scale 20 µm. A-D: On Forest Kelp (*Laminaria hyperborea*), Læsø Trindel, 11 m, 3.6.1993.

B: *Laminariocolax tomentosoides.* Cylindrical cells with 2 ribbon-shaped plastids. Scale 10 µm.

C: *Laminariocolax tomentosoides.* Perpendicular, protruding plurilocular sporangia in a long filament. Scale 10 µm.

D: *Laminariocolax tomentosoides.* Plurilocular sporangia on consecutive cells. Scale 10 µm.

## *Laminariocolax tomentosoides*

**(Farlow) Kylin**

Oar Weed's Felt

**Appearance:** A felty cover of tiny upright filaments, up to 2 mm in height, appearing as dark spots on the host alga.

**Structure:** Creeping endophytic filaments, which spread in cell walls inside the host. From the creeping filaments, upright filaments arise, which are unbranched apart from protruding plurilocular sporangia. Filaments consist of cylindrical cells, 5-8 µm in width and 3-4 times as long as wide, typically with two short ribbon-shaped plastids. No hairs.

**Reproduction:** Plurilocular sporangia are uniseriate. They are terminal on the upright filaments or lateral and approximately perpendicular to the branches, occasionally with a stalk of 1-2 cells. Sporangia may be more than 100 µm long and 4-8 µm in width. Terminal sporangia are occasionally branched. Development is direct, swarmers from plurilocular sporangia develop into individuals similar to the former generation (Pedersen, 2011).

**Seasonal variation:** Collected in April-June with plurilocular sporangia.

**Habitat:** Epiphytic on Oar Weed (*Laminaria digitata*) and Forest Kelp (*L. hyperborea*), particularly on the blades, but may occur on the stipes, 6-15 m depth.

**Comment:** By comparing molecular studies, Peters (2003) has documented that *Streblonema deformans* (P.J.L.Dangeard) Hamel is a subspecies of Oar Weed's Felt (*L. tomentosoides*). Reports of unilocular sporangia are doubtful, apparently being ascocysts.

**References:** Kornmann & Sahling (1977), Kylin (1947), Lein et al. (1991), Pedersen (2011), Peters (2003), Rosenvinge & Lund (1941, *Ectocarpus tomentosoides*), Russell (1964).




# *Leathesia marina*

**(Lyngbye) Decaisne**

Punctured Ball Weed

**Appearance:** Yellow-brown spherical or irregularly shaped lumpy thalli with a cartilaginous consistency and a smooth surface. The size varies from a few millimetres up to 5 cm in width. Young thalli are compact while older ones are hollow.

**Structure:** A syntagma of radiating filaments, which are di- or trichotomously branched. The medulla consists of pale, large and irregularly rounded cells, which become smaller, egg-shaped or spherical towards the surface. The centre gradually becomes hollow as the thallus increases in size. The surface consists of radiating short, 3-4 cells long assimilating filaments and true brown algal hairs. Lower cells in the assimilating filaments are cylindrical, and the apical cell approximately spherical. Each cell contains a few disc-shaped plastids. True brown algal hairs arise from the outermost medullary cells.

**Reproduction:** Uni- or plurilocular sporangia occur at the base of the assimilating filaments. They are on the same or different individuals. Unilocular sporangia are ellipsoid or ovoid and lateral on the outer medullary cells, c. 25-30 µm long and 15-18 µm in width. Plurilocular sporangia are cylindrical and uniseriate, c. 15-20 µm long and 4-6 µm in width, and occur individually or in small fascicles between the assimilating filaments.

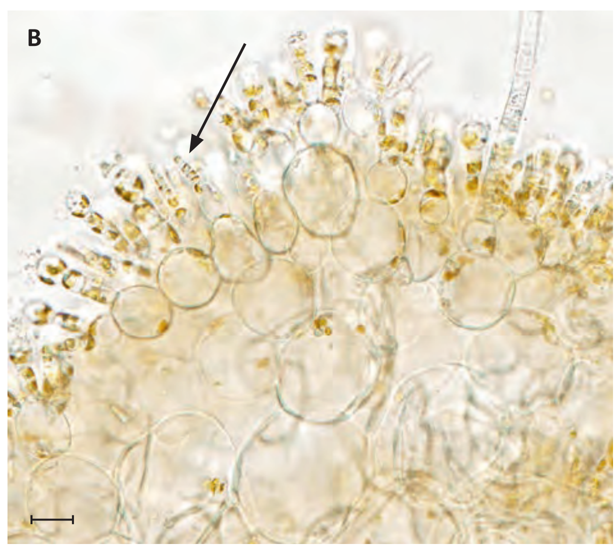
**Seasonal variation:** Collected in May-October. Thalli with only unilocular sporangia recorded in June, July and September, whereas those with only plurilocular sporangia in July-October; few thalli with both uni- and plurilocular sporangia in August.

**Habitat:** Typically epiphytic on Black Scour Weed (*Ahnfeltia plicata*) and may occur on other algae, Eelgrass (*Zostera marina*) and other sea grasses, 2-6 m depth, a few collections by dredge, 9 m depth.

**Comment:** Culture studies of Punctured Ball Weed (*L. marina*) from various European localities showed that the macroscopic sporophyte alternates with microscopic gametophytes. Direct development of new macroscopic or new microscopic thalli from swarmers of plurilocular sporangia may also occur.

**References:** Fletcher (1987, *Leathesia difformis*), Kim 2010, Rosenvinge & Lund (1943, *L. difformis*).


A: *Leathesia marina*. Lumpy thalli on Black Scour Weed (*Ahnfeltia plicata*) (arrow). Nordre Rønner, Læsø, 0.5 m, 17.8.2005.




B: *Leathesia marina*. Part of alga with rounded pale medullary cells; surface of short assimilating filaments and true brown algal hairs. Plurilocular sporangia (arrow) between the assimilating filaments. Scale 20 µm. B-D: Squash preparation. Beach north of Vesterø Havn, Læsø, drift, 9.7.2013.


C: *Leathesia marina*. Mature unilocular sporangium, on an outer medullary cell, assimilating filament and empty sporangium (arrow). Scale 10 µm.


D: *Leathesia marina*. Plurilocular sporangia (arrow). Scale 10 µm.

## *Leptonematella fasciculata*

**(Reinke) P.C.Silva**

Fine Bundle Weed

**Appearance:** Tufts of tiny unbranched filaments, 0.5-3 mm in height. They arise from a basal system of creeping filaments.

**Structure:** Basal system of radiating, closely connected filaments. Upright filaments are uniseriate and unbranched, 7-16 µm in width, but occasionally with branches at the base. Filaments have an intercalary growth zone slightly above the base. Cylindrical vegetative cells contain many disc-shaped plastids without pyrenoids. No hairs.

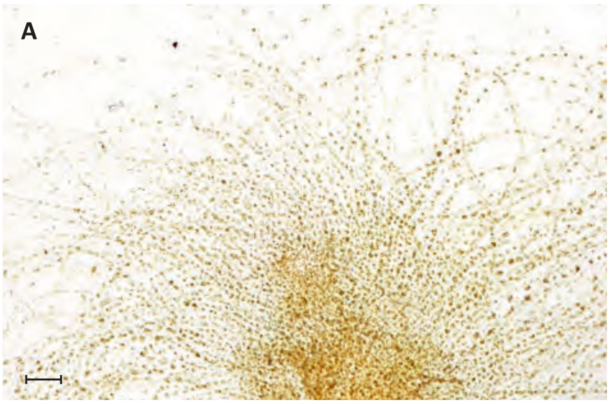
**Reproduction:** Plurilocular sporangia are intercalary in the upright filaments. They are typically many in a series and form from vegetative cells after initial longitudinal and transverse divisions. Sporangia are evacuated through a small papilla. Unilocular sporangia occasionally occur at the base of upright filaments, sessile or on a short stalk. They are obovate, 56-112 µm long and 25-32 µm in width. Culture studies showed a direct development of swarmers from both plurilocular and unilocular sporangia (Pedersen, 1978b).

**Seasonal variation:** Collected in January-September. Plurilocular sporangia recorded in March-August and unilocular sporangia in April-July.

**Habitat:** On larger algae, seagrasses, hermit crabs and ascidians, 0.5-22 m depth.

**Resembles:** The structure is reminiscent of Woolly Wristlet (*Halothrix lumbricalis*), but this species has broader filaments, 30-50 µm in width, and the plurilocular sporangia in sori around the filaments.

**References:** Fletcher (1987), Kornmann & Sahling (1977), Lee et. al. (2002), Pedersen (1978b, 2011), Rosenvinge (1935, *Leptonema fasciculatum*).

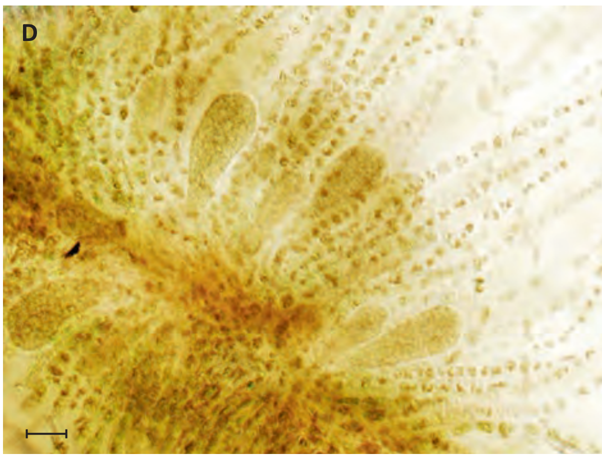



A: *Leptonematella fasciculata*. Tuft of upright filaments from a thin basal layer. Schultz's Grund, 7 m, 27.5.1992. Scale 50 µm.



B: *Leptonematella fasciculata*. Filament with plurilocular sporangia. Beach north of Vesterø Havn, Læsø, drift, 5.6.2017. Scale 10 µm.

C: *Leptonematella fasciculata*. Filament with mature and empty (arrow) plurilocular sporangia. Store Middelgrund, 12 m, 9.6.1993. Scale 10 µm.




D: *Leptonematella fasciculata*. Unilocular sporangia at the base of upright filaments. Briseis Flak, 7 m, 29.5.1992. Scale 20 µm.

## *Litosiphon laminariae*

**(Lyngbye) Harvey**

Kelp Thread

**Appearance:** Unbranched light brown or dark brown compact thread, 3-5 (-6) cm in height. They are typically constricted at the base and have a rounded apex. They are epiphytes which grow individually or a few together from the same base.

**Structure:** Thalli are constructed as parenchyma with a medulla of large slightly elongate cells and cortex of 1-2 cell layers of quadratic or rectangular cells. Surface cells are in longitudinal rows, occasionally slightly twisted. They contain several disc-shaped plastids with pyrenoid. Many true brown algal hairs are scattered on the surface. Young thalli have a true brown algal hair at the apex. On the lower part of the thallus rhizoids occur, which may grow between the cells of the host alga.

**Reproduction:** Uni- and plurilocular sporangia are embedded among the surface cells on the same or different individuals. Unilocular sporangia develop directly from surface cells and are slightly vaulted. They are approximately spherical, 16-32 µm in width.

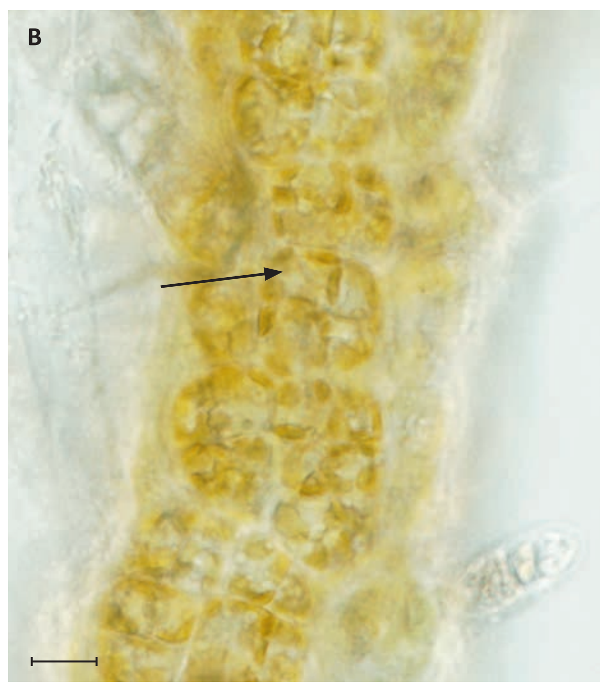
Plurilocular sporangia form after a couple of vegetative divisions of surface cells and are more or less level with the surface.

**Seasonal variation:** Collected in April-September and in November. Plurilocular sporangia recorded in July-September and unilocular sporangia in July-November.

**Habitat:** On Bootlace Weed (*Chorda filum*), Bladder Wrack (*Fucus vesiculosus*) and Sugar Kelp (*Saccharina latissima*). Common in shallow water, collected by divers to 9 m depth and by dredge, 12 m depth.

**Comment:** Culture studies of the alga from Danish waters (Pedersen, 1981a, 1984) showed that the life history comprised a filamentous microthallus, from which upright individuals may arise. Both uni- and plurilocular sporangia occurred on the microthallus. The life history was direct, and sexual reproduction not documented. Swarmers from both uni- and plurilocular sporangia, both on the upright alga as on the microthalli, germinated and grew into thalli which were similar to the thalli from which they developed. Development depended on physical factors such as salinity and light intensity. The microthallus was identified as *Streblonema danicum* Kylin, *S. oligosporum* Strömfelt, *S. thuretii* Sauvageau and *S. volubile* (P.Crouan & H.Crouan) Pringsheim, and these names are considered synonyms of *L. laminariae* (Pedersen, 1984 as *L. pusillus*). Of these *Streblonema* species, only *S. danicum* is recorded in Danish waters.


A: *Litosiphon laminariae*. Unbranched filaments on Bootlace Weed (*Chorda filum*). Deget, Frederikshavn, drift, 13.7.1966. Leg.: L. Mathiesen. Scale 2 cm.




B: *Litosiphon laminariae*. Vegetative cells with several disc-shaped plastids (arrow). Scale 10 µm. B-E: Beach east of Holtemmen, Læsø, drift, 23.7.2013.

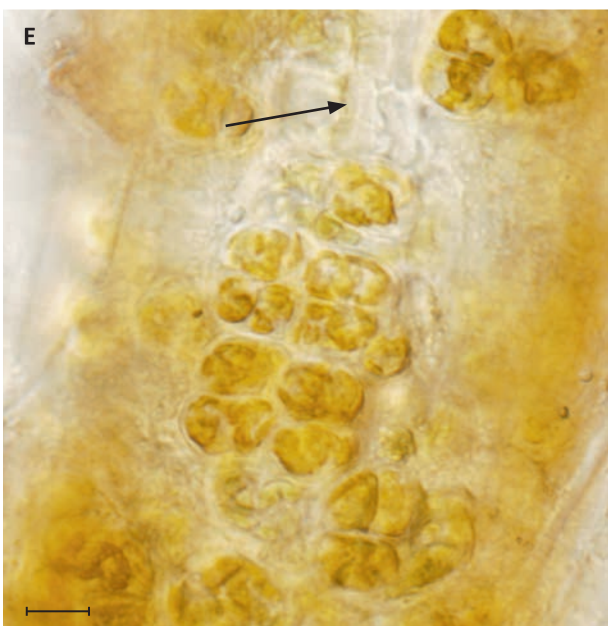
## *Microthallus*

### (Previously *Streblonema danicum*)

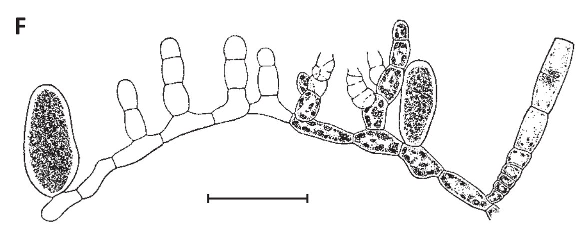
**Appearance:** Microscopic, endophytic filaments.
**Structure:** Uniseriate creeping filaments with scattered branches and upright, unbranched or branched filaments of a few cells with true brown algal hairs.
**Reproduction:** Unilocular sporangia are ellipsoid, ovoid or obovate. Plurilocular sporangia are uni- or multiseriate and occur individually or in clusters. Sporangia are sessile on the creeping filaments or on upright filaments, where they might be apical.
**Seasonal variation:** Collected in July with sporangia.
**Habitat:** Endophytic in Slimy Wormweed (*Mesogloia vermiculata*), 5 m depth.
**References:** Fletcher (1987), Kuckuck (1954, *Pilocladus danicus*, *P. thuretii*, *P. volubilis*), Kylin (1947, *Streblonema danicum, Entonema oligosporum*), Pedersen (1981a, 1984), Rosenvinge & Lund (1941, *S. thuretii* (?), 1947, *L. pusillus*), Wærn (1952, *S. oligosporum*).


C: *Litosiphon laminariae.* True brown algal hair. Scale 10 µm.


D: *Litosiphon laminariae.* Unilocular sporangia (arrow) among vegetative cells. Scale 10 µm.




E: *Litosiphon laminariae.* Plurilocular sporangia, mature and empty (arrow). Scale 10 µm.




F: *Litosiphon laminariae.* Microthallus. Creeping filaments with true brown algal hair, upright uni- and plurilocular sporangia. Several plastids in vegetative cells. Endophytic in Slimy Wormweed (*Mesogloia vermiculata*), Kølpen, Hirsholmene, 5 m, 14.7.1932. Scale 50 µm. After Rosenvinge & Lund (1941).

# *Mesogloia vermiculata*
**(Smith) S.F.Gray**
Slimy Wormweed

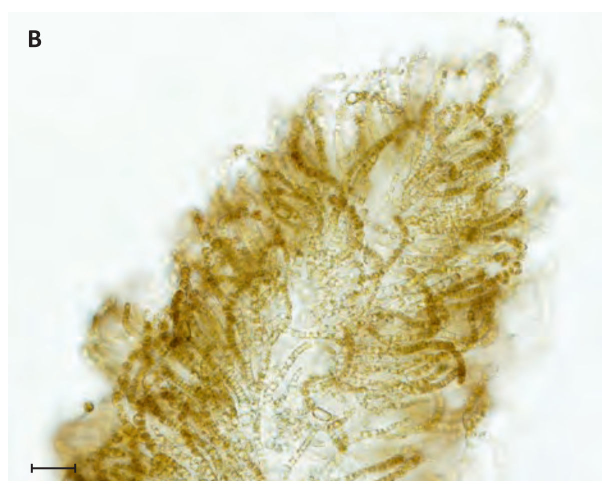
**Appearance:** Very soft, jelly-like, smooth and much branched yellow-brown to dark brown thalli, up to 32 cm in height, with terete branches. There is a distinct main branch and scattered branches of several orders on all sides. Branches, 1-5 mm in width, widest in the middle part with a constricted base and attenuated at the top.

**Structure:** Syntagma with only a single filament at the apex and more central filaments further down the alga. Growth monopodial of the apical filament which has an intercalary growth zone and terminates in an assimilating filament. Scattered cell divisions further down in the filaments result in longitudinal growth and development of branches which become close together with the central filament and form a medulla of several longitudinal filaments slightly below the apex. Cells of medullary filaments are elongate cylindrical, more rounded to spherical towards the surface. Two or more unbranched assimilating filaments and true brown algal hairs arise from each of the outermost medullary cells. Assimilating filaments are slightly curved and club-shaped, 8-12 µm in width. Lower cells of the assimilating filaments are cylindrical, but the cells become rounded to spherical at the end simultaneous with an increase in width. Filaments are kept together by a jelly-like wall substance but slide apart easily by slight pressure.

**Reproduction:** Unilocular sporangia occur at the base of assimilating filaments. They are ovoid or short ellipsoid. Culture studies showed that the life history comprises a filamentous microthallus with plurilocular sporangia. Upright thalli are the sporophyte generation, in which meiosis takes place in unilocular sporangia. Copulation between swarmers from plurilocular sporangia on microthalli sometimes observed, but also a direct development of filamentous thalli. The culture studies were undertaken in Norway, Great Britain and Sweden.

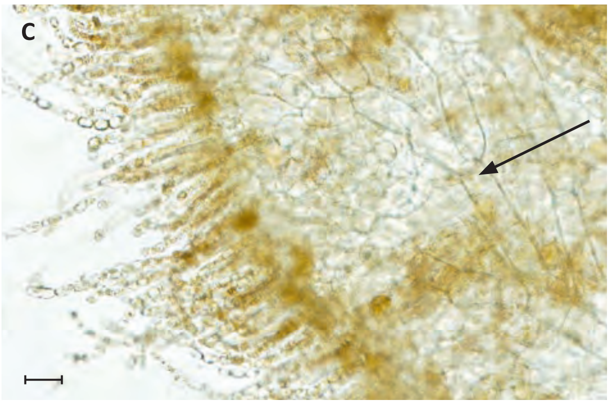
**Seasonal variation:** Collected in June-October with unilocular sporangia.

A: *Mesogloia vermiculata.* Much branched alga with distinct main branch. Deget, Frederikshavn, 1 m, 11.8.1974. Scale 2 cm.



B: *Mesogloia vermiculata.* Apex, surface of assimilating, slightly curved filaments. Scale 50 µm. B-E: Squash preparation. Beach south of Vesterø Havn, Læsø, drift, 9.7.2013.

**Habitat:** On stone and epiphytic on larger algae such as Wrack (*Fucus*) and coarse red algae. Most frequent in shallow water, collected by divers to 4 m depth. In older collections by dredge, 10-26 m depth.
**References:** Kylin (1933), Rosenvinge & Lund (1943).




C: *Mesogloia vermiculata.* Medulla of branched filaments of large cylindrical cells (arrow), and cells becoming smaller towards the surface, of assimilating filaments.
Scale 50 µm.

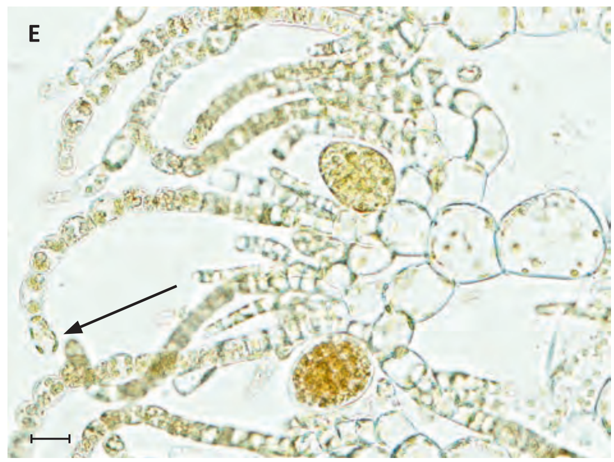
## *Mesogloia lanosa*

### P.Crouan & H.Crouan

Woolly Wormweed

Differs from Slimy Wormweed (*M. vermiculata*), by the surface being velvet-like, while it is very smooth in Slimy Wormweed (*M. vermiculata*). Furthermore, the assimilating filaments in Woolly Wormweed (*M. lanosa*) are cylindrical and relatively wide, 14-20 µm in width, and do not increase in thickness towards the surface as in Slimy Wormweed (*M. vermiculata*), where they are club shaped.


D: *Mesogloia vermiculata.* Assimilating filaments and true brown algal hairs with growth zone (arrow). Scale 20 µm.




E: *Mesogloia vermiculata.* Assimilating filaments, in which the cells increase in size outwards. Cells with several disc-shaped plastids (arrow). Unilocular sporangia.
Scale 20 µm.

**Comment:** A few small thalli of this species are mentioned by Rosenvinge & Lund (1943), but there are no later collections and no herbarium specimens of *M. lanosa* from Danish waters in the algal herbarium, Natural History Museum of Denmark. According to Kylin (1940), the species is close to Slimy Wormweed (*M. vermiculata*) and by some authors considered a form of this species.
**References:** Kylin (1940), Rosenvinge & Lund (1943).

## *Microcoryne ocellata*

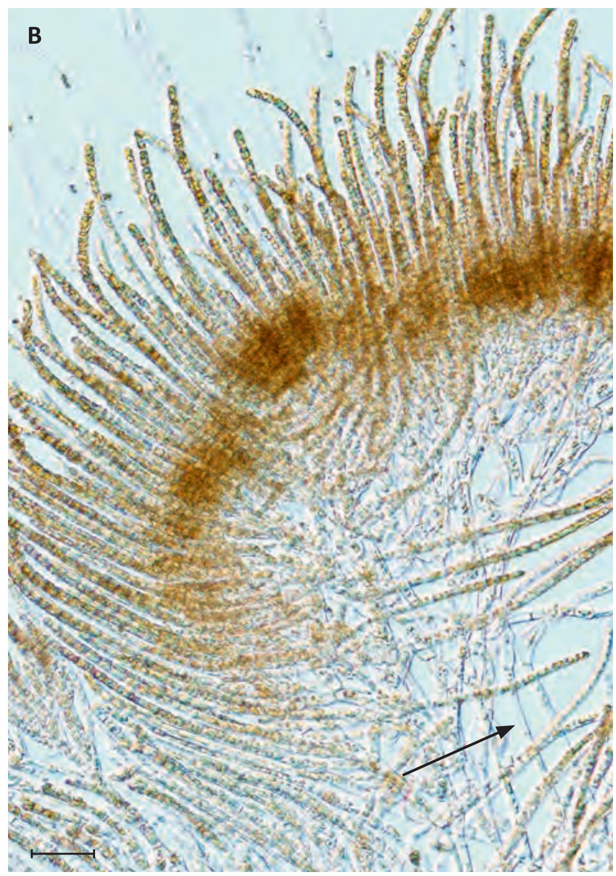
**Strömfelt**

Mini Jelly Clublet

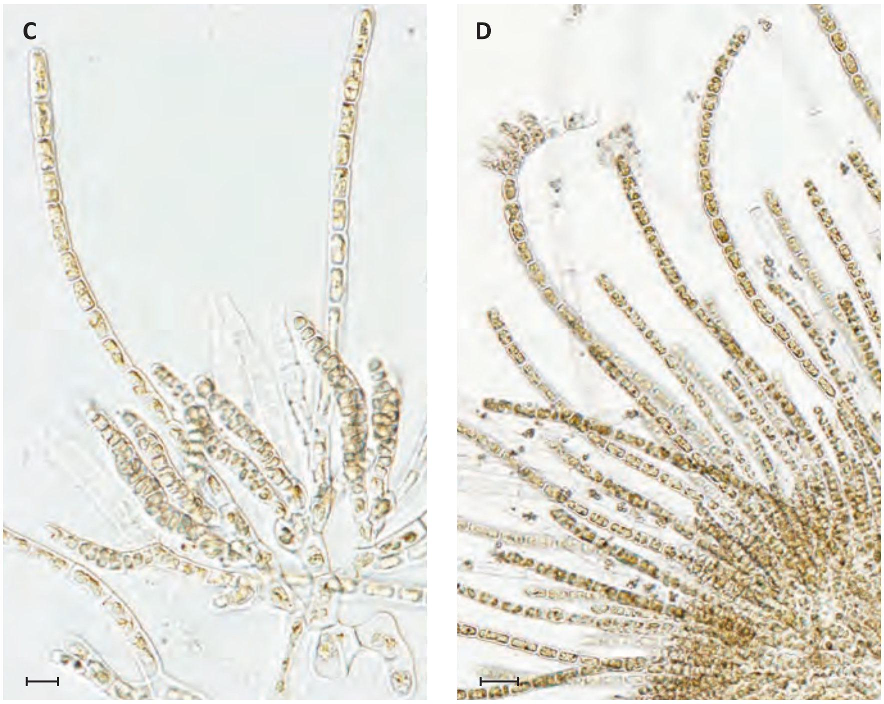
**Appearance:** Small cylindrical to club-shaped yellow-brown, soft, jelly-like alga, 0.1-2 (-5) mm in height. Thalli are unbranched or have single dichotomous branching, seldom scattered branches on all sides.


A: *Microcoryne ocellata*. Small dark brown algae (arrows) on Bootlace Weed (Chorda filum). Purple Siphon Weed (*Leptosiphonia fibrillosa*) is also epiphytic. Hirsholm, 21.9.1893. Leg.: Rosenvinge. Scale 2 cm.

**Structure:** Multiaxial syntagma of very loosely connected filaments, which slide from each other by light pressure of a coverslip. Inner medulla consists of filaments of long cylindrical colourless cells. From these arise filamentous branches which are di- or trichotomously branched. They consist of large ellipsoid cells, which become smaller towards the surface. Assimilating filaments arise from the outer medullary cells, and form the surface, they consist of (10-) 15-30 cylindrical or slightly swollen cells, 7-9 µm in width and 1-2 times as long as wide. Each of the cells contains several plate-shaped plastids with pyrenoids. Between the assimilating filaments there are true brown algal hairs which arise from the outer medullary cells or from the basal cells of the assimilating filaments. The hairs have a growth zone 2-3 cells above the base.




B: *Microcoryne ocellata*. Central colourless filaments (arrow) with branches, surface of loosely connected assimilating filaments and true brown algal hairs. Scale 50 µm. B-D: Beach south of Vesterø Havn, Læsø, drift, 11.7.2014.




C: *Microcoryne ocellata*. Mature and empty plurilocular sporangia in fascicles at the base of assimilating filaments. Scale 10 µm.

D: *Microcoryne ocellata*. Plurilocular sporangia at the apex of assimilating filament. Scale 20 µm.

**Reproduction:** Plurilocular sporangia occur at the base of the assimilating filaments, they are cylindrical or spindle-shaped, 116-134 µm long and c. 14 µm in width and widest where longitudinal divisions may occur. Sporangia are typically so numerous, that they appear to be in fascicles. Plurilocular sporangia may also occur in the upper part of the assimilating filaments, where they develop as uniseriate papillae. The two locations of plurilocular sporangia may occur on the same or different thalli. Unilocular sporangia are unknown.

**Seasonal variation:** Collected in July-October. Plurilocular sporangia recorded in July.

**Habitat:** Epiphytic on larger algae such as Bladder Wrack (*Fucus vesiculosus*), Serrated Wrack (*F. serratus*) and Bootlace Weed (*Chorda filum*), 1-5 m depth and a single collection, 12 m depth.

**References:** Fletcher (1987), Rosenvinge & Lund (1943).

## *Microspongium*

Microscopic to c. 1 mm large epiphytes of uniseriate branched filaments with true brown algal hairs and small plurilocular sporangia. Vegetative cells contain 1-3 plastids. Plurilocular sporangia are uniseriate or in part biseriate.

**Identification key to species of *Microspongium***

| | | |
|---|---|---|
| 1a. | Forming a small knot on the host | *M. globosum* |
| 1b. | Creeping filaments between the assimilating filaments of the host | *M. stilophorae* |

# *Microspongium globosum*

**Reinke**

Pearl Micropillow

**Appearance:** Semiglobular epiphytes, 0.5-1 mm in width. They have a solid cartilaginous consistency.

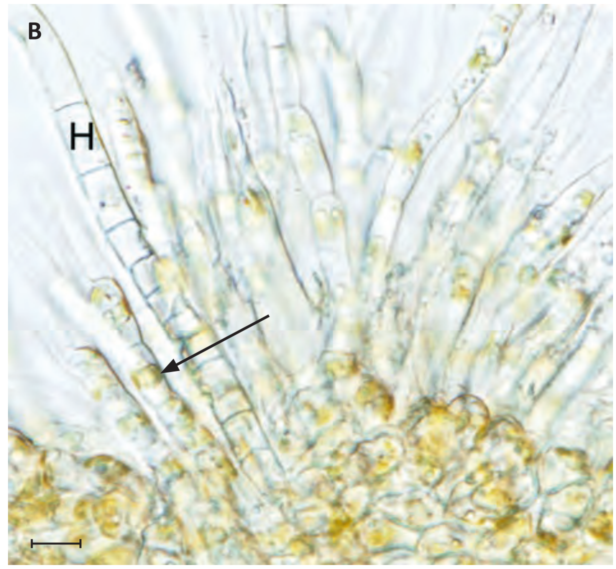
**Structure:** Uniseriate filaments arise from a monostromatic basal crust, 9.5 µm in thickness. Upright filaments are unbranched or have scattered branches, they consist of long cylindrical cells, 5.5-9.5 µm in width and 2-8 times as long as wide. Each cell has 1-3 disc-shaped plastids with one pyrenoid. True brown algal hairs, arise from the basal crust or are apical on the upright filaments. Brown algal hairs with sheath are recorded in specimens from Greenland (Lund, 1959); but hairs with sheaths are not recorded in material from Danish waters.

**Reproduction:** Plurilocular sporangia are uniseriate, seldom partly biseriate, 3.8-7.5 µm in width and 21-40 (-95) µm in height. They are lateral or terminal on the upright filaments. Unilocular sporangia are not recorded. Culture studies showed a direct life history, in which swarmers from plurilocular sporangia grew into thalli which were similar to the parent generation (Kornmann & Sahling, 1983).

**Seasonal variation:** Collected in March-June and August with plurilocular sporangia.

**Habitat:** Epiphytic on Black Scour Weed (*Ahnfeltia plicata*), Black Siphon Weed (*Vertebrata fucoides*), Bladder Wrack (*Fucus vesiculosus*) and drift leaves of Eelgrass (*Zostera marina*), also on stone, 0.5-1 m depth.

**References:** Fletcher (1987), Kornmann & Sahling (1983), Kristiansen (1960, 1978a), Lund (1959), Russell & Pedersen (1994).




B: *Microspongium globosum*. True brown algal hair (H) from basal crust, vegetative cells with one plastid and one pyrenoid (arrow). Scale 10 µm.

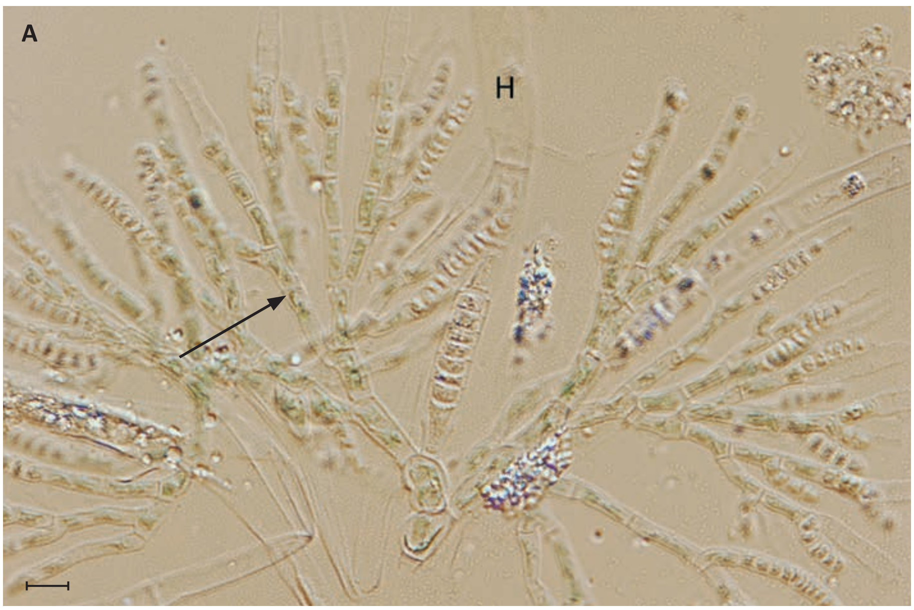

A: *Microspongium globosum*. Semiglobular knot of upright filaments close together. Scale 20 µm. A-C: On Bladder Wrack (*Fucus vesiculosus*). Beach north of Vesterø Havn, Læsø, drift, 29.4.2016.


C: *Microspongium globosum*. Basal layer, upright uniseriate filaments with scattered branches, lateral and terminal plurilocular sporangia (arrows). Scale 10 µm.

## *Microspongium stilophorae*

**(P.Crouan & H.Crouan) Cormaci & G.Furnari**

**Appearance:** Microscopic filaments between assimilating filaments of the host alga.
**Structure:** Upright filaments with scattered branches, 3.5-6 µm wide arise from creeping uniseriate filaments. Each vegetative cell contains one plastid according to Rosenvinge & Lund (1941), but 2-3 plastids according to Kuckuck (1954). Apical brown algal hairs with sheath occur on short upright branches.
**Reproduction:** Plurilocular sporangia are close together, scattered lateral or terminal on the upright filaments. Plurilocular sporangia are uniseriate and cylindrical, 4-5 µm wide and relatively long.
**Seasonal variation:** Collected in May, August and November with plurilocular sporangia.
**Habitat:** Endophytic in Sea Noodle Worm Weed (*Nemalion multifidum*) and in Furry Rope Weed (*Halosiphon tomentosus*), collected in shallow water and at 7 m depth.
**References:** Cormaci et al. (2012), Kuckuck (1954, *Phycocelis tenuissima*), Peters (2003, *M. tenuissimum*), Rosenvinge & Lund (1941, *Streblonema tenuissimum*).




A: *Microspongium stilophorae*. Upright filaments, several plastids per cell (arrow), true brown algal hair (H) and terminal plurilocular sporangia. In Furry Rope Weed (*Halosiphon tomentosus*), Schultz's Grund, 7 m, 27.5.1992. Scale 10 µm.

## *Mikrosyphar*

Brown Puzzle

Microscopic epi- and endophytes of creeping filaments with scattered branches, which may be confluent and form pseudoparenchyma. Vegetative cells contain 1-3 plate-shaped plastids. True brown algal hairs may occur. Plurilocular sporangia are transformed vegetative cells in short branches and typically close together in large area.
**References:** Kuckuck (1897), Kylin (1947), Pedersen (1984).

**Identification key to species of *Mikrosyphar***

| | | |
|---|---|---|
| 1a. | Filaments, 6-9 µm in width, no hairs, pseudoparenchymatous on or in *Polysiphonia stricta* and *Cladophora rupestris* | *M. polysiphoniae* |
| 1b. | Filaments, 3-5 µm in width, true brown algal hairs may occur, endophytic filaments in cell walls of *Porphyra* | *M. porphyrae* |

# *Mikrosyphar polysiphoniae*

**Kuckuck**

Siphonous Brown Puzzle

**Appearance:** Microscopic, creeping filaments on or in the cell walls of other algae.

**Structure:** Uniseriate, filaments with scattered branches, 6-9 µm in width. Occasionally confluent and forming monostromatic pseudoparenchyma which cover the host alga. Each vegetative cell contains 1-3 plastids. No hairs.

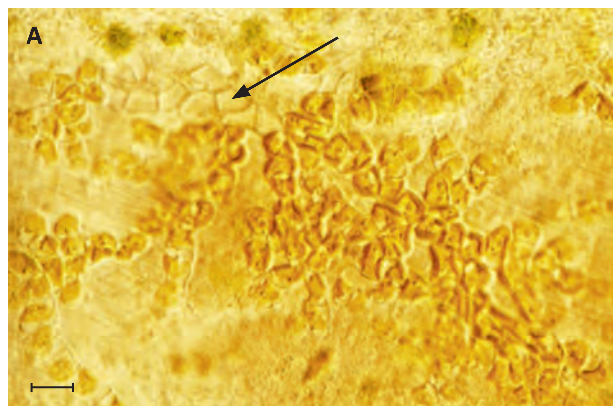
**Reproduction:** Plurilocular sporangia develop after divisions of vegetative cells and typically contain 2-4 compartments. They resemble vegetative cells in shape, possibly slightly larger. Thalli may be polystromatic in fertile area. Sporangia develop typically in neighbouring cells so the fertile part may account for a major area of the thallus.

**Habitat:** On Pitcher Siphon Weed (*Polysiphonia stricta*) and Common Green Branched Weed (*Cladophora rupestris*), 4-14 m depth. The identity of *Mikrosyphar* sp. on the hydroid *Dynamena pumila* has to be verified in future investigations.

**Seasonal variation:** Collected in January, March and June. Plurilocular sporangia recorded in March.

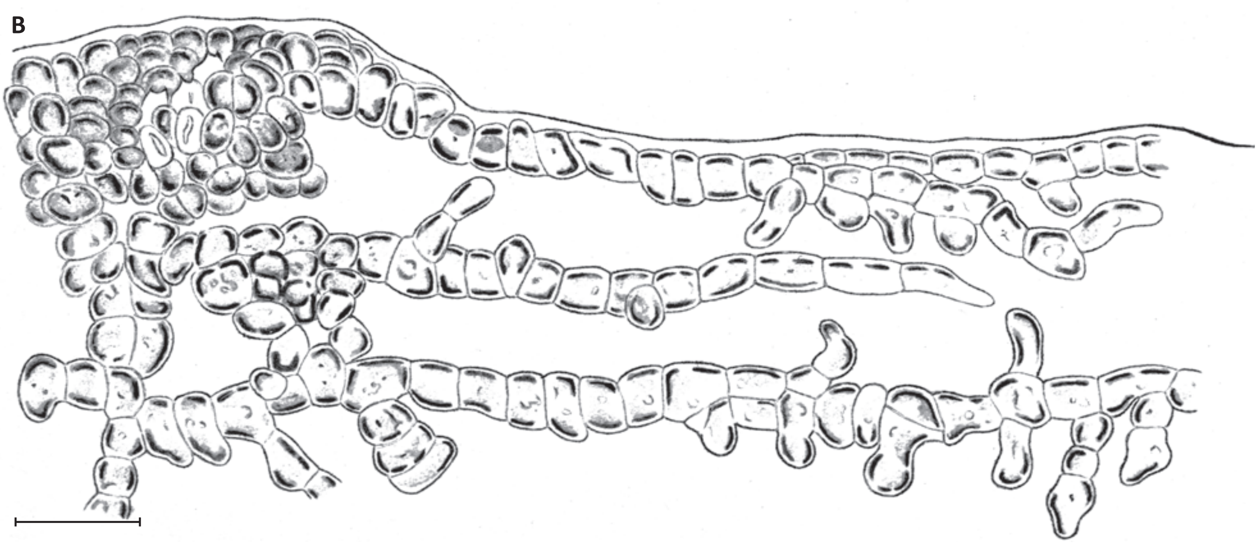
**Comment:** Culture studies of this alga from Isle of Man (Pedersen, 1984) showed a direct life history, in which swarmers from plurilocular sporangia developed into thalli similar to the previous generation. Pseudoparenchyma only developed when in contact with a host alga in these studies.

**References:** Kornmann & Sahling (1977), Kuckuck (1897), Kylin (1947), Pedersen (1984, 2011).




A: *Mikrosyphar polysiphoniae.* Pseudoparenchyma with mutually free filaments at the edge. Empty plurilocular sporangia (arrow). On Common Green Branched Weed (*Cladophora rupestris*). Vesterø Havn, Læsø, 0.5 m, 19.3.2015. Scale 10 µm.

B. *Mikrosyphar polysiphoniae.* Uniseriate filaments of vegetative cells with plastids, pseudoparenchyma with sporangia, a few empty. In wall of Pitcher Siphon Weed (*Polysiphonia stricta*). From Kuckuck (1897). Scale 20 µm.

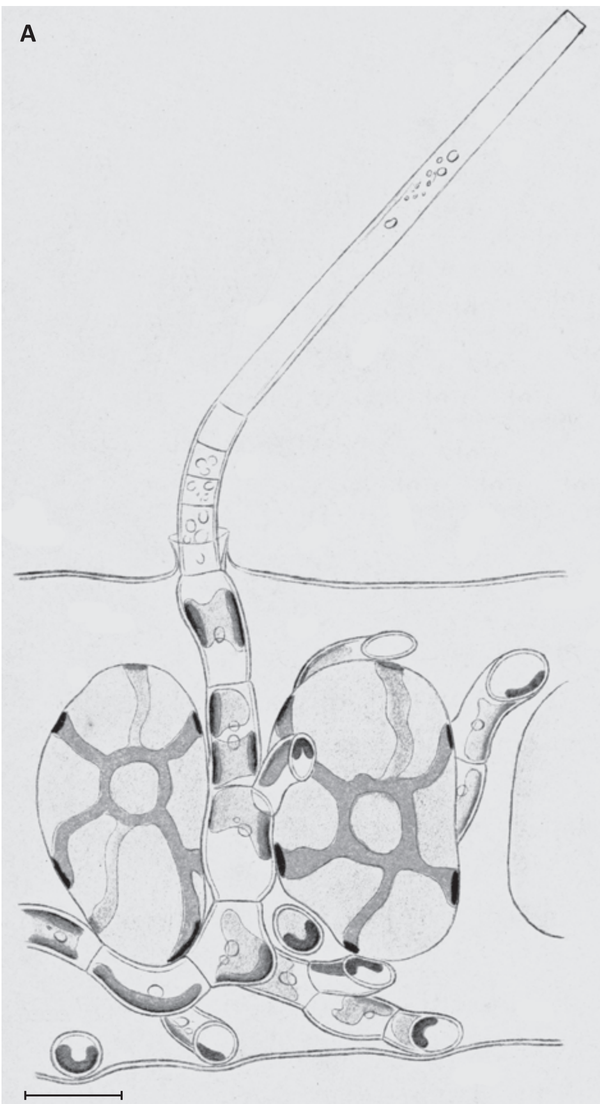


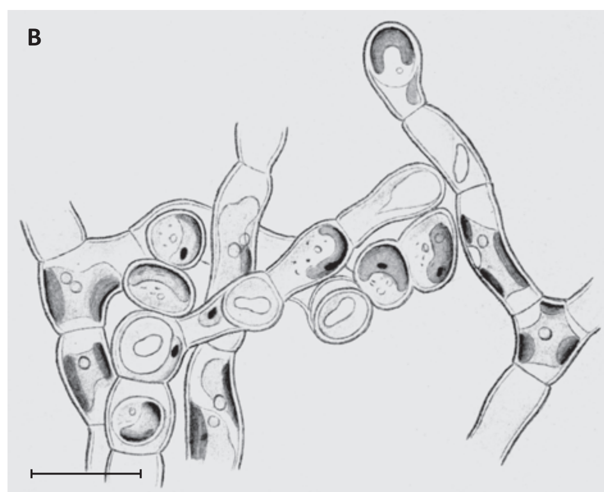
## *Mikrosyphar porphyrae*

**Kuckuck**

Porphyra's Brown Puzzle

**Appearance**: Small endophytic brown spots, approximately circular, up to 1 mm in width.
**Structure**: Filaments in the middle part of the spot are close together and form a pseudoparenchyma, while they are mutually free at the margin, 3-5 µm in width. Few-celled upright branches grow towards the surface of the host alga. True brown algal hairs are outside the host. Vegetative cells contain 1-2 plate-shaped slightly lobed plastids (Kuckuck, 1897).
**Reproduction:** Sporangia develop from apical cells of short branches close to the surface of the host which is broken through by the sporangia. Plurilocular sporangia with 2-4 compartments develop from a vegetative cell after 1-2 cell divisions.
**Seasonal variation:** Collected in March.
**Habitat:** Filaments grow inside cell walls of Laver (*Porphyra*), in the blade from one to the other side, and may grow into the cells of the host alga. It turned up in a crude culture of *Ralfsia* sp., collected in 0.5 m depth (Pedersen 1984).
**Comment:** Culture studies by Pedersen (1984) showed a direct life history. Swarmers from plurilocular sporangia germinated and grew into uniseriate branched filaments, which formed pseudoparenchyma and developed few-celled plurilocular sporangia. True brown algal hairs occurred.
**References:** Kuckuck (1897), Pedersen (1984), Rosenvinge & Lund (1941).




A: *Mikrosyphar porphyrae.* Branched filaments within *Porphyra* sp., true brown algal hair outside the host alga. Scale 10 µm. A-B: From Kuckuck (1897).

B: *Mikrosyphar porphyrae.* Fertile filaments with empty sporangia on the surface of the host. Scale 10 µm.

# *Myriactula*

Minituft

**Appearance:** Epiphytes, appearing as small knots or tufts of assimilating filaments, up to 1 mm in height.
**Structure:** Basal system of filaments, which may be creeping or form a small knot or cushion. Uniseriate, unbranched assimilating filaments arise from the basal system. In the lower part of the upright filaments narrow approximately cylindrical cells occur, followed by a growth zone and above this, more or less barrel-shaped to cylindrical cells. Each cell contains many disc-shaped plastids with pyrenoids. Among the assimilating filaments are true brown algal hairs.
**Reproduction:** Uni- and plurilocular sporangia occur at the base of assimilating filaments in the same or different thalli. Sporangia develop from the upper cells of the basal system. Plurilocular sporangia are cylindrical and uniseriate, they may also form from cells in the assimilating filaments, typically from the lowest cells. Unilocular sporangia are obovate or pyriform.
**References:** Fletcher (1987), Kylin (1947), Levring (1937), Lund (1949), Rosenvinge (1935, *Gonodia*), Rosenvinge & Lund (1943).

**Identification key to species of *Myriactula***

| | | |
|---|---|---|
| 1a. | Base of thallus a small knot | 2 |
| 1b. | Base of thallus creeping filaments, not condensed into a knot | 3 |
| 2a. | In hair cavities (cryptostomata) of *Fucus serratus*, *F. vesiculosus* and *Sargassum muticum* | *M. rivulariae* |
| 2b. | On various terete algae without hair cavities | *M. chordae* |
| 3a. | On *Scytosiphon lomentaria*. Upright filaments, 20-29 cells in height | *M. haydenii* |
| 3b. | On *Dictyota dichotoma*. Upright filaments, 12 cells in height | *M. stellulata* |

# *Myriactula chordae*

**(Areschoug) Levring**

Knotted Minituft

**Appearance:** Appears as a small knot on terete algae such as Bootlace Weed (*Chorda filum*) with assimilating filaments, 0.7-1 mm in height.

**Structure:** Basal knot consists of filaments of relatively large colourless cells, which are closely connected. From the basal knot assimilating filaments arise, (15-) 18-21 (-31) cells in height, where basal cells close to the growth zone are approximately barrel-shaped, while upper cells are cylindrical. Filaments, 15-28 µm in width, gradually decrease in width upwards. Brown algal hairs have a growth zone 2-3 cells above the base, are 12-14 µm in width and longer than the assimilating filaments.


A: *Myriactula chordae*. Tuft of upright assimilating filaments, cells become slender and relatively long towards the upper end. Scale 20 µm. A-B: On Bootlace Weed (*Chorda filum*), Geller Odde outside Hygum Church, 3.5 m, 23.8.2000.

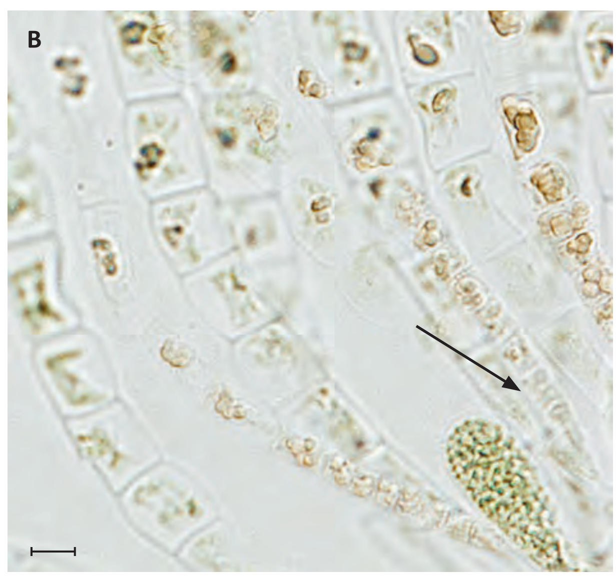
**Reproduction:** Unilocular sporangia occur at the base of the assimilating filaments, and are obovate, 82-93 µm long and 25-33 µm in width. Plurilocular sporangia arise in closely packed fascicles from the surface cells of the small basal knot or from the upper part of assimilating filaments. They are uniseriate, 6-8 µm in width. Uni- and plurilocular sporangia may occur on the same or different individuals.

**Seasonal variation:** Collected in July-September, unilocular sporangia recorded in July-August and plurilocular sporangia in July.

**Habitat:** Recorded from the Northern Kattegat, epiphytic on Pointed Hair Weed (*Acrothrix gracilis*), Bootlace Weed (*Chorda filum*), Winding Broomweed (*Stictyosiphon tortilis*), Pitcher Siphon Weed (*Polysiphonia stricta*) and Black Siphon Weed (*Vertebrata fucoides*), 3-8 m depth.

**Comment**: Rosenvinge (1935) referred an epiphyte on *Ceramium* sp. (as *C. rubrum*) to the same species. Assimilating filaments in this alga were 10-13 cells long and 16-28 µm in width, plurilocular sporangia were uniseriate, 7-9 µm in width. It is uncertain if the identification of the alga was correct, which must be clarified in future investigations.

**References:** Fletcher (1987), Kylin (1947), Rosenvinge (1935, *Gonodia pulvinata* f. *chordæ*).

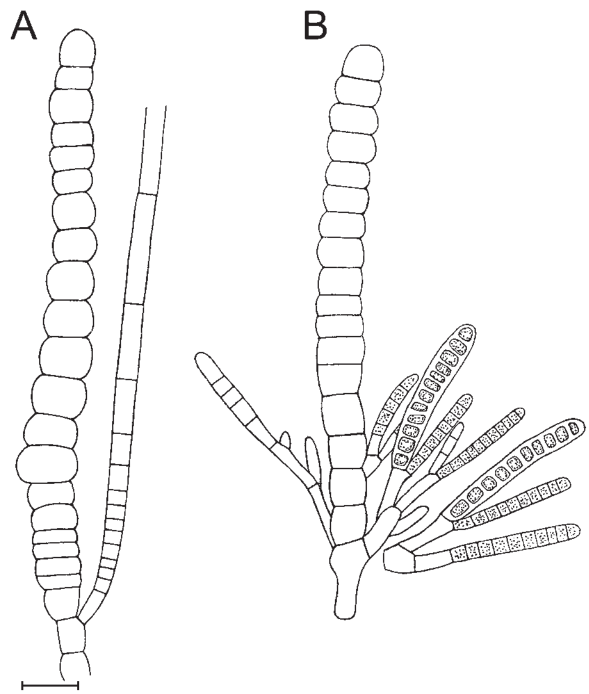



B: *Myriactula chordae*. Unilocular sporangium at the base of assimilating filaments; true brown algal hair with growth zone (arrow). Scale 10 µm.

## *Myriactula haydenii*

**(Gatty) Levring**
Scytosiphon's Minituft

**Appearance:** Upright brown filaments, up to 0.5 mm in height, arise from a flat endophytic basal system.
**Structure:** Upright filaments arise from the basal system of loosely connected filaments which grow between paraphyses and plurilocular sporangia of the host alga. Upright assimilating filaments, 20-25 µm in width, consist of 20-29 cells, gradually becoming narrower downwards. The lowest 2-3 cells are narrow and cylindrical. Above these cells is a growth zone. The upper part of filaments consists of swollen, barrel-shaped cells, which are barely as long as wide. Among the assimilating filaments true brown algal hairs occur.
**Reproduction:** Uniseriate plurilocular sporangia, 33-74 µm long and 6-8 µm in width, occur at the base of the filaments on special short branches or on the lower cells of assimilating filaments.
**Seasonal variation:** Collected in July with plurilocular sporangia. Unilocular sporangia not observed in algae from Danish waters.
**Habitat:** Epiphytic on Chipolata Weed (*Scytosiphon lomentaria*) near the edge of the water.
**References:** Kylin (1947), Lund (1949).




*Myriactula haydenii.* Assimilating filament of barrel-shaped cells and true brown algal hair (A). Small branches with plurilocular sporangia (B). Deget, Frederikshavn, 0.5 m, 15.7.1929. Scale 20 µm. After Lund (1949).

## *Myriactula rivulariae*

**(Suhr ex Areschoug) Feldmann**
Wrack Minituft

**Appearance:** Epiphytes forming tufts less than 1 mm in height. They arise from a bulbous base in cryptostomata of Wrack (*Fucus*) and Wire Weed (*Sargassum muticum*).
**Structure:** Assimilating filaments consist of up to 26 cells and arise from a basal knot of rounded cells. The lower 2-3 cells of the filaments are relatively long and narrow, above which cells are barrel-shaped, the widest slightly above the base where they measure 21-29 µm. From here filaments gradually decrease to c. 17 µm or to 6.3-8 µm just below the apex. Barrel-shaped cells are (0.5-) 1-1.5 (-2) times as long as wide. The narrow distal cells are cylindrical and up to 3 times as long as wide. Each cell contains disc-shaped plastids. True brown algal hairs occur among assimilating filaments.
**Reproduction:** Plurilocular sporangia arise from the lower cells of the assimilating filaments or are lateral. They arise individually or form small fascicles. Sporangia are 21-70 µm long and c. 8.5 µm in width, with a series of 2-15 compartments. Small plurilocular sporangia may occur laterally on assimilating filaments

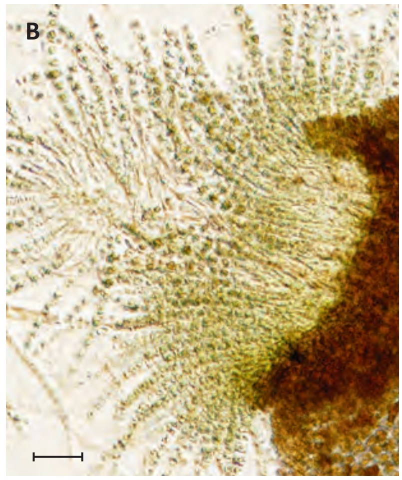
and on rhizoids. Unilocular sporangia are not recorded in this alga from Danish waters.

**Seasonal variation:** Collected in July-August and October-November with plurilocular sporangia in July, October and November.

**Habitat:** Epiphytic on Serrated Wrack (*Fucus serratus*), Bladder Wrack (*F. vesiculosus*) and Wire Weed (*Sargassum muticum*), 0.5-1 m depth.

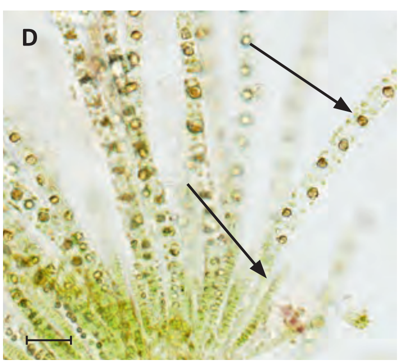
**References:** Fletcher (1987), Kylin (1947, *Myriactula fucorum*), Nielsen 2002, Rosenvinge (1935, *Gonodia pulvinata* f. *fucorum*), Rosenvinge & Lund (1943, *M. pulvinata*).


A: *Myriactula rivulariae*. Small tufts (arrow) on Wire Weed (*Sargassum muticum*). Tile works, Helligsø, 0.5 m, 20.7.1996. Scale 2 cm.




B: *Myriactula rivulariae*. Squeezed out of cryptostomata on the host alga. Scale 50 µm. B-C, F: On Wire Weed (*Sargassum muticum*). Præstebugten, Hirsholm, 1.5 m, 6.7.2001.


C: *Myriactula rivulariae*. Base of assimilating filament and true brown algal hair (arrow). Scale 10 µm.




D: *Myriactula rivulariae*. Plurilocular sporangia (lowest arrow), vegetative cells with disc-shaped plastids (upper arrow). Scale 20 µm. D-E: On Wire Weed (*Sargassum muticum*). Hirsholm 0.5 m, 23.7.1998.


E: *Myriactula rivulariae*. Plurilocular sporangium (arrow) at base of assimilating filament. Scale 10 µm.


F: *Myriactula rivulariae*. Plurilocular sporangia, lateral on lower part of assimilating filament, in which the upper part is broken off. Scale 10 µm.

# *Myriactula stellulata*

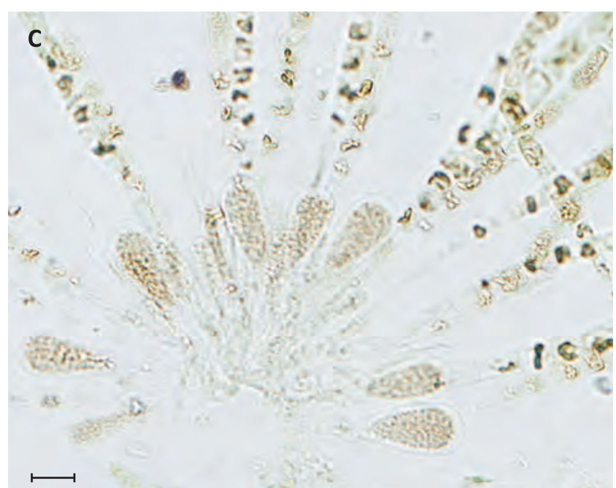
**(Harvey) Levring**

Brown Fan Weed's Minituft

**Appearance:** Small insignificant tufts on Brown Fan Weed (*Dictyota dichotoma*).
**Structure:** Basal system of filaments that are closely connected and consist of large pale cells, which may in part be endophytic. Short slightly club-shaped assimilating filaments arise from the base. The upright filaments, up to 12 (-17) cells in height have a pair of narrow long pale cells at the basal part, a growth zone and cylindrical to slightly barrel-shaped cells above. A few scattered true brown algal hairs occur among the assimilating filaments.
**Reproduction:** Uni- and plurilocular sporangia arise from the basal system. They occur on the same or different individuals.. Unilocular sporangia are elongate obovate, 44-49 µm long and 19-22 µm wide. Plurilocular sporangia are cylindrical, uniseriate and c. 5 µm in width.
**Seasonal variation:** Collected in August with uni- and plurilocular sporangia.
**Habitat:** Epiphytic on Brown Fan Weed (*Dictyota dichotoma*), 3-4 m depth.
**References:** Fletcher (1987).


B: *Myriactula stellulata*. Plurilocular sporangia (P), upright club-shaped assimilating filaments and base of true brown algal hair (H). Scale 10 µm.


A: *Myriactula stellulata*. Tuft of few celled filaments and unilocular sporangia (S). Scale 20 µm. A-C: On Brown Fan Weed (*Dictyota dichotoma*). Tile works, Helligsø, 3.5 m, 22.8.2000.




C: *Myriactula stellulata*. Unilocular sporangia. Scale 10 µm.

# *Myriocladia lovenii*

**J.Agardh**

Flabby Mucilage Thread

**Appearance:** Olive-brown thalli of very soft terete scattered branches on all sides. They are slightly flaccid and appear like a woollen thread. Typically 1-7 cm in height but may be up to 12-13 cm in height and branches up to 1 mm in width.

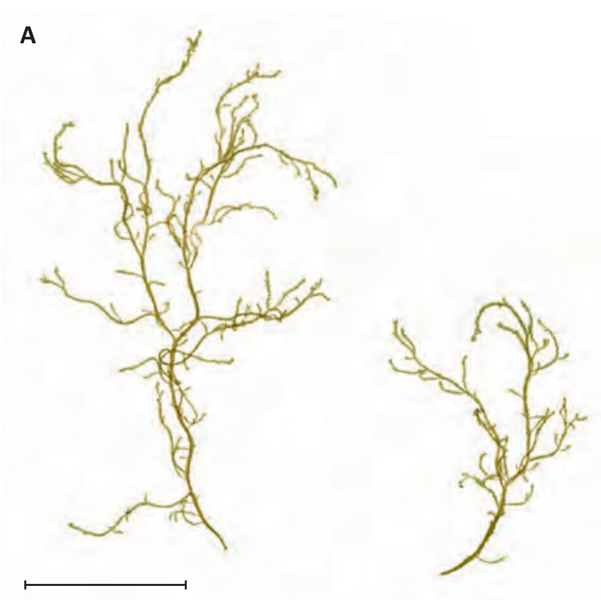
**Structure:** Syntagma of a central filament with branches, which develop into short assimilating filaments or to long filaments that grow parallel with the central filament and have pale elongate cylindrical cells. These filaments form the medulla. Downward-growing narrow hyphae-like filaments arise from the basal cells of the short assimilating filaments. They strengthen and increase the medullary filaments which are close together and secondary assimilating filaments arise from them. Assimilating filaments in fascicles form from the surface and are distinctly separated from the central medulla. Assimilating filaments are unbranched or dichotomously branched at the base. The filaments are mutually free, not kept together in a jelly-like wall substance, and consist of cylindrical cells, 5-6 µm in width and up to 4 times as long as wide. True brown algal hairs arise from the base of the assimilating filaments.

**Reproduction:** Unilocular sporangia develop from the lower cells of assimilating filaments. They are elongate ellipsoid, pyriform or obovate, 40-70 µm long and 20-32 (-53) µm in width. Plurilocular sporangia unknown according to Kylin (1933) and Rosenvinge & Lund (1943).

**Seasonal variation:** Collected in May-September. Unilocular sporangia recorded in June-September.

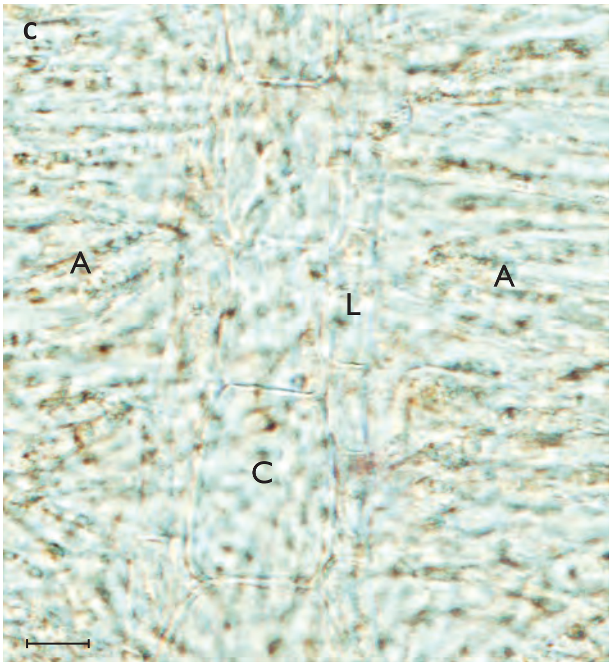
**Habitat:** On stone and epiphytic on Forest Kelp (*Laminaria hyperborea*), leaves of Eelgrass (*Zostera marina*) and once collected on Sea Chervil (*Alcyonidium*) in the North Sea. Collected by divers, 4-11 m depth and by dredge, 16.5 (-24.5) m depth.

**References:** Kylin (1933), Rosenvinge & Lund (1943).

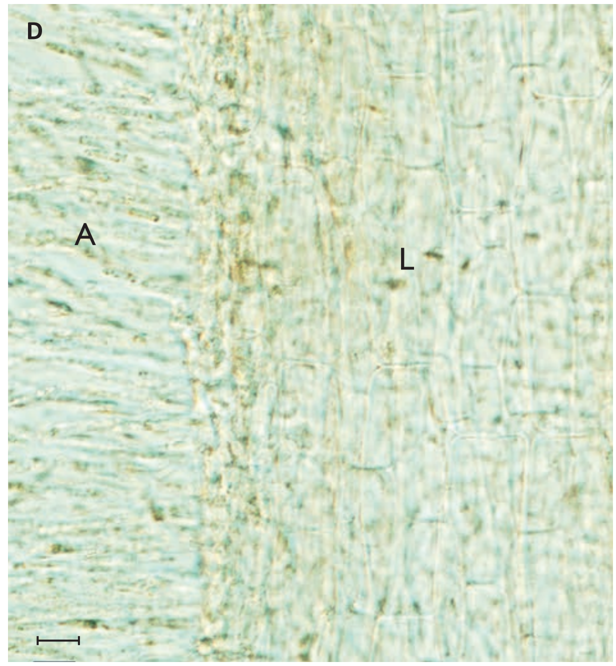



A: *Myriocladia lovenii.* Light brown algae with scattered branches. Bredsund, Hirsholm, 4 m, 29.6.1992. Scale 2 cm.


B: *Myriocladia lovenii.* Medullary filaments close together, mutually free assimilating filaments and unilocular sporangia. Scale 50 µm. B, E-F: Briseis Flak, 9 m, 6.6.1993.




C: *Myriocladia lovenii.* Central filament of cylindrical cells (C) surrounded by filaments of long cylindrical cells (L) and the lower part of out-stretching assimilating filaments (A). Optical longitudinal section, near the apex. Scale 20 µm. C-D: Læsø Trindel, 5 m, 31.5.1992.




D: *Myriocladia lovenii.* Medulla of several filaments of long cylindrical cells (L), surrounded by assimilating filaments (A). Optical longitudinal section, at some distance from the apex. Scale 20 µm.


E: *Myriocladia lovenii.* Young unilocular sporangium and true brown algal hair (arrow) from basal cells of assimilating filament. Scale 10 µm.


F: *Myriocladia lovenii.* Mature and an empty unilocular sporangia from base of branched assimilating filament. Scale 10 µm.

## *Myrionema*

Brown Dot Weeds

Small disc-shaped, approximately circular alga, with a monostromatic basal layer of creeping radiating and confluent filaments. In the central part short upright filaments arise from each of the cells. They are uniform in height and unbranched or rarely branched. Vegetative cells have 1-3 plate-shaped plastids with pyrenoids. Brown algal hairs with sheath occur. Upright plurilocular sporangia are uni- or multiseriate.
**References:** Fletcher (1987), Kylin (1947, *Myrionema* and *Ascocyclus*).

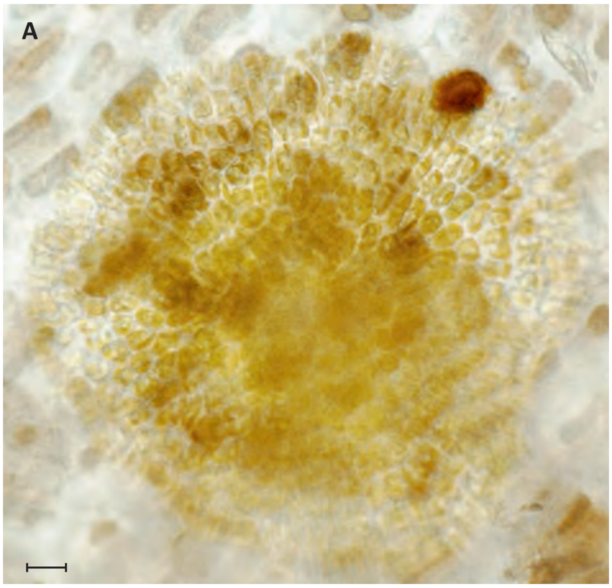
**Identification key to species of *Myrionema***

| | | |
|---|---|---|
| 1a. | With ascocysts, which are longer than the upright filaments; common on leaves of *Zostera marina* | *M. magnusii* |
| 1b. | Without ascocysts, on *Ulva fenestrata* | *M. strangulans* |

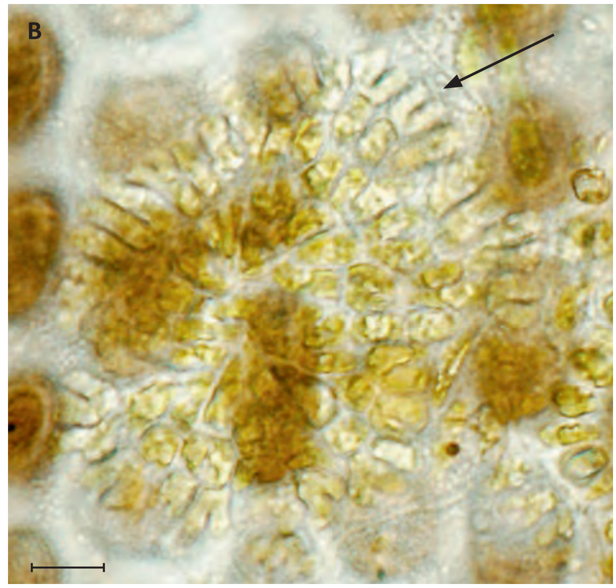
## *Myrionema magnusii*

**(Sauvageau) Loiseaux**
Large Brown Dot Weed

**Appearance:** Circular light- or dark brown spots, up to 0.5 mm in width.
**Structure:** Monostromatic basal disc of confluent radiating filaments. Growth at the margin and some marginal cells forked. Cells contain a single plate-shaped lobed plastid with pyrenoid. Short, upright, uniseriate, and unbranched filaments arise from the central cells, together with brown algal hairs with sheath and ascocysts with thick walls. Ascocysts are cylindrical colourless cells, 11.3-14.2 µm in width and much longer than the upright vegetative filaments.
**Reproduction:** Upright plurilocular sporangia also arise from the central cells of the disc. They are 40.5-60.5 µm long and 6.8-13.5 µm in width. Typically uniseriate but occasionally biseriate. Unilocular sporangia are not recorded on Large Brown Dot Weed (*M. magnusii*) from Danish waters but occur in the British Isles. Culture studies of the alga from Brittany and the Swedish west coast showed a direct life history, in which swarmers from plurilocular sporangia germinated and developed filamentous or disc-shaped alga, both with plurilocular sporangia. See also comment about *Cladosiphon*.
**Seasonal variation:** Collected in April-October with plurilocular sporangia.
**Habitat:** Epiphytic on leaves of Eelgrass (*Zostera marina*), 0.5-9 m depth, and in an older collection, 17 m depth.
**Comment:** According to Kylin (1907) *Ascocyclus affinis* Svedelius, which has relatively small ascocysts, is young individuals of Large Brown Dot Weed (*M. magnusii*). These are recognised as separate species by Lund (1934) in Stege Nor.
**References:** Fletcher (1987), Kylin (1907, 1947, *Ascocyclus orbicularis*), Lund (1934, *A. affinis, A. orbicularis*).

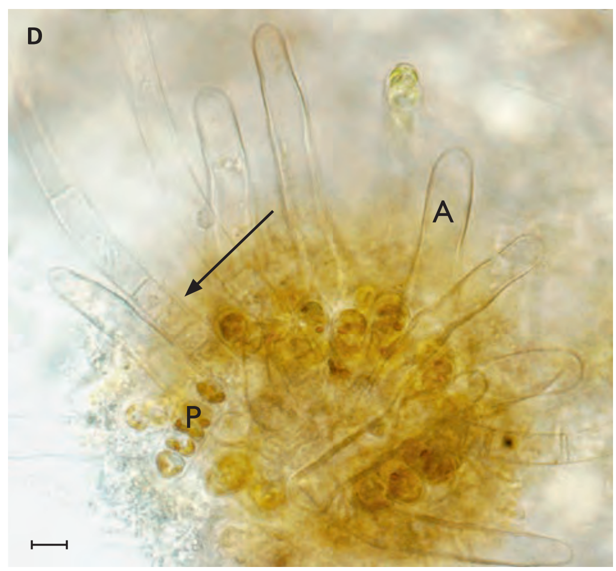



A: *Myrionema magnusii*. Circular disc of radiating filaments. Scale 10 µm. A-D: On Eelgrass (*Zostera marina*), beach north of Vesterø Havn, Læsø, drift, 1.9.2014.




B: *Myrionema magnusii*. Young monostromatic disc of radiating filaments, with forked marginal cells (arrow). Scale 10 µm.


C: *Myrionema magnusii*. Upright ascocysts (A) and brown algal hairs with sheath (arrow). Scale 10 µm.




D: *Myrionema magnusii*. Ascocysts (A), brown algal hairs with sheath (arrow) and plurilocular sporangium (P). Scale 10 µm.

# *Myrionema strangulans*

**Greville**

Green Blades' Brown Dot Weed

**Appearance:** Small circular light- or dark brown disc-shaped epiphytes, which may be confluent to form larger spots, 0.5-3 mm in width.

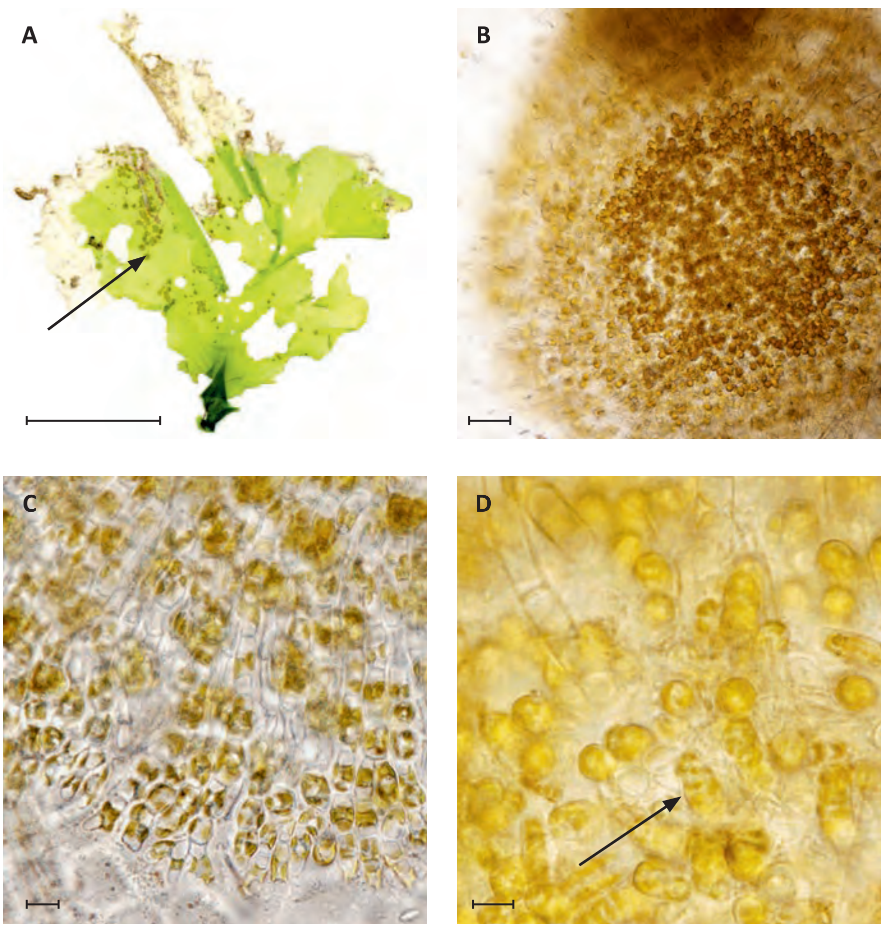
**Structure:** Disc consists of radiating filaments, which are mutually free at the margin. There are mutually free short upright filaments or brown algal hairs with sheath from virtually all cells in the central part of the disc, no ascocysts. Cells contain 1-3 disc-shaped plastids with pyrenoids.

**Reproduction:** Unilocular sporangia are spherical or ellipsoid. Plurilocular sporangia are upright and uniseriate or biseriate, 25-28 µm long and 7-9.5 µm in width. They are sessile on the disc or terminal on short upright filaments. From swarmers of plurilocular sporangia are direct development. Swarmers of unilocular sporangia develop upright irregular filaments, which are the gametophyte generation.

**Seasonal variation:** Collected in June-August and October. Plurilocular sporangia recorded in April and June.

**Habitat:** Epiphytic on Sea Lettuce (*Ulva fenestrata*), 0.5-3.5 m depth, and an older collection from 17 m depth.

**References:** Fletcher (1987), Kim (2010), Kylin (1934, 1947), Pedersen (1981a), Peters (1988).




A: *Myrionema strangulans*. Brown discs on the host alga (arrow). Scale 2 cm. A-D: On Sea Lettuce (*Ulva fenestrata*). Pole south of the harbour, Vesterø Havn, Læsø, 0.5 m, 5.6.2017.

B: *Myrionema strangulans*. Circular disc with upright filaments and brown algal hairs. Scale 50 µm.

C: *Myrionema strangulans*. Mutually free filaments at the edge of disc. Scale 10 µm.

D: *Myrionema strangulans*. Plurilocular upright sporangia (arrow). Scale 10 µm.

# *Myriotrichia clavaeformis*

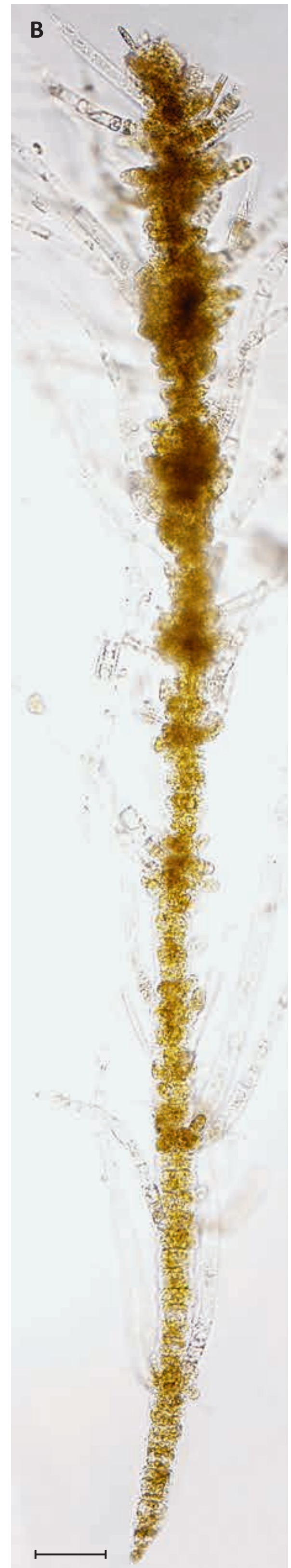
**Harvey**

Club Brown Tuft Weed

**Appearance:** Dark brown epiphytic tufts of short, slightly club-shaped threads, 0.3-1.5 cm in height. Short protruding branches on all sides are scattered, opposite or in whorls. Branches are mutually free or approximately confluent in larger parts of the alga, typically in the upper end and contribute to the club-shaped appearance.

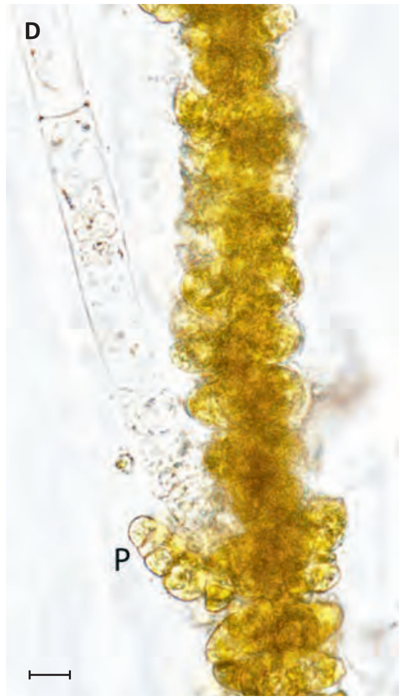
**Structure:** Uprights arise from a system of uniseriate filaments with scattered branches, epiphytic or endophytic in soft host algae. Rhizoidal filaments may arise from the lower cells and contribute to the attachment of the alga. Young individuals are uniseriate with an apical true brown algal hair, which is pushed aside by continued growth from the cells below the growth zone of the hair. A parenchymatous area gradually develops after longitudinal cell divisions. This happens at first in the upper part of the alga and also takes place at intervals down the alga. Therefore, parenchymatous and uniseriate parts alternate and


A: *Myriotrichia clavaeformis*. Small tufts on Chipolata Weed (*Scytosiphon lomentaria*). Frederikshavn, 0.2 m, 28.6.1972. Leg.: H. Nielsen. Scale 2 cm.




B: *Myriotrichia clavaeformis*. Club-shaped alga. Scale 50 µm. B-E: Pole, south of the harbour, Vesterø Havn, Læsø, 0.5 m, 5.6.2017.


C: *Myriotrichia clavaeformis*. Initiation of parenchyma by longitudinal cell divisions and apical true brown algal hair. Scale 20 µm.




D: *Myriotrichia clavaeformis*. Plurilocular sporangium (P) and true brown algal hair. Scale 10 µm.


E: *Myriotrichia clavaeformis*. Unilocular sporangium (S). Scale 20 µm.

thalli become slightly uneven or rough. The parenchymatous area may be confluent but the lower part is typically uniseriate. Cells in the uniseriate part are elongate cylindrical. Vegetative cells contain several disc-shaped plastids without pyrenoids. True brown algal hairs without sheath arise from scattered surface cells and are frequent. Short uniseriate branches occasionally occur. Uniseriate upright thalli, where true brown algal hairs are rare, sometimes occur. Such forms were previously known as *M. repens* Hauck. In this, the cells are relatively long and 10-17 µm in width while they are shorter and slightly barrel-shaped in parenchymatous thalli.

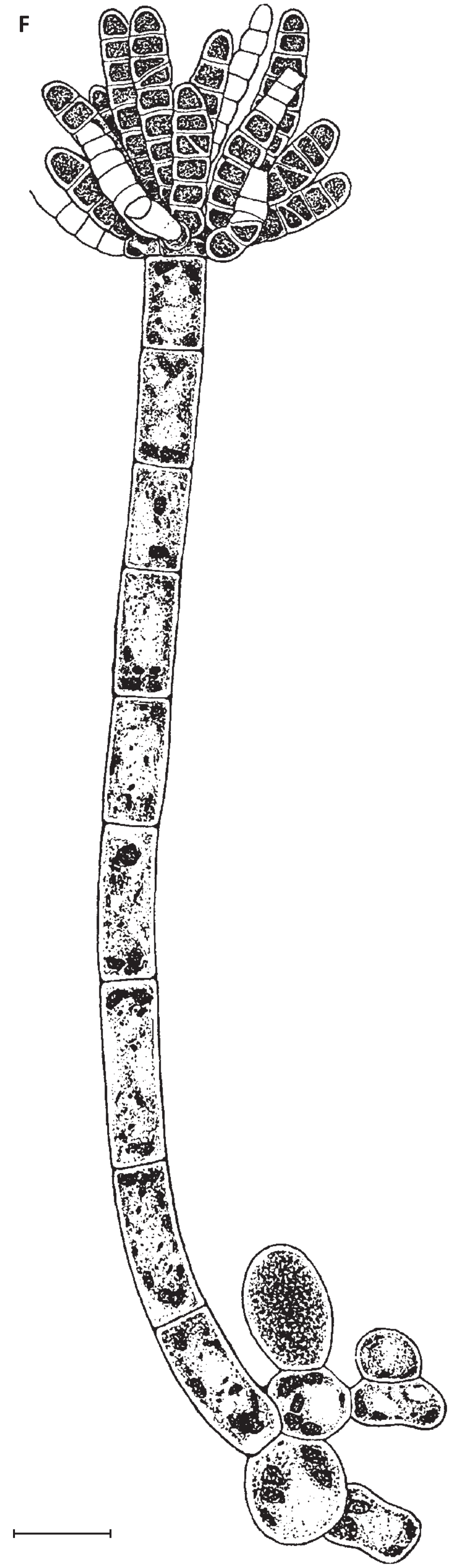
**Reproduction:** Uni- and plurilocular sporangia occur on the same or different thalli. Several sporangia are frequently close together, opposite or in whorls. Unilocular sporangia develop from surface cells on the main branch or branches. They are sessile or have short stalks, ellipsoid to approximately spherical, 57-65 (-80) µm long and 50-57 (-65) µm in width. Plurilocular sporangia develop from cells in branches typically from all cells so the whole branch turns into a sporangium which is cylindrical or cone-shaped. Although several vegetative cells are involved in the process, it is a single sporangium, evacuated through a common exit pore at the apex. There is considerable morphological variation and the life history comprises a microthallus.

**Seasonal variation:** Collected in April-October. Plurilocular sporangia recorded in April, June-October, and unilocular sporangia in June-August.

**Habitat:** Epiphytic on Chipolata Weed (*Scytosiphon lomentaria*), but also on other algae, particularly brown algae and on Eelgrass (*Zostera marina*). Most collections from shallow water but in older collections by dredge recorded to 12 m depth.

**Comment:** Culture studies of Danish Club Brown Tuft Weed (*M. clavaeformis*) by Pedersen (1978a) showed the morphology to be dependent on physical factors, particularly salinity and temperature. The morphological variation comprised forms described as *M. clavaeformis*, *M. filiformis* Harvey and *M. repens* and therefore these names are considered synonyms. Pedersen (1978a). also found a microthallus of creeping filaments as part of the life history, and this was identified with *Streblonema sphaericum* (Derbès & Solier) Thuret, which is not observed in nature in Danish waters, but known as an endophyte in Slimy Wormweed (*Mesogloia vermiculata*) at the Swedish west coast. Some of the Danish collections which were identified as *M. repens*, grew also on Slimy Wormweed (*Mesogloia vermiculata*). Both this alga and *S. sphaericum* have spherical unilocular sporangia on creeping filaments. *Myriotrichia repens* also has short upright filaments with plurilocular sporangia. In culture studies of the alga from Ireland (Peters, 1988), sexual reproduction was found, in which swarmers from plurilocular sporangia on dioecious microthalli were isogametes. The zygotes germinated and developed into upright macrothalli.

**References:** Fletcher (1987), Kuckuck (1954, *Streblonema sphaericum*), Kylin (1947, *Myriotrichia filiformis*, *M. repens, S. sphaericum*), Pedersen (1978a), Peters (1988), Rosenvinge & Lund (1947, *M. clavaeformis*, *M. repens*), Wærn (1952, *M. repens*).




F: *Myriotrichia clavaeformis.* Creeping filament with unilocular sporangium, short upright branch with plurilocular sporangia (previously, *M. repens*). After Rosenvinge & Lund (1947). Scale 20 µm.

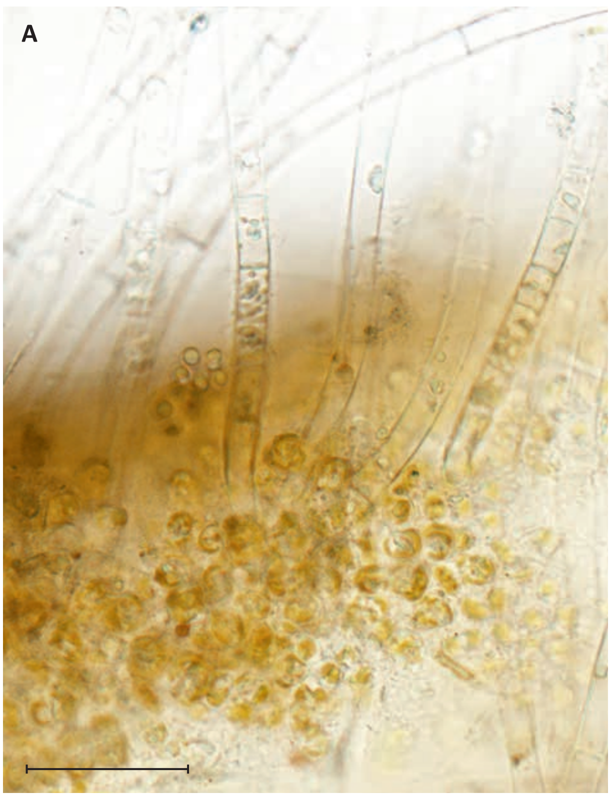
## *Phaeostroma pustulosum*

**Kuckuck in Reinbold**

Long Cell Pustule

**Appearance:** Microscopic, epiphytic creeping filaments or disc-shaped alga.

**Structure:** Uniseriate filaments with scattered branches, which may be confluent to pseudoparenchymatous discs of 2-3 cell layers and up to c. 0.5 mm in width. Vegetative cells contain several disc-shaped plastids. Brown algal hairs are distinct with a characteristic long cell just below the growth zone (phaeostroma-hair). The long cell has a small constriction above a broad base.




A: *Phaeostroma pustulosum*. Pseudoparenchyma of vegetative cells with several disc-shaped plastids. Upright phaeostroma-hairs with a long basal cell below the growth zone. Scale 20 µm. A-C: On Black Siphon Weed (*Vertebrata fucoides*). Just north of the jetty, Nordre Rønner, Læsø, 0.5 m, 24.5.2005.

**Reproduction:** Uni- and plurilocular sporangia occur on different individuals. Plurilocular sporangia develop after division of all cells in a branch system. They develop into a complex structure with a lumpy rounded shape. Unilocular sporangia are not observed in the alga from Danish waters, but recorded from the Swedish west coast, where they are spherical or pyriform and develop from a vegetative cell. Culture studies of the alga from Greenland (Pedersen, 1981d, 2011) showed a direct life history, with no difference in the fate of swarmers from uni- or plurilocular sporangia.

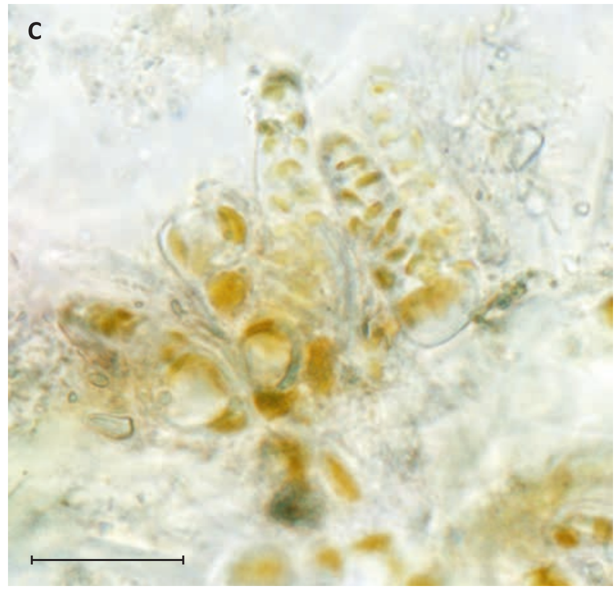
**Seasonal variation:** Collected in January, May, July and September. Plurilocular sporangia recorded in May and July.

**Habitat:** Epiphytic on Bootlace Weed (*Chorda filum*), Purple Siphon Weed (*Leptosiphonia fibrillosa*), Black Siphon Weed (*Vertebrata fucoides*) and old leaves of Eelgrass (*Zostera marina*). Collected in 0.5-2 m depth and once from 8 m depth by dredge.

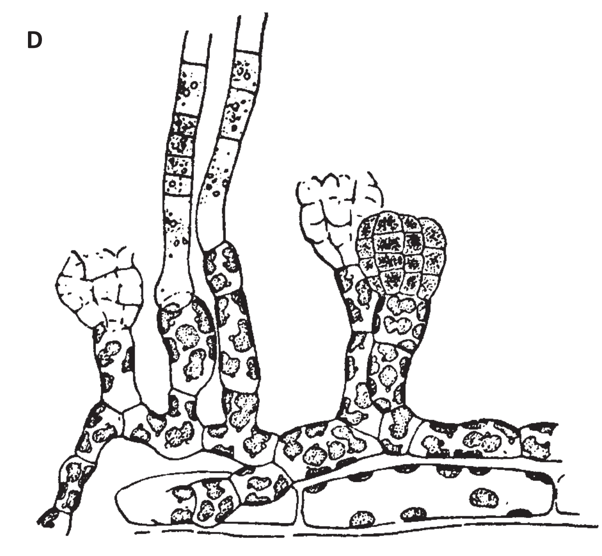
**Comment:** Culture studies of the alga from Greenland (Pedersen, 1981d) support the proposal that *Streblonema aequale* Oltmanns is a synonym of *P. pustulosum*. *Streblonema aequale* has creeping uniseriate filaments, from which typically unbranched filaments, 1-4 cells long, arise. Vegetative cells contain several disc-shaped plastids. Uni- or plurilocular sporangia are apical on the upright filaments. Unilocular sporangia are ellipsoid; plurilocular sporangia multiseriate and club-shaped. *Streblonema aequale* is endophytic, observed in the same host species as Long Cell Pustule (*P. pustulosum*) and also has brown algal hairs with a long basal cell. In Danish waters it is collected on Bootlace Weed (*Chorda filum*), with plurilocular sporangia recorded in January.

**References:** Kylin (1947, *P. pustulosum* and *Entonema aequale*), Pedersen (1981d, 2011), Rosenvinge & Lund (1941, *P. pustulosum* and *Streblonema aequale*).


B: *Phaeostroma pustulosum*. Phaeostroma-hairs, long basal cell with a small constriction at base (arrow). Scale 10 µm.




C: *Phaeostroma pustulosum*. Plurilocular sporangia. Scale 10 µm.




D: *Phaeostroma pustulosum*. Creeping filaments, upright branches with phaeostroma-hairs, rounded plurilocular sporangia (previous *Streblonema aequale*). Scale 50 µm. After Kuckuck (1897, in Kylin, 1947).

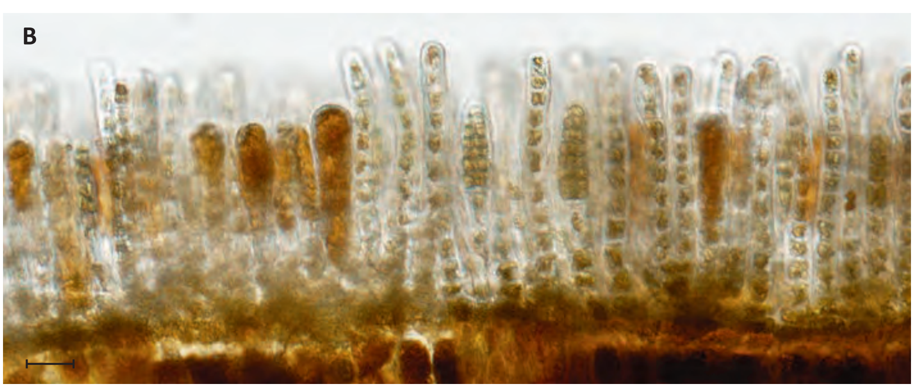
# *Phycocelis foecunda*

**Strømfelt**

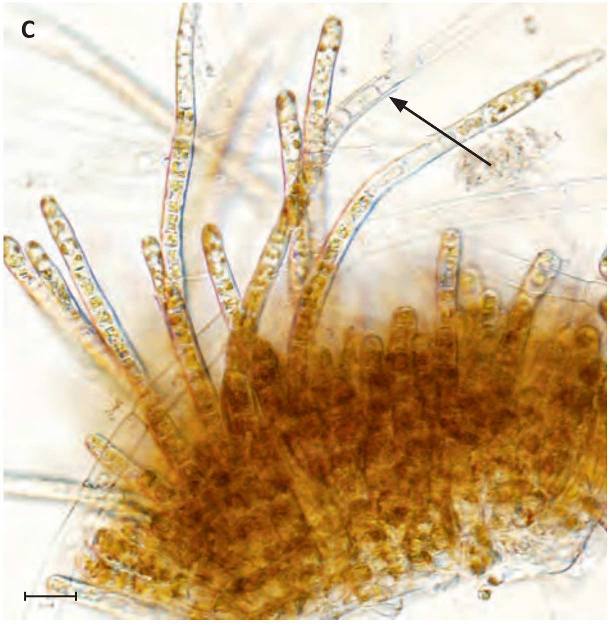
Wrack Spot

**Appearance:** Brown circular epiphytic discs, c. 1 mm in width or confluent to form irregular spots. The surface may be smooth and glossy.
**Structure:** Radiating confluent filaments form a basal layer which is entirely or in part distromatic. From each of the upper cells arise upright unbranched filaments or ascocysts, which typically are shorter than the upright filaments. Vegetative cells have a relatively large plastid with several lobes and one pyrenoid. Terminal brown algal hairs with sheath may occur on the upright filaments and, according to Fletcher (1987), also on the basal disc.
**Reproduction:** Plurilocular sporangia arise from cells in the basal layer or are apical on short upright filaments. The sporangia are bi- or multiseriate, almost cylindrical and slightly conical at the apex.
**Seasonal variation:** Collected with plurilocular sporangia in July-August.
**Habitat:** On Bladder Wrack (*Fucus vesiculosus*), 0.5 m depth. In the British Isles, on other host algae also (Fletcher, 1987).
**References:** Fletcher (1987, *Chilionema foecundum*).

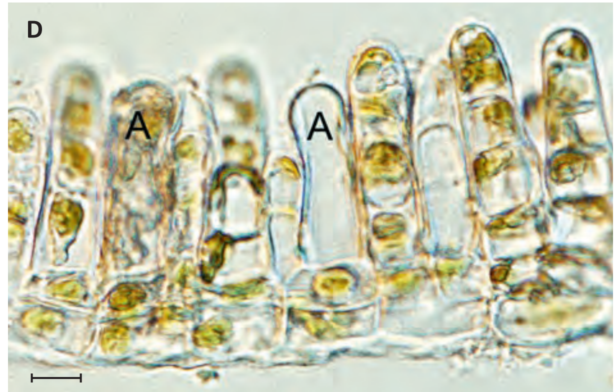

A: *Phycocelis foecunda*. Spots on Bladder Wrack (*Fucus vesiculosus*) (arrows). Scale 2 cm. A, C-D, F: On Bladder Wrack (Fucus *vesiculosus*), beach north of Vesterø Havn, Læsø, 0.5 m, 2.9.2017.



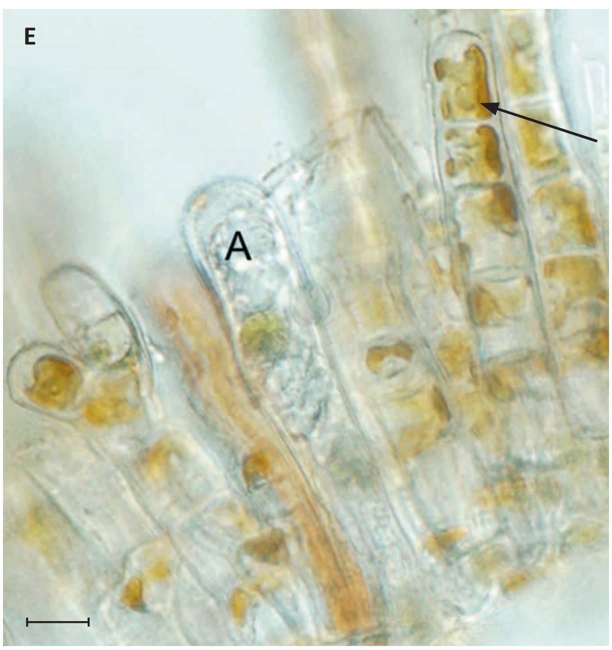

B: *Phycocelis foecunda*. Disc with many upright filaments, plurilocular sporangia and dark brown ascocysts. Scale 20 µm. B, E: On Bladder Wrack (*Fucus vesiculosus*), beach north of Vesterø Havn, Læsø, drift, 29.7.2014.



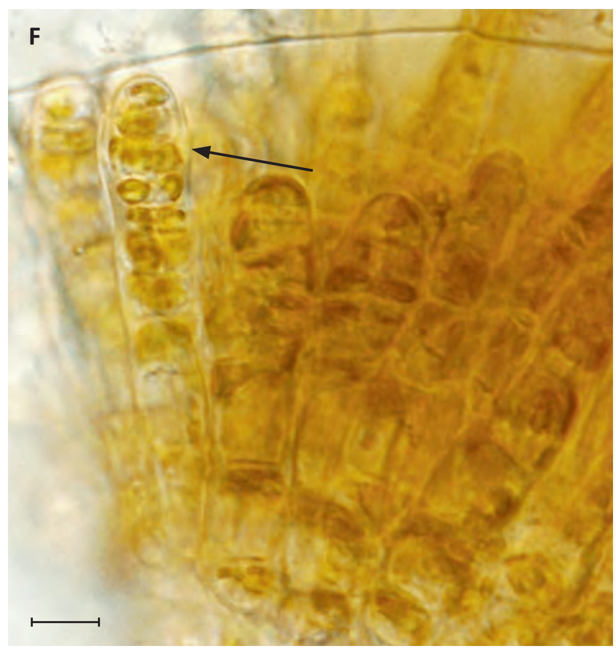

C: *Phycocelis foecunda*. Disc with upright short and longer filaments, apical brown algal hair with sheath (arrow). Scale 20 µm.




D: *Phycocelis foecunda*. Distromatic basal disc, short upright filaments and ascocyst (A). Scale 10 µm.




E: *Phycocelis foecunda*. Vegetative cell with a large lobed plastid with one pyrenoid (arrow), colourless ascocyst (A). Scale 10 µm.




F: *Phycocelis foecunda*. Apical plurilocular sporangia (arrow) on short upright filaments. Scale 10 µm.

# *Pilinia rimosa*

**Kützing**

Brown Filifelt

**Appearance:** Yellow-brown or light brown covering of close, short upright filaments.

**Structure:** Upright filaments, c. 250 µm in height, are uniseriate, unbranched or have scattered branches. Branches typically unilateral with a pointed apical cell. Cylindrical cells, 6-8 µm in width and 1.5-2 times as long as wide. Cells occasionally divided by longitudinal walls before the development of few-celled branches or sporangia which cluster around the main branch. Vegetative cells contain few disc-shaped plastids with slightly lobed margin, without pyrenoids. No hairs. Upright filaments arise from a basal system of creeping filaments.

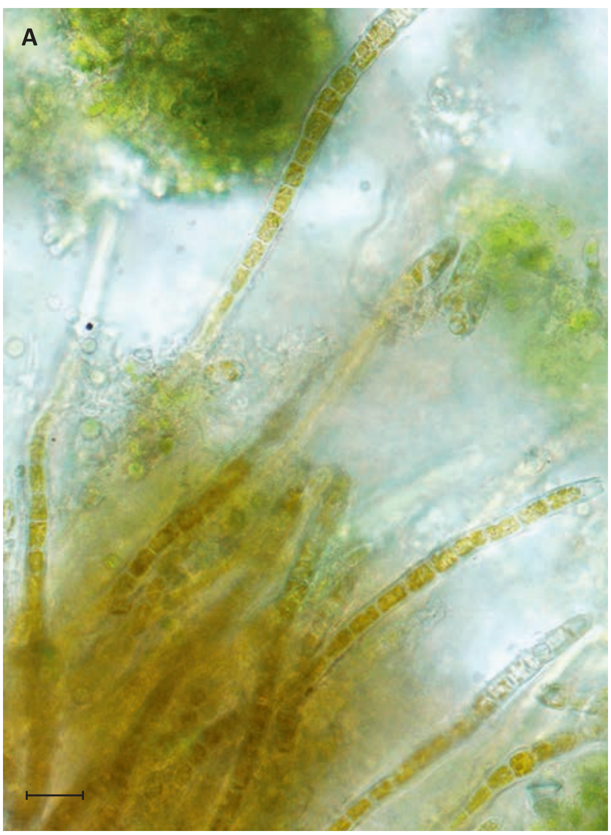
**Reproduction:** Sporangia develop from vegetative cells in the upper part of upright filaments. They form in several consecutive cells and commonly in consecutive branches. Unilocular sporangia are seriate and each of them is evacuated through a small exit papilla. Plurilocular sporangia with 2-3 compartments develop after longitudinal divisions of cells in short branches.

**Seasonal variation:** Collected in April-May and July with sporangia.

**Habitat:** Shaded localities in the salt-dust zone, on wooden poles, and fissures between boulders and at the under surface of hanging boulders above the normal water level.

**Comment:** Probably more widely distributed in Danish waters than the few records indicate.

**References:** Hooper et al. (1987), Kuckuck (1897, *Leptonema lucifugum*), Kylin (1947, *Waerniella lucifuga*), Rosenvinge (1935, *Leptonema* (?) *lucifugum*).




A: *Pilinia rimosa*. Filaments close together. Scale 20 µm.
A-G: On wooden pole under a bridge at the shipyard, Vesterø Havn, Læsø, 1.5.2016.


B: *Pilinia rimosa*. Long, unilateral branches. One apparently converted into a plurilocular sporangium (arrow). Scale 20 µm.



C: *Pilinia rimosa*. Apex with branches on all sides. Scale 10 µm.

D: *Pilinia rimosa*. Lumpy apex with longitudinal wall (arrow), and unilateral branches. Scale 10 µm.


E: *Pilinia rimosa*. Vegetative cells with disc-shaped plastids (arrow). Scale 10 µm.


F: *Pilinia rimosa*. Branch with a lumpy area, and at the apex a series of unilocular sporangia (arrow). Scale 10 µm.


G: *Pilinia rimosa*. Seriate unilocular sporangia with exit papilla (upper arrow) and a few empty sporangia (lower arrow). Scale 10 µm.

## *Polytretus reinboldii*

**(Reinke) Sauvageau**

Club Thread Weed

**Appearance:** Small delicate, branched bush-like alga, up to 5 cm in height.

**Structure:** Uniseriate filaments of cylindrical to barrel-shaped cells with scattered branches, which terminate in true brown algal hairs. Hairs are pushed aside with continued sympodial growth. Cells contain many disc-shaped plastids each with one pyrenoid.

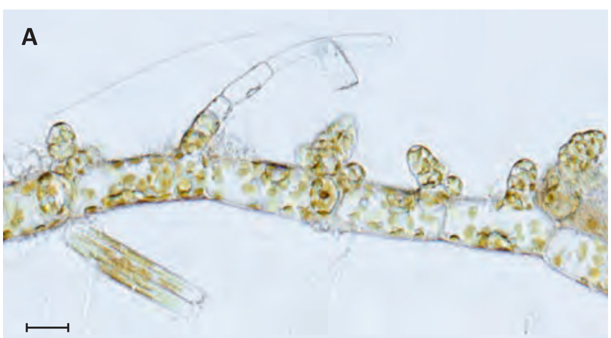
**Reproduction:** Plurilocular sporangia develop from cells in short branchlets, in which each of the vegetative cells becomes a plurilocular sporangium after divisions into a few cells. At maturity, each sporangium is emptied separately, which shows that there are several sporangia in a sorus. Rounded cells thought to be unilocular sporangia are recorded by Rosenvinge & Lund (1941). Culture studies of the alga from Danish waters by Pedersen (1977) showed that swarmers from plurilocular sporangia germinated and developed attached creeping filaments. These uniseriate filaments resembled vegetative thalli, and new upright filaments arose from them.

**Seasonal variation:** Only a few collections from Danish waters, March-May with plurilocular sporangia.

**Habitat:** On stone, 1.5-3 m depth and a single collection, 11-12 m depth.

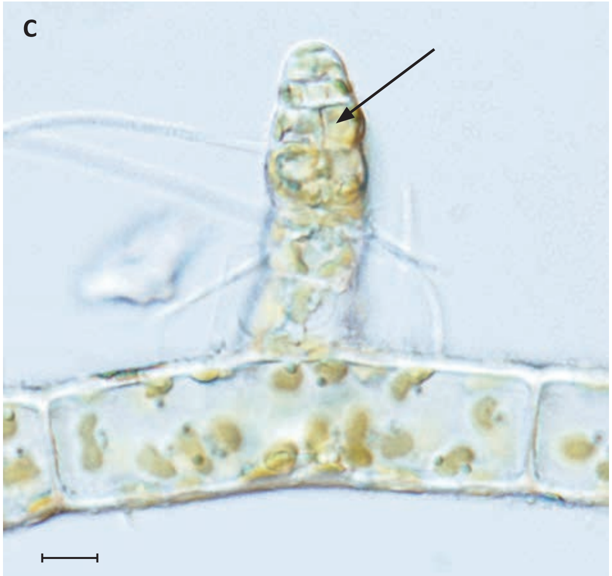
**Resembles:** Appearance reminiscent of Mini Brown Mulberry Weed (*Botrytella micromora*), from which it is best distinguished by the development of sporangial sori. These are club-shaped in Club Thread Weed (*P. reinboldii*), conical and consist of elongate ovoid sporangia in Mini Brown Mulberry Weed (*B. micromora*).

**References:** Kornmann & Sahling (1977, *Sorocarpus micromorus* Abb. 59), 1988, *Botrytella reinboldii*), Kurogi (1978), Pedersen (1977, 1989), Rosenvinge & Lund (1941, *Ectocarpus reinboldii*), Taskin & Pedersen (2012).




A: *Polytretus reinboldii.* Part of filament with true brown algal hair and sessile sporangial sori. Many disc-shaped plastids in vegetative cells. Scale 20 µm. A-F: Bovet, Læsø, drift, 28.4.2016.

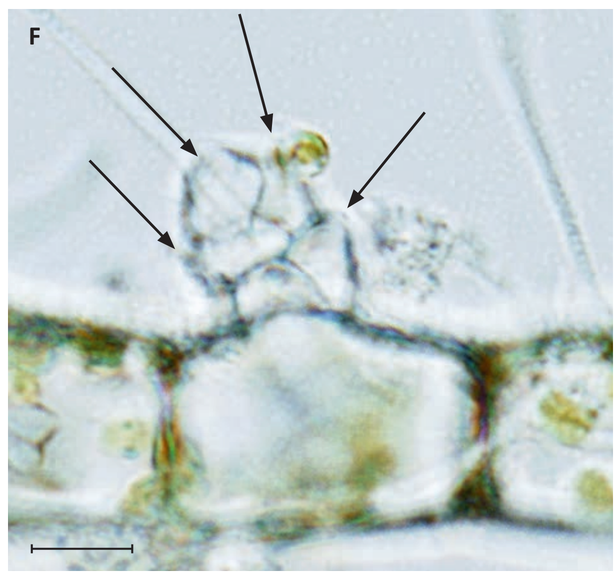

B: *Polytretus reinboldii.* Branchlet with apical true brown algal hair. Scale 10 µm.




C: *Polytretus reinboldii.* Branchlet with longitudinal wall (arrow), initiation of a young sporangia sorus. Scale 10 µm.


D: *Polytretus reinboldii.* Older sporangia sorus. Scale 10 µm.


E: *Polytretus reinboldii.* Almost mature sporangia sorus. Eyespots of swarmers appear as dark points (arrow).
Scale 10 µm.

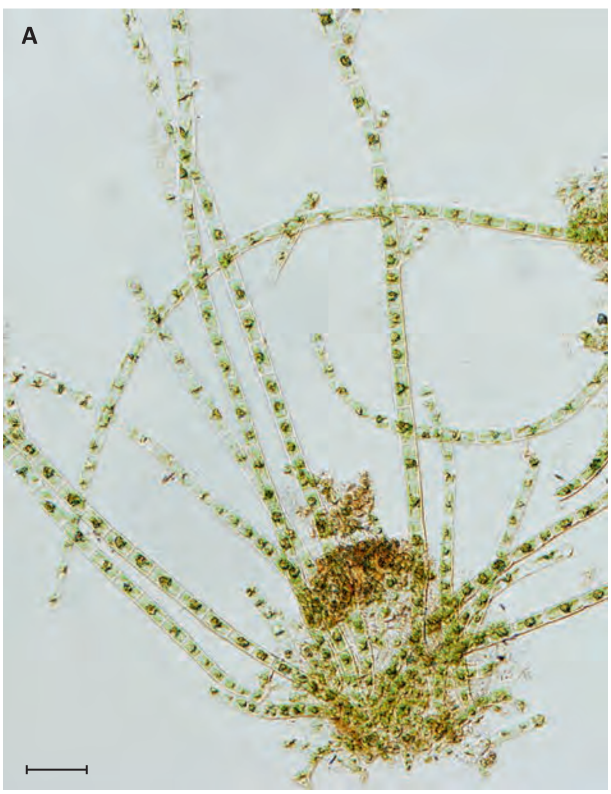



F: *Polytretus reinboldii.* Empty sporangial sorus, each sporangium with its own exit pore (arrows). Scale 10 µm.

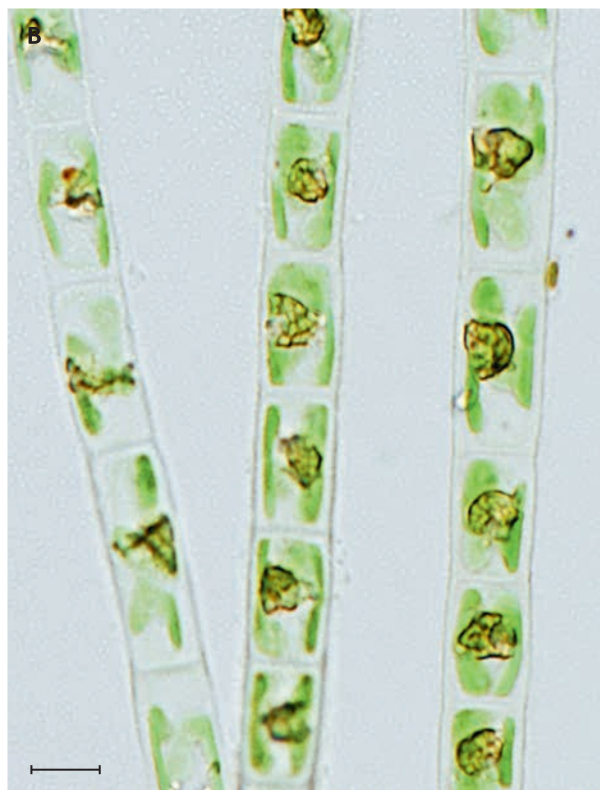
## *Protectocarpus speciosus*

**(Børgesen) Kornmann in Kuckuck**
Felty Cotton Thread

**Appearance:** Felty cover of brown filaments, < 1 mm in height, or small spots, < 1 mm in width.
**Structure:** Creeping filaments, which are confluent and form a monostromatic disc-shaped base. Mutually free filaments arise from the base. They are uniseriate, unbranched or sparsely branched, 6-8 µm in width. Branches are short, typically unilateral and without further branches. Filaments have diffuse growth with cylindrical cells, 1-4 times as long as wide. Cells contain a single large bilobed plastid with one pyrenoid. Brown algal hairs with sheath are terminal or lateral on upright filaments or arise from the basal system, but not always present.
**Reproduction:** Plurilocular sporangia are cylindrical, slightly narrow towards the apex with a few longitudinal walls and may be branched. They arise from the basal system, sessile or on a short stipe or they are apical on the upright filaments or branches. When a sporangium has unilateral branches, it might appear as a cock's comb.
**Seasonal variation:** Collected in February-October. Plurilocular sporangia recorded in April, June and September.
**Habitat:** On stone and epiphytic on larger algae and hydroids, 0.5-18 m depth.
**References:** Fletcher (1987), Kim (2010), Kornmann & Sahling (1977), Kuckuck (1955), Tanaka (1986).




A: *Protectocarpus speciosus.* Basal system of creeping filaments with sparsely branched uprights. Scale 50 µm. A-B: Slide preparation of formalin fixed material in Karo. Hatter Barn, 7 m, 18.9.1993.




B: *Protectocarpus speciosus.* Vegetative cells with a single bilobed plastid. A brownish mass of fucosan also in cells. Scale 10 µm.

C: *Protectocarpus speciosus*. Branched plurilocular sporangium. On Bladder Wrack (*Fucus vesiculosus*), beach north of Vesterø Havn, Læsø, 0.5 m, 1.9.2014. Scale 10 µm.


## *Punctaria*

Brown Tongue

Ribbon-shaped thalli, appear rough and slightly hairy because of protruding sporangia and many brown algal hairs with sheath. One of the species is mainly ribbon-shaped but in some areas it also occurs as branched filaments. The algae are parenchymatous with cells in rows. Surface cells contain many disc-shaped plastids with pyrenoids. Young algae are uniseriate filaments with an apical brown algal hair with sheath, many surface cells in older algae also have brown algal hairs with sheath.

**Identification key to species of *Punctaria***

| | | |
|---|---|---|
| 1a. | Ribbon-shaped, 8-25 cm long and 1-2 (-3) cm in width with 4-8 cell layers. Hairs typically in groups | *P. plantaginea* |
| 1b. | Ribbon-shaped, up to 5 cm long and 5-7 mm in width with 2-4 cell layers or filiform. Hairs scattered | *P. tenuissima* |

# *Punctaria plantaginea*

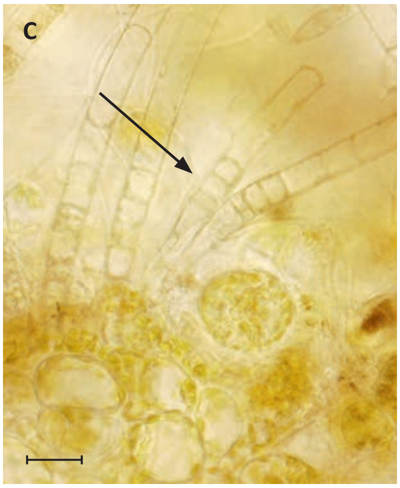
**(Roth) Greville**

Pointed Brown Tongue

**Appearance:** Ribbon- or tongue-shaped, light brown thalli, typically 8-25 cm in height and 1-2 cm in width but may be up to 40 cm long and 3 cm wide. The blades arise from a disc-shaped base with a short stipe and gradually expanding in width. Blades are typically finely pointed with hairs in small groups.
**Structure:** The blade is 4-8 cell layers thick. Central cells are colourless and slightly rounded. Surface cells in young blades are approximately quadrangular or rectangular and become rounded in older thalli, 26-44 µm in width. Cells contain many disc-shaped plastids with pyrenoids. Many brown algal hairs with sheath arise from surface cells, typically in small groups.
**Reproduction:** Unilocular sporangia, 40-45 µm in width develop from surface cells and protrude slightly from the surface. Plurilocular sporangia are only reported on peculiarly small individuals in Danish waters (Rosenvinge & Lund, 1947). Culture studies of the alga from Greenland and Canada (Pedersen 1984, South 1980) showed a direct life history. Swarmers from unilocular sporangia germinated and developed microthalli, from which new upright thalli arose. Neither plurilocular sporangia nor sexual reproduction were found in these culture studies.
**Seasonal variation:** Collected in March-August and December, most frequent in early summer. Unilocular sporangia recorded in April-August and December.
**Habitat:** On stone, 0-5 m depth and a single collection by dredge, 10 m depth at Læsø Trindel.
**Resembles:** Appearance similar to Broad Leaf Weed (*Petalonia fascia*) but blades in this species are smooth with scattered true brown algal hairs without sheath. They have many cell layers and only a single plastid per cell. Pointed Brown Tongue (*P. plantaginea*) has a few cell layers, true brown algal hairs with sheath, typically in groups, and several plastids in the assimilating cells.
**References:** Fletcher (1987), Pedersen (1984, 2011), Rosenvinge & Lund (1947), South (1980).


A: *Punctaria plantaginea*. Ribbon-shaped blades with groups of hairs. Hirsholm, 0.5 m, 20.6.1985. Scale 2 cm.


B: *Punctaria plantaginea*. Vegetative cells with many disc-shaped plastids. Scale 20 µm. B-H: Beach south of Vesterø Havn, Læsø, drift, 3.6.2017.

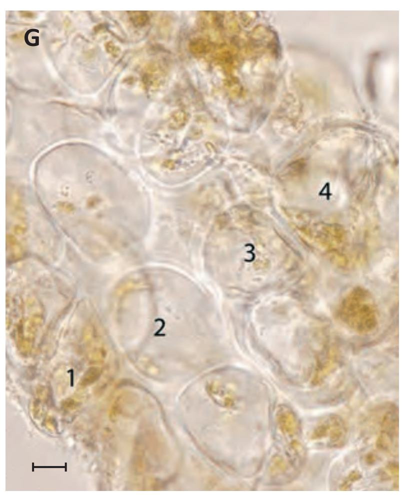



C: *Punctaria plantaginea*. Group of brown algal hairs with sheath (arrow). Scale 20 µm.

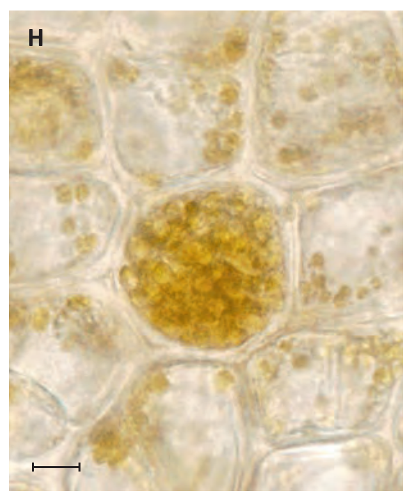

D: *Punctaria plantaginea*. Apical hair with sheath in young alga. Scale 10 µm.


E: *Punctaria plantaginea*. Brown algal hairs with sheath from the edge of a young blade. Scale 10 µm.


F: *Punctaria plantaginea*. Young blade with slender filaments for attachment. Scale 50 µm.




G: *Punctaria plantaginea*. Blade with 4 cell layers (1-4). Transverse section. Scale 10 µm.




H: *Punctaria plantaginea*. Unilocular sporangium among surface cells. Scale 10 µm.

# *Punctaria tenuissima*

**(C.Agardh) Greville**

Wavy Brown Tongue

A

A: *Punctaria tenuissima.* Narrow, ribbon-shaped blades on Eelgrass (*Zostera marina*). Deget, Frederikshavn, 0.5 m, 13.7.1967. Leg.: L. Mathiesen. Scale 2 cm.

**Appearance:** Well-developed thalli are light brown narrow ribbons, occasional slightly twisted with a wavy margin. Typically around 5 cm in height and 0.5-0.7 cm in width but may be up to 20 cm in height and very narrow. Furthermore, thalli might be filiform. Several thalli commonly occur together but may occur individually. Individual blades have irregularly alternating wide and narrow parts, and there might be small projections from the margin. The thalli typically expand in width from a short stipe-like part at the base and decrease towards the top.

**Structure:** Young individuals are uniseriate with a brown algal hair with sheath at the apex. Longitudinal cell divisions occur in some or all the cells, and the thalli become parenchymatous and consist of (1-) 2-4 cell layers. Surface cells are quadrangular or rectangular, 15-27 µm long and 12-20 µm in width, occurring in rows. Each cell contains several plastids with pyrenoids. Many brown algal hairs with sheath arise from scattered surface cells and at the edge of the blades.

**Reproduction:** Uni- or plurilocular sporangia protrude, developing from surface cells on both sides of the blades. Unilocular sporangia, approximately spherical, c. 35 µm in width. Plurilocular sporangia are conical with a broad base, 12-20 µm in width and 15-28 µm in height. Plurilocular sporangia in the narrow and the filiform individuals might be elongate ellipsoid and have a stalk cell. Uni- and plurilocular sporangia occur on the same or different thalli.

**Seasonal variation:** Collected in March-October. Plurilocular sporangia recorded in March-October and unilocular sporangia in August and September.

**Habitat:** Epiphytic on leaves of Eelgrass (*Zostera marina*) and on larger algae, 0.5-10 m depth.

**Resembles:** Very slender or uniseriate individuals may resemble other filiform species. This species is best identified on the brown algal hairs with sheath and the protruding plurilocular sporangia.

**Comment:** Culture studies of the alga from Danish waters (Pedersen 1984) showed a direct life history with uprights from a filamentous microthallus. This could have creeping filaments, from where brown algal hairs with sheath and upright plurilocular sporangia arose. Vegetative cells contained several disc-shaped plastids. Morphology and particularly the plurilocular sporangia varied according to the physical conditions. The microthallus was identified as *Streblonema effusum* Kylin. Parente et al. (2010), who also studied the species in culture, found unilocular sporangia.

**References:** Fletcher (1987), Kylin (1933, 1947, *Desmotrichum undulatum*, *Entonema effusum*), Parente et al. (2010), Pedersen (1984, *D. undulatum*), Rosenvinge & Lund (1941, *D. undulatum, Streblonema effusum*).

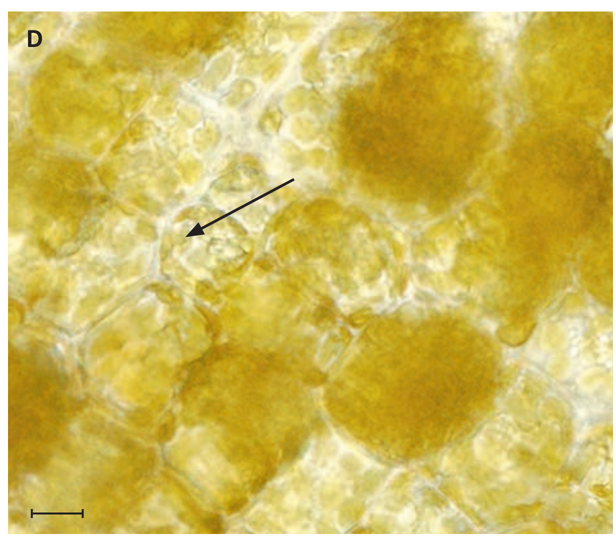
# *Microthallus*

## (previously *Streblonema effusum*)

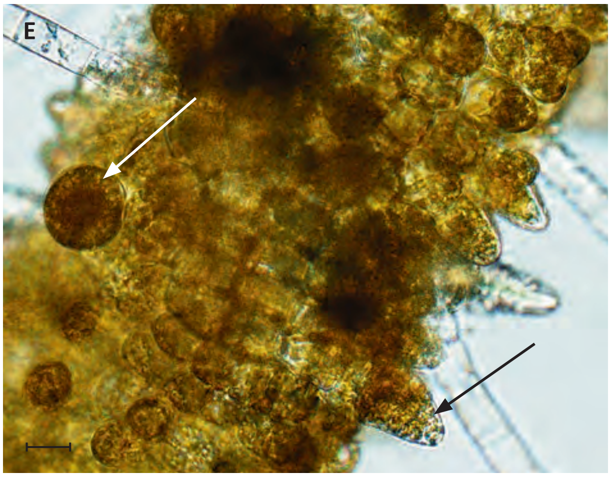
**Appearance:** Endophytic creeping filaments.
**Structure:** Creeping irregularly branched filaments. True brown algal hairs and plurilocular sporangia arise from the filaments and are the only structures outside the host alga. Each of the vegetative cells contain several disc-shaped plastids.
**Reproduction:** Plurilocular sporangia are ovoid and multiseriate. They are sessile on the creeping filaments or on a unicellular stalk.
**Seasonal variation:** Observed with plurilocular sporangia in July-September.
**Habitat:** Endophytic in the wall of Banded Pincer Weed (*Ceramium* sp.), Purple Claw Weed (*Cystoclonium purpureum*) and Pitcher Siphon Weed (*Polysiphonia stricta*).


B: *Punctaria tenuissima*. Ribbon-shaped blade with many brown algal hairs with sheath, protruding uni- and plurilocular sporangia. Scale 50 µm. B-E: Beach north of Vesterø Havn, Læsø, drift, 1.9.2014.


C: *Punctaria tenuissima*. Brown algal hair with sheath (arrow) and plurilocular sporangia from edge of blade. Scale 10 µm.



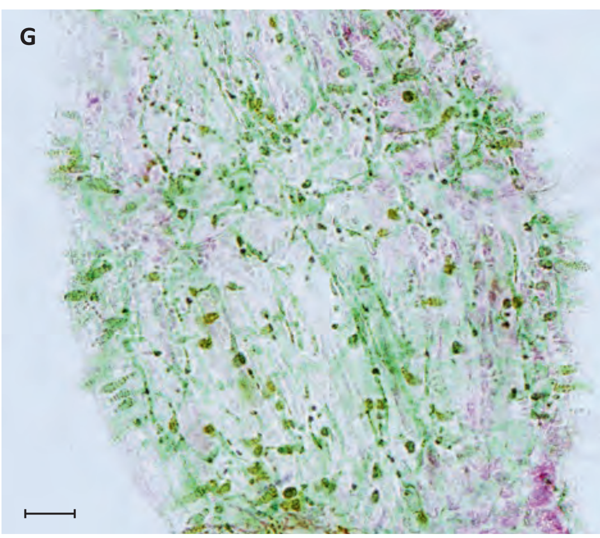

D: *Punctaria tenuissima*. Sporangia and vegetative cells, many disc-shaped plastids with pyrenoids (arrow). Scale 10 µm.



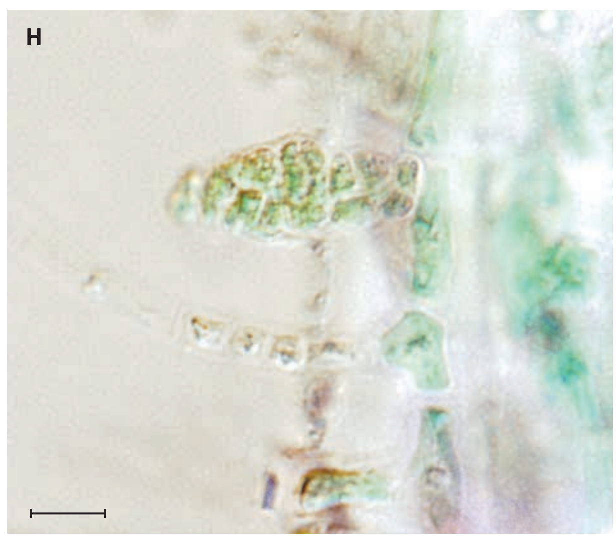


E: *Punctaria tenuissima*. Protruding unilocular sporangium (upper arrow) and plurilocular sporangium (lower arrow). Scale 20 µm.

F: *Punctaria tenuissima*. Narrow alga with protruding, mature and empty plurilocular sporangia. Beach north of Vesterø Havn, Læsø, drift, 23.6.2013. Scale 10 µm.




G: *Punctaria tenuissima*, microthallus. Endophytic filaments with upright sporangia and true brown algal hairs. Scale 50 µm. G-H: In Banded Pincer Weed (*Ceramium* sp.), Sjællands Rev, 4.5 m, 11.9.1996.




H: *Punctaria tenuissima*, microthallus. Creeping filament with upright sporangium and true brown algal hair. Scale 10 µm.

# *Spermatochnus paradoxus*

**(Roth) Kützing**

Evenly-Divided Branched Weed

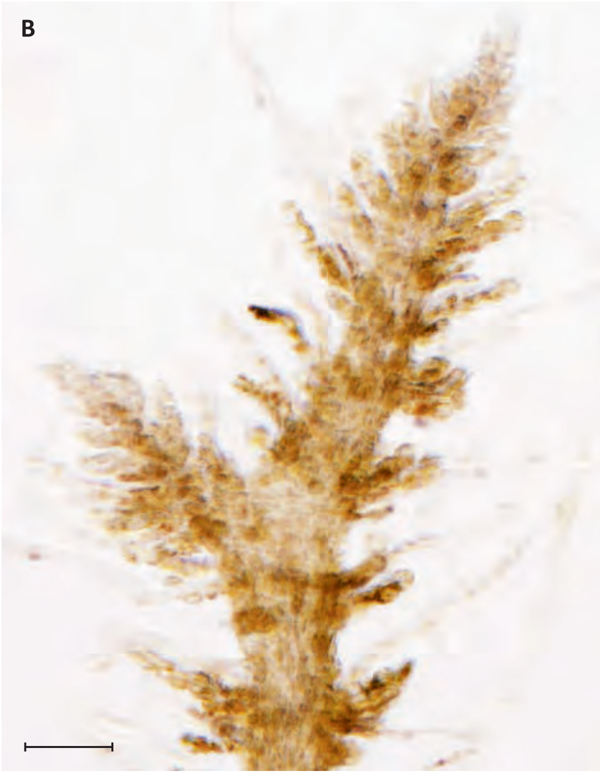
**Appearance:** Bushy thalli of terete, light yellow-brown branches which are repeatedly dichotomously branched, scattered branches occasional. Thalli are up to 40 cm in height. Branches up to 2 mm in width at the base, gradually decrease in width to the top and terminate in filamentous apices. Consistency slightly cartilaginous, flexible with hollow branches.

**Structure:** Uniaxial syntagma with a central axis of cylindrical cells in branches which terminate in a single apical cell. From each of the central axial cells 4-5 filaments arise in a whorl (primary assimilating filaments). They consist of 7-9 cells and curve slightly upwards. The primary assimilating filaments are in obvious whorls when the cells of the central axis stretch. The first cell of primary assimilating filaments stretches perpendicular to the central axis at the same time, to become elongate cylindrical, and a cavity forms around these cells and the central axial cells. A thick cortical tissue develops from the second cell of the primary assimilating filaments. It consists of several cell layers, the inner ones of relatively large colourless cells and the outer ones of small assimilating cells. Very narrow hyphae-like filaments may arise from the innermost cortical cells and entangle the lower part of the thallus. The part of the primary assimilating filaments which are outside the cortex gradually disappear and are replaced by secondary assimilating filaments (paraphyses). These, together with unilocular sporangia form wart-like spots (sori) on the branches. The sori are initially in whorls but later more sori develop at irregular intervals. The paraphyses are slightly curved, club-shaped and up to 6 cells long. Lower cells are cylindrical and relatively long, upper cells are rounded, and the apical cell is almost spherical. True brown algal hairs occur in the youngest part of branches and in sori. They arise from the assimilating filaments or paraphyses, from the basal of the cells outside the cortex.

**Reproduction:** Unilocular sporangia occur in sori, are obovate and develop from the innermost cells of the paraphyses. Culture studies of the alga from the Mediterranean Sea (Müller, 1981) showed that the life history, comprised a microthallus with plurilocular sporangia, and an upright sporophyte generation with unilocular sporangia. Swarmers from plurilocular sporangia differed according to the temperature. At temperatures of 20°C, zoospores germinated and developed into new microthalli. At temperatures of 9°C, some swarmers were gametes which copulated and the zygotes grew up to new diploid macrothalli. Other swarmers germinated without fertilization and developed haploid macrothalli.

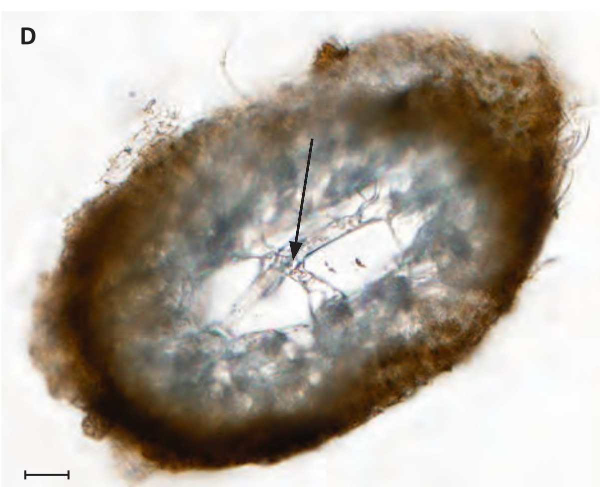
**Seasonal variation:** Collected in June-September with unilocular sporangia.


A: *Spermatochnus paradoxus*. Dichotomously branched bushy alga with terete branches gradually becoming narrower in the apical part. Dammen, Nordre Rønner, Læsø, 0.5 m, 17.8.2005. Scale 2 cm.

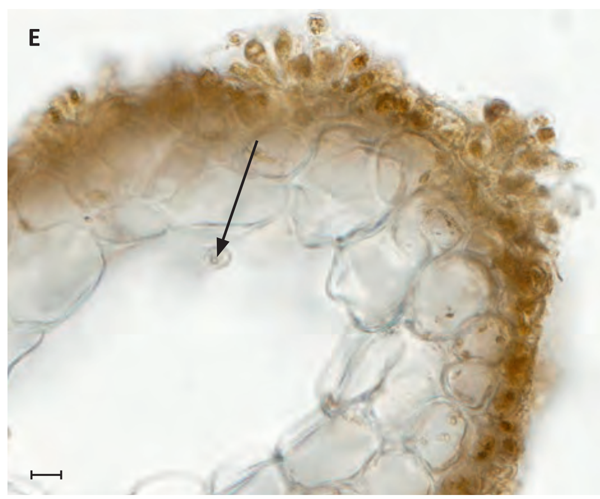



B: *Spermatochnus paradoxus*. Primary assimilating filaments and true brown algal hairs, in whorls at the apex. Lunkebugten, Tåsinge, 1.5 m, 11.7.2011. Scale 50 µm.


C: *Spermatochnus paradoxus*. Central axis with apical cell, primary assimilating filaments and true brown algal hair (arrow). Klatterne, south-east coast, Nordre Rønner, Læsø, 0.5 m, 15.8.2005. Scale 10 µm.




D: *Spermatochnus paradoxus*. Central axis (arrow) and a whorl of 4 cylindrical cells in cavity surrounded by cortical cells. Thick transverse section. Scale 50 µm. D-E: Beach south of Vesterø Havn, Læsø, drift, 29.7.2014.




E: *Spermatochnus paradoxus*. Central cavity with central axis (arrow) surrounded by cortex of large pale cells towards the cavity and small assimilating cells at the surface. Sori with paraphyses and unilocular sporangia. Transverse section. Scale 20 µm.

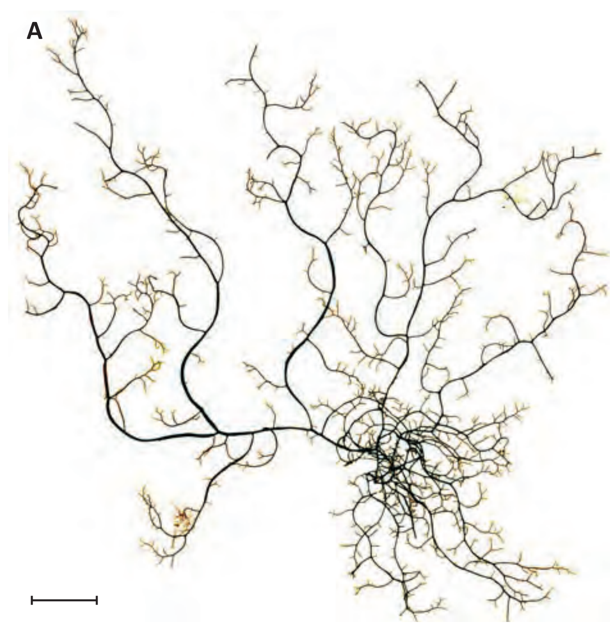
**Habitat:** Epiphytic on Bladder Wrack (*Fucus vesiculosus*), Serrated Wrack (*F. serratus*) and on leaves of Eelgrass (*Zostera marina*), rare on stone. Typically in shallow water, but specimens collected by dredge, 15 m depth.
**Resembles:** The appearance is similar to Knobbly Branched Weed (*Stilophora tenella*), best distinguished by the hollow cavity thallus and the single central filament. Knobbly Branched Weed (*Stilophora tenella*) has several central filaments, visible as several apical cells or probably easier seen in transverse sections in the microscope.
**References:** Müller (1981), Rosenvinge & Lund (1943).

## *Sphaerotrichia divaricata*

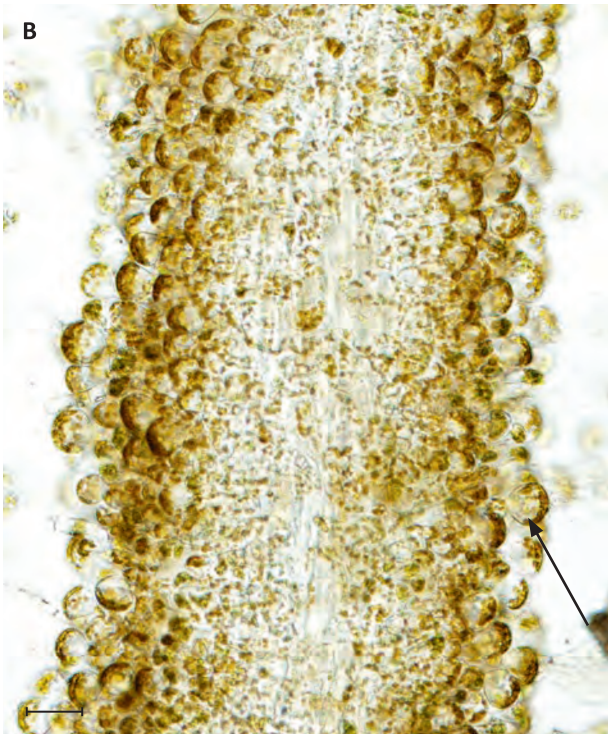
**(C.Agardh) Kylin**
Soft Angle Weed

**Appearance:** Much and repeatedly branched, very smooth bushy thalli, brown to dark brown and up to 54 cm in height. Branches are slightly curved with scattered branches on all sides, and typically arise at 90° branch angles, are 0.5 (-1) mm in width and become narrower towards the apex. Variation can include dark, thick and sparsely branched specimens with short branches.
**Structure:** Syntagma with a single central filament that terminates in an assimilating filament of 2-4 cells. A medulla of several parallel filaments of large pale cells occurs in the centre of branches. Innermost cells are longitudinally elongate, becoming shorter and more rounded towards the surface. Medullary filaments in the lower part may be entangled by very narrow hyphae-like filaments. Assimilating filaments, which form the surface, arise from the outermost medullary cells. Several assimilating filaments arise from a single basal cell together with true brown algal hairs. Cells of assimilating filaments are cylindrical except the apical which is relatively large and swollen as a balloon or spherical. Each cell contains several disc-shaped plastids. Filaments are loosely connected in a gelatinous wall substance. The lower part of the thalli may become hollow with age.
**Reproduction:** Unilocular sporangia are obovate, pyriform- or spherical. They develop at the base of assimilating filaments.
**Seasonal variation:** Summer to early autumn, collected in May-October. Unilocular sporangia recorded in June-October.

**Habitat:** On stone and epiphytic on larger algae and Eelgrass (*Zostera marina*) at sheltered localities. Most of the collections in the algal herbarium, Natural History Museum of Denmark, are from 1-8 m depth, and a few by dredge, 17 m depth.
**Comment:** Culture studies of Soft Angle Weed (*S. divaricata* ) from the Atlantic Sea, which included a strain from Denmark, showed that the life history comprised a microthallus. This reproduced sexually given the right conditions of temperature and day-length (Peters et al., 1987).
**References:** Peters et al. (1987), Rosenvinge & Lund (1943).

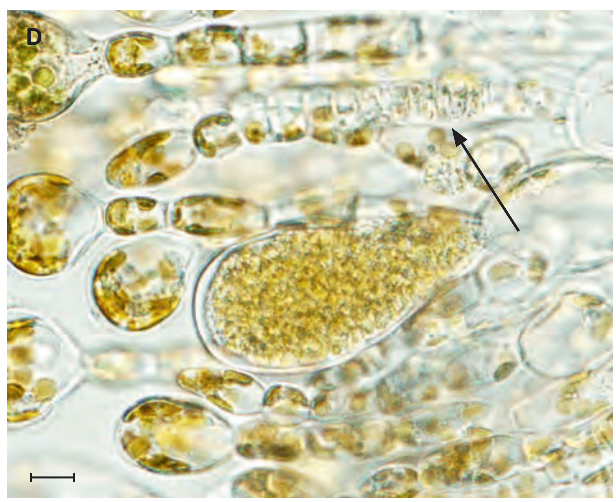



A: *Sphaerotrichia divaricata*. Much and repeatedly branched thalli. Stone reef at Frederikshavn, dredge, 10-4 m, 20.7.1998. Scale 2 cm.




B: *Sphaerotrichia divaricata*. Syntagma, medulla of large, colourless cells and surface of assimilating filaments, with a large balloon-shaped apical cells (arrow). Optical longitudinal section of branch in squash preparation. Scale 50 µm. B-D: Beach north of Vesterø Havn, Læsø, drift, 23.6.2013.


C: *Sphaerotrichia divaricata*. Assimilating filaments, cells with several disc-shaped plastids. Squash preparation. Scale 10 µm.




D: *Sphaerotrichia divaricata*. Unilocular sporangium, growth zone of true brown algal hair (arrow). Squash preparation. Scale 10 µm.

## *Stictyosiphon*

Broom Weeds

**Appearance:** Much branched bushy thalli with terete branches on all sides.
**Structure:** Parenchymatous, the apical part uniseriate with one terminal true brown algal hair. Further down in the branches is a medulla of four central filaments in the alga from Danish waters. The medullary cells are surrounded by a cortex of small cells in one to two layers. These cells contain several disc-shaped plastids. True brown algal hairs occur from scattered surface cells.
**Reproduction:** Plurilocular sporangia are frequent and unilocular sporangia occasional occur. The sporangia develop from surface cells and are more or less protruding.
**References:** Naylor (1958), Rosenvinge (1935), Rueness (1977).

**Identification key to species of *Stictyosiphon***

| | | |
|---|---|---|
| 1a. | Thalli yellow-brown with scattered branches. Medullary cells approximately spherical and visible through the cortex | *S. soriferus* |
| 1b. | Thalli brown to dark brown, much branched, but only few branches in the lower part. Medullary cells cylindrical and difficult to see through the cortex | *S. tortilis* |

## *Stictyosiphon soriferus*

**(Reinke) Rosenvinge**

Dotty Broom Weed

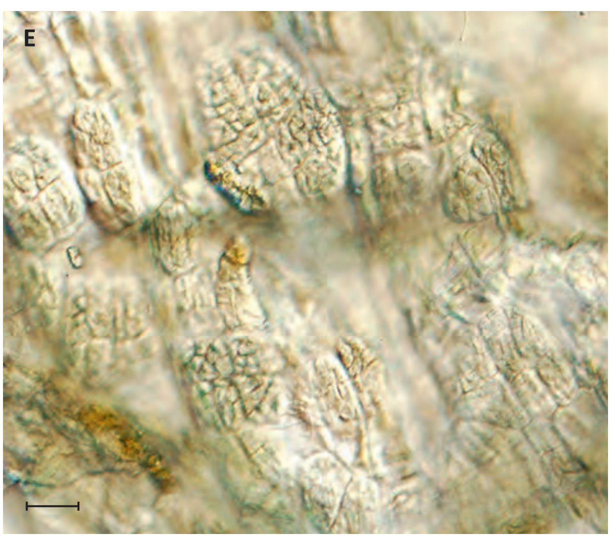
**Appearance:** Yellow-brown bushy thalli with branches on all sides, mainly 5-10 cm in height, but can be up to 22 cm in height. Branches scattered, seldom opposite, becoming pointed towards the apex.
**Structure:** Medulla typically consists of four rows of large spherical cells. These are covered by a single layer of small cortical cells, which are quadrangular or rectangular when seen in surface view. Small cells may also occur between the cortical cells. The apex is uniseriate and consists of a row of short cells terminating in a true brown algal hair. Scattered true brown algal hairs also occur from surface cells. Vegetative cells contain many elongate or disc-shaped plastids. Thalli are attached to the substratum by numerous rhizoidal filaments from the lowest cells.


A: *Stictyosiphon soriferus*. Bush-like alga with branches on all sides. Rygård Strand, 3 m, 3.9.1990. Leg.: K. Nielsen. Scale 1 cm.


B: *Stictyosiphon soriferus*. Part of alga with opposite branches (upper arrow) and narrow apex (lower arrow). Scale 1 mm. B-D: Alsund, 4.6 m, 9.06.2009. Photo by S. Lundsteen.


C: *Stictyosiphon soriferus*. Spherical medullary cells surrounded by a single layer of small cortical cells. Optical longitudinal section. Scale 100 µm.


D: *Stictyosiphon soriferus*. Unilocular sporangia among surface cells. Scale 200 µm.




E: *Stictyosiphon soriferus*. Plurilocular sporangia developed from surface cells. Rehydrated herbarium material. Rønnerne, Frederikshavn, drift, 24.6.1987. Scale 100 µm.

**Reproduction:** Plurilocular sporangia develop from surface cells. They occur between the surface cells of the parenchyma, may be intercalary in the uniseriate part of the thallus, and have a protruding outer cell wall. Sporangia are scattered but may occur in confluent spots. Unilocular sporangia, which are seldom observed, are rounded and form from scattered surface cells.

**Seasonal variation:** Collected in April-August. Plurilocular sporangia recorded in April-August and unilocular sporangia in April and June.

**Habitat:** Epiphytic on larger algae, on Common Whelk (*Buccinum undatum*), hydroids, wood and stone. In shallow water and collected by divers to 11.5 m depth and by dredge at 37.5 m depth.

**References:** Kornmann & Sahling (1977), Kylin (1947, *Stictyosiphon subarticulatus*), Rosenvinge (1935), Rueness (1977).

# *Stictyosiphon tortilis*

**(Gobi) Reinke**

Winding Broom Weed

**Appearance:** Much branched dark brown bushy thalli, typically 20-32 cm in height, but can be up to 50 cm. Branches are terete with scattered, seldom opposite, branches on all sides. In the lower part the branches are often few and short, whereas in the upper part, there are many longer branches which gives the alga a broom-like outline. Upright thalli arise from a compact crustose base, often several together.

**Structure:** Young uprights are uniseriate filaments and become parenchymatous by development of longitudinal cell divisions. The medulla consists of four filaments of elongate cylindrical cells that is surrounded by a cortex of small cells in a single layer or two layers. Surface cells contain several disc-shaped plastids. The apex is uniseriate and terminates in a true brown algal hair, often with a pair of opposite hairs or a whorl of hairs just below.

**Reproduction:** Plurilocular sporangia occur scattered among the surface cells. They are slightly protruding and reminiscent of unilocular sporangia, because the separating walls between the compartments are very thin. Culture studies showed a direct life history, swarmers germinated and developed into creeping confluent filaments from which new upright thalli arose.

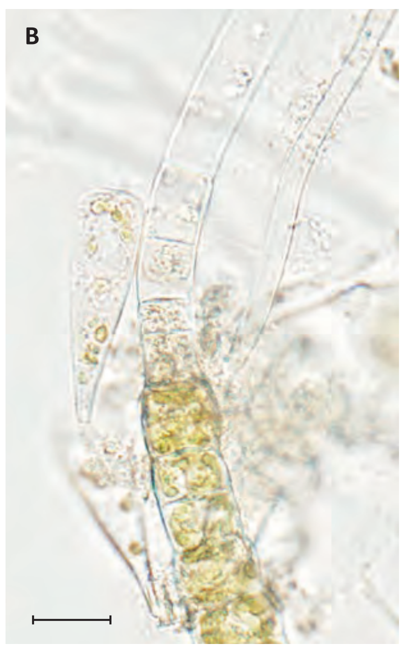
**Seasonal variation:** Occurs all year, best developed in early summer. Collected in January and March-September. Plurilocular sporangia recorded in January and April-September.

**Habitat:** On stone and mollusc shells, including Common Pelican's Foot (*Aporrhais pespelecani*). In shallow water and collected by divers to 15 m depth, and by dredge to 24.5 m depth at Bornholm.

**Resembles:** Similar in appearance to Tubular Net Weed (*Dictyosiphon foeniculaceus*), where branches have an apical cell, not a terminal hair.

**References:** Kylin (1947), Rosenvinge (1935), Rueness (1977).


A: *Stictyosiphon tortilis.* Upright thallus, most branches in the upper part. Deget, Frederikshavn, 2 m, 22.6.1974. Scale 2 cm.




B: *Stictyosiphon tortilis.* Uniseriate apex with terminal true brown algal hair. Scale 10 µm. B-C: Sjællands Odde, 0.5 m, 24.4.2017.


C: *Stictyosiphon tortilis.* Terete parenchyma with true brown algal hair, vegetative cells with several plastids. Scale 10 µm.

## *Stilopsis lejolisii*

**(Thuret) Kuckuck & Nienburg ex Hamel**

Pointed Fork Weed

**Appearance:** Terete, pseudodichotomously branched, hollow alga, up to 20 cm in height. Branches, up to 0.5 mm in width decreasing towards the apex. They are brown to yellow-brown when dried on herbarium sheets.

**Structure:** Syntagma with a central filament, which is visible at the apex of young branches. Primary assimilating filaments develop from the cells of the central filament. They are in whorls, closely branched and cover the central filament as a thick cell layer. Older branches have relatively large cells in the inner part and a surface of short confluent filaments, 1-2 cells long, of small assimilating cells. These short filaments arise from the basal cells of the primary assimilating filaments which stretches simultaneous with the longitudinal growth of the thallus. True brown algal hairs occur among assimilating filaments and in sporangial sori.

A

A: *Stilopsis lejolisii.* Bush-like alga of terete dichotomous branches, which become narrow towards the apex. Mullerne, Nissum Bredning, 5 m, 26.7.1905. Leg. & det.: Rosenvinge. Scale 2 cm.

B: *Stilopsis lejolisii.* Pseudodichotomously branched apical part. Uniaxial syntagma, central axial cells (arrow) surrounded by branches of primary assimilating filaments. Large medullary cells further down in the branch. Surface of short assimilating cells and true brown algal hairs. After Kuckuck (1930). Scale 20 µm.

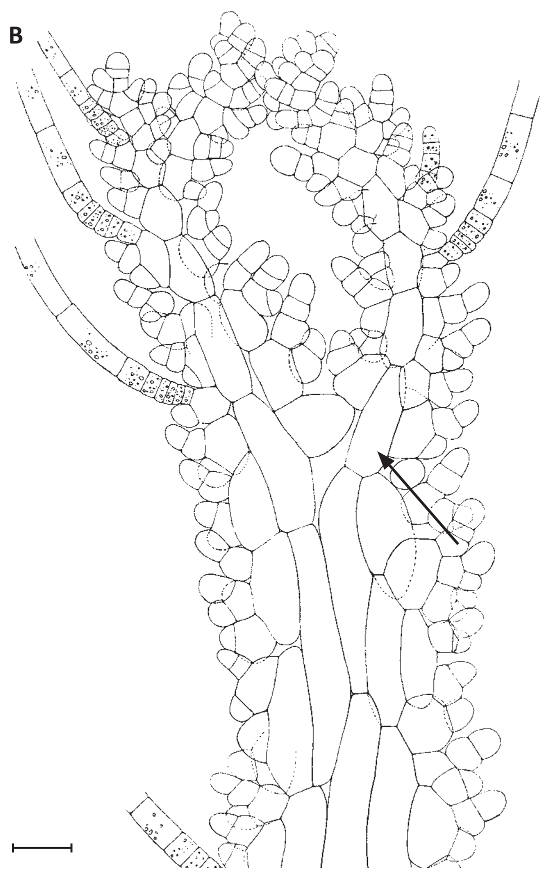
**Reproduction:** Unilocular sporangia occur in well-defined sori on the surface together with secondary assimilating filaments (paraphyses) and true brown algal hairs. Paraphyses are unbranched or branched, club-shaped, straight or slightly curved and consist of 4-6 cells, with long thin cells at the lower part and swollen cells in the upper part. Unilocular sporangia are obovate, pyriform or ellipsoid, and arise from the base of paraphyses. Uniseriate plurilocular sporangia are reported to occur on separate individuals from those with unilocular sporangia, but not recorded in the alga from Danish waters.

**Seasonal variation:** Collected in July-August with unilocular sporangia.

**Habitat:** Epiphytic on Serrated Wrack (*Fucus serratus*), 3-5 m depth.

**References:** Kuckuck (1930), Kylin (1940), Rosenvinge & Lund (1943).

B



## *Streblonema*

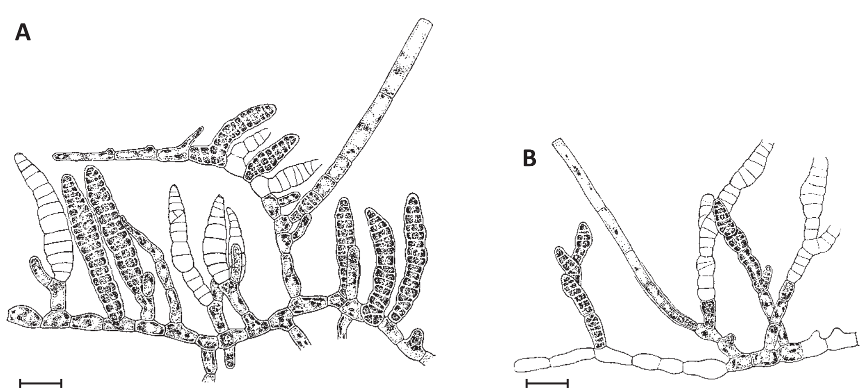
Microscopic epi- or endophytic uniseriate filaments with scattered branches were commonly referred to *Streblonema* but recently, most have been transferred to other genera or their identity as microthalli of larger algae revealed. Rosenvinge & Lund (1941) mentioned six species of *Streblonema* from Danish waters. Among these, *S. infestans* (Gran) Batters was transferred to *Endodictyon infestans, S. tenuissimum* Hauck to *Microspongium stilophorae* and *S. aequale* is considered a morphological variant of *Phaeostroma pustulosum*. *Streblonema effusum* is considered to be the microthallus of *Punctaria tenuissima*. The alga Rosenvinge & Lund (1941) mention as *S. thuretii* (?) from Danish waters, was described as *S. danicum* by Kylin (1947), but today is considered to be the microthallus of *Litosiphon laminariae*. *Streblonema fasciculatum*, the only one left in the genus that is found in Denmark, occurs in Sea Noodle Worm Weed (*Nemalion multifidum*). Rosenvinge & Lund (1941) also mention a *Streblonema* sp. from this same host alga, which is also *S. fasciculatum* according to Kuckuck (1954). These small brown algae are seldom recorded and our knowledge of their occurrence and distribution is therefore limited.

**References:** Guiry in Guiry & Guiry (2021), Kuckuck (1954, *Streblonema*, *Pilocladus*), Kylin (1907, 1947, *Streblonema, Entonema*), Pedersen (1984, 2011), Rosenvinge & Lund (1941), Rueness (1977).

## *Streblonema fasciculatum*

### Thuret

**Appearance:** Microscopic, endophytic filaments.
**Structure:** Creeping filaments with scattered branches, with few-celled upright filaments and brown algal hairs, occasionally with sheath. Vegetative cells are cylindrical or slightly swollen. Each cell contains several disc-shaped plastids.
**Reproduction:** Upright plurilocular sporangia are uni- or multiseriate with c. 20 layers of compartments. They are sessile on the creeping filaments or have a short upright stalk. Plurilocular sporangia are cylindrical or elongate lanceolate and may have short branches.
**Seasonal variation:** Collected in August-September and November.
**Habitat:** Among assimilating filaments of Sea Noodle Worm Weed (*Nemalion multifidum*) in shallow water and reported in other soft algae such as Slimy Wormweed (*Mesogloia vermiculata*), Brown Jelly Weed (*Eudesme virescens*) by Kuckuck (1954) and Slimy Whip Weed *Chordaria flagelliformis* by Pedersen (2011).
**Comment:** The species has brown algal hairs with sheath and according to Pedersen (2011), therefore belongs into the genus *Hecatonema*.
**References:** Kuckuck (1954), Pedersen (2011), Rosenvinge & Lund (1941, *S. fasciculatum* and *Streblonema* sp.).




A: *Streblonema fasciculatum*. Creeping filaments with upright plurilocular sporangia and true brown algal hair. Scale 20 µm. A-B: After Rosenvinge & Lund (1941).

B: *Streblonema fasciculatum*. Brown algal hair with sheath and branched plurilocular sporangia. Scale 20 µm.

## *Striaria attenuata*

**(Greville) Greville**

Striped Branched Weed

**Appearance:** Yellow-brown bush-like thalli of terete branches, typically 7-18 cm in height, but may be up to 45 cm. Distinct main branch has scattered, or opposite branches on all sides, rarely in a whorl. Branches, 0.5-1 (-2) mm in width, slightly constricted at base and gradually terminating in a long thread-like top. Sporangial sori are typically in whorls, appearing as dark transverse stripes on the branches.

**Structure:** Young upright thalli are uniseriate with a terminal true brown algal hair. Parenchyma of several cell layers are later formed by longitudinal and transverse cell divisions. Medulla of large rounded colourless cells is surrounded by a layer of small assimilating cells. Older thalli are hollow.

**Reproduction:** Unilocular sporangia develop on the surface cells, are obovate or almost spherical and form sori with unicellular paraphyses and true brown algal hairs.

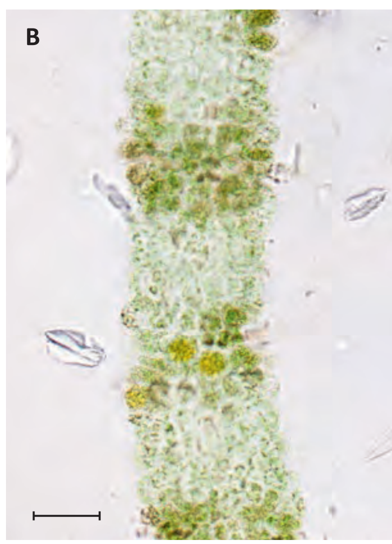
**Seasonal variation:** Collected in April-August and November. Unilocular sporangia recorded in April and June-August.

**Habitat:** On stone and epiphytic on other algae, collected by divers to 15 m depth and by dredge, 2-27 m depth.

**Comment:** Culture studies of the alga from Denmark, France, Helgoland and the Swedish west coast showed that swarmers from unilocular sporangia germinated and developed into microthalli. The microthallus consisted of creeping filaments, which might develop into small crusts. Uni- or plurilocular sporangia were reported on the microthallus and in some cases new upright thalli also. Sexual reproduction was only observed in the alga from France. Pedersen (1984) included a summary of these studies and confirmed the results with culture studies of the alga from Danish waters. Peters (1991) found sexual reproduction in microthalli of *S. attenuata* from Chile.

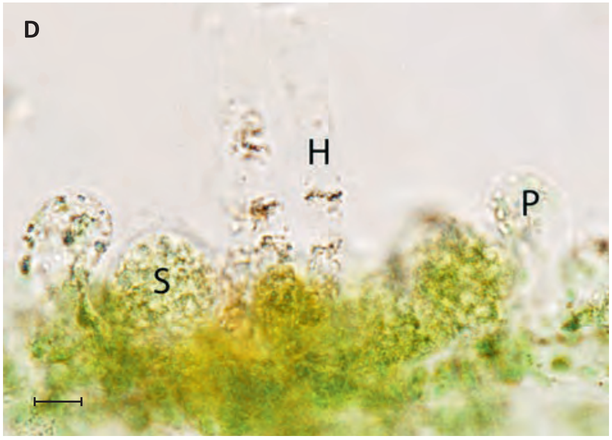
**References:** Caram (1965, 1966), Caram & Nygren (1970), Kornmann & Sahling (1973), Nygren (1975a, b), Pedersen (1984), Peters (1991), Rosenvinge & Lund (1947).


A: *Striaria attenuata*. Bush-like alga of terete branches, terminating in thin thread-like apices. Main branch with scattered and a few opposite branches. Rønnerne, Frederikshavn, drift, 19.6.1998. Scale 2 cm.




B: *Striaria attenuata*. Parenchymatous surface with stripes of sporangial sori. Scale 50 µm. B-D: Rygård Strand, 1 m, 23.6.1992.


C: *Striaria attenuata*. Large rounded medullary cells surrounded by a layer of small assimilating surface cells. Scale 10 µm.




D: *Striaria attenuata*. Sorus with spherical unilocular sporangia (S), unicellular paraphyses (P) and true brown algal hair (H). Scale 10 µm.

## *Trachynema mortensenii*

**(S.Lund) P.M.Pedersen**

**Appearance:** Terete, compact unbranched threads, c. 150 µm in width; in Greenland up to 2 cm in height (Lund 1959). The top is rounded and the basal part slightly pointed.

**Structure:** Parenchyma initiated as a uniseriate filament with a terminal brown algal hair with sheath (Pedersen 1985). Growth is diffuse and parenchyma develop by longitudinal cell divisions. Cortex of angular surface cells, slightly swollen and with a thick outer wall and internal larger cells. Surface cells contain several plastids. Scattered or opposite brown algal hairs with sheath, present in the area of division in the uniseriate filaments.

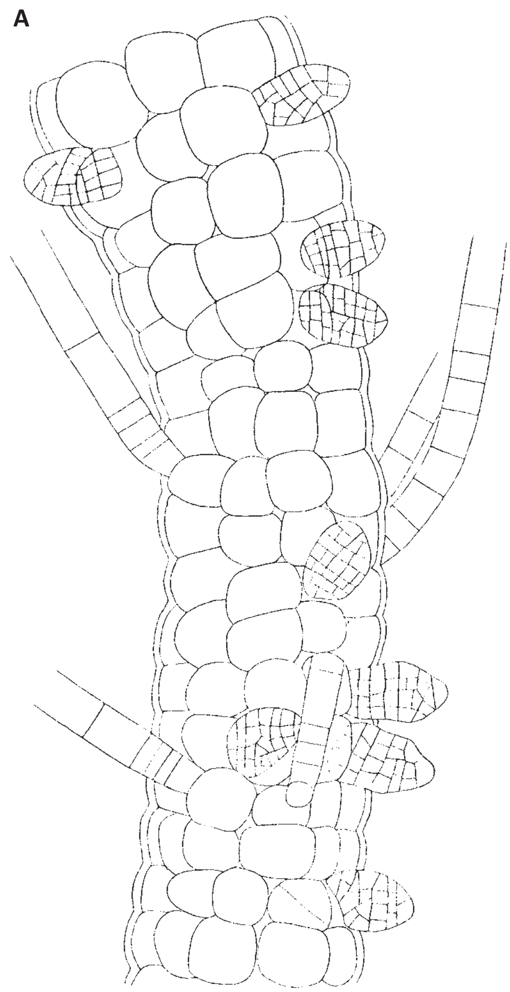
**Reproduction:** Plurilocular sporangia develop from surface cells. They are ellipsoid or conical, 29-33 µm long and 25-29 µm in width. They are scattered or in groups and protrude from the surface for most of their length.

**Habitat:** Only a single collection from Danish waters, Vodstrup hage, the Limfjord, 1895.

**Resembles:** Kelp Thread (*Litosiphon laminariae*) appears similar but has true brown algal hairs without sheath and plurilocular sporangia in level with the surface.

**Comment:** Culture studies of the alga from Greenland showed swarmers from plurilocular sporangia to germinate and develop into a filamentous microthallus. It had brown algal hairs with sheath and elongate conical plurilocular sporangia. Upright thalli arose from the microthallus. Sexual reproduction was not observed. The microthallus was reminiscent of Hundred Thread Weed (*Hecatonema*).

**References:** Lund (1959), Pedersen (1985, 2011), Rosenvinge & Lund (1947, *Litosiphon* sp.).




A: *Trachynema mortensenii*. Upright thallus with plurilocular sporangia and brown algal hairs (sheaths not illustrated). Vodstrup Hage, 15.5.1895. After Rosenvinge & Lund (1947). Scale 50 µm.

# *Ulonema rhizophorum*
## Foslie

**Appearance:** Microscopic epiphytic filaments which form light brown spots, up to 1 mm in diameter.
**Structure:** Creeping filaments with scattered branches, which are more or less confluent in monostromatic discs. Mutually free short upright filaments arise from the central cells, together with brown algal hairs with sheath and sporangia. Upright filaments are uniseriate, cylindrical or slightly club-shaped, up to 7 cells long, with cells, 1-4 times as long as wide. Branches of 1-3 cells may occur. Cells contain 1-3 disc-shaped plastids with pyrenoids. Rhizoids, which grow into the host alga, develop on the underside of the cells in the creeping filaments. Rhizoids are uni- or multicellular, uniseriate and sometimes branched.
**Reproduction:** Unilocular sporangia are upright on the creeping filaments or lateral on the lower part of upright filaments. They are spherical or pyriform, sessile or have a unicellular stalk. Plurilocular sporangia are uniseriate, but rare.
**Habitat:** On Dumont's Tubular Weed (*Dumontia contorta*). There is only a single collection from Danish waters in the algal herbarium, Natural History Museum of Denmark.
**Seasonal variation:** Collected in June.
**Comment:** The description above is based on information from the literature and must be verified with new collections of the alga in Danish waters. The status of the species is uncertain, it is included in *Myrionema strangulans* by some authors while others (Fletcher, 1987) retain it as a separate genus and species.
**References:** Fletcher (1987), Foslie (1894), Jaasund (1951, 1965).

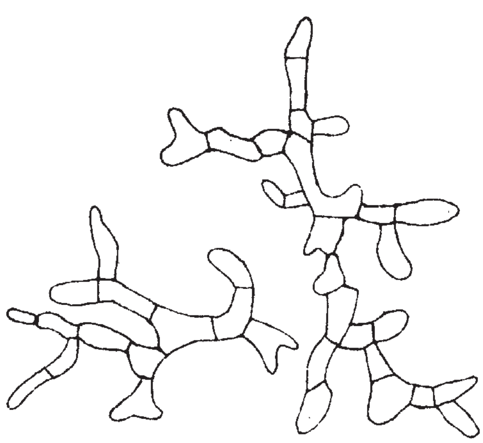
A

A: *Ulonema rhizophorum*. Brown spots (arrow) on Dumont's Tubular Weed (*Dumontia contorta*). Bastholm, 15.6.1922. Leg. et det.: Rosenvinge. Scale 2 cm.

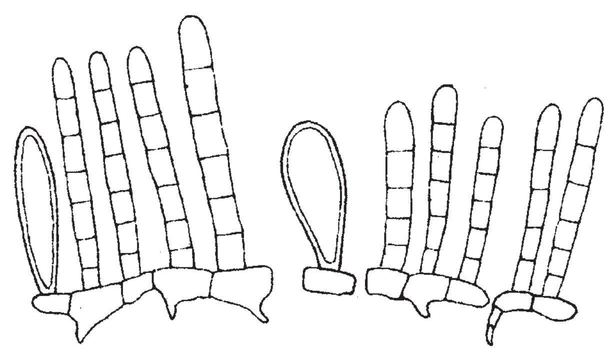
B: *Ulonema rhizophorum*. Creeping branched filaments. B-C: After Foslie (1894).

C: *Ulonema rhizophorum*. Creeping filaments with short rhizoids, upright unbranched filaments and unilocular sporangia.

B



C



## Family: Ectocarpaceae

### *Ectocarpus*

Cotton Wool Weeds

**Appearance:** Much branched bush-like alga of thin, mutually free filaments with branches on all sides.
**Structure:** Uniseriate filaments with diffuse growth. Upright filaments arise from a basal system of creeping, uniseriate, branched filaments. The main branch is repeatedly pseudodichotomously branched with scattered branches on all sides. Cells are cylindrical, and elongate towards the end of branches, becoming relatively long, narrow and pale (false hairs). True brown algal hairs do not occur. Vegetative cells contain several ribbon-shaped, often branched plastids with many pyrenoids, which are visible as clear spots. Rhizoids may arise from the lower cells in the main branches and contribute to the attachment of the alga.
**Reproduction:** Uni- or plurilocular sporangia occur on the same or different thalli. They are sessile or on a short stalk. Plurilocular sporangia have many small compartments, each with a swarmer. They are evacuated through an apical papilla at maturity, after the walls between the individual compartments are dissolved and swarmers slide out through the middle of the sporangium. Unilocular sporangia are ellipsoid or ovoid. Swarmers from plurilocular and unilocular sporangia are isomorphic and of the typical brown algal kind with lateral flagella and a red eyespot. The life history in *Ectocarpus* has been investigated in numerous culture studies of isolates from different parts of the world (Maier & Müller, 1986, Müller, 1975, 1977). More or less isomorphic haploid gametophytes (n), diploid sporophytes (2n) and individuals with higher ploidy-levels were found. Both sexual and vegetative propagation were observed. In plurilocular sporangia, only mitotic divisions took place and swarmers were either vegetative (zoospores) or sexual (gametes). During sexual reproduction female gametes are at first attached to the substratum and attract male gametes chemically by a special pheromone (ectocarpin). Meiosis takes place in unilocular sporangia, but not always. When it happens, meiosis starts the process followed by several vegetative (mitotic) divisions. At maturity swarmers are released through a small exit pore in the upper part of the sporangium and act as zoospores.
**Comment:** Morphological variation is large, and species discrimination not always easy. Rosenvinge & Lund (1941) mentioned *E. confervoides*, *E. fasciculatus* and *E. draparnaldioides* as well as species which were later transferred into other genera. The relationships of some of the forms, which Rosenvinge & Lund (1941) referred to *E. confervoides*, are questionable and have to be solved by future investigations including molecular studies.

The name *E. confervoides* was originally introduced with reference to *E. siliculosus*, and therefore superfluous (Silva in Silva et al., 1996). In checklists of algae in Danish waters (Christensen et al., 1985, Nielsen, 2005) species of *Ectocarpus* were referred to *E. siliculosus* or *E. fasciculatus* in agreement with studies of Russell (1966). In the algal flora of Korea (Kim 2010) Danish algae are mentioned, and *E. penicillatus* accepted as a separate species.
**References:** Christensen et al. (1985), Kim (2010), Kornmann & Sahling (1977), Kristiansen (1972), Maier & Müller (1986), Müller (1975, 1977), Müller & Eichenberger (1995), Nielsen (2005), Rosenvinge & Lund (1941), Russell (1966), Silva in Silva et al. (1996).

**Identification key to species of *Ectocarpus***

| | | |
|---|---|---|
| 1a. | Main branches with a gradual transition to lateral branches and much pseudodichotomous branching | 2 |
| 1b. | Main branches distinct and wider than lateral branches, which form fascicles in the upper part of the alga | *E. fasciculatus* |
| 2a. | Plurilocular sporangia, cone-shaped without terminal hair | *E. penicillatus* |
| 2b. | Plurilocular sporangia, elongate cone-shaped with terminal hair | *E. siliculosus* |

## *Ectocarpus fasciculatus*

### Harvey

Clustered Cotton Wool Weed

**Appearance:** Bush-like brown or dark brown thalli of thin, mutually free, filaments with branches on all sides, 3-12 cm in height. Branches may be loosely twisted and in the upper part of the thallus typically appear in small tufts.

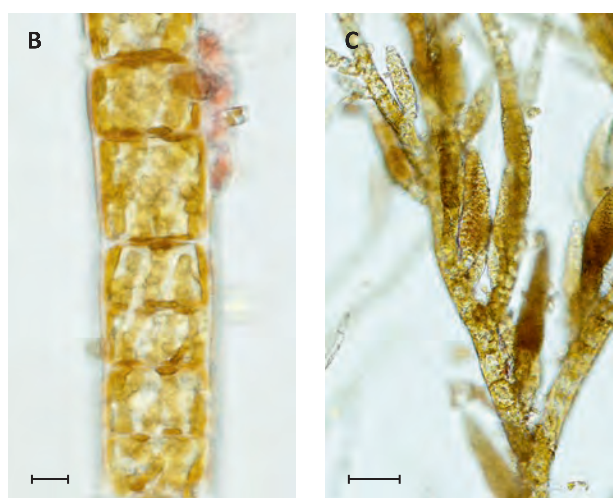
**Structure:** Uniseriate, scattered branched filaments with distinct main branches, broader than lateral branches. Most of the lateral branches are typically close together in the upper end of main branches and appear as fascicles of branches. Main branches, 30-60 (75) µm in width, are covered by numerous rhizoidal filaments in the lower part. Cells are only slightly longer than wide, and contain several more or less branched, ribbon-shaped plastids per cell.


**Reproduction:** Plurilocular sporangia are numerous on the upper side of branches and typically without apical hairs. They are elongate ovoid to conical, 30-130 µm long and 14-37 µm wide, but occasionally up to 200-225 µm long and narrow. Unilocular sporangia are ellipsoid to ovoid, 25-50 µm long and 25-37 µm wide. They occur on the same individual as the plurilocular sporangia, and often between these. Sporangia have a short stalk, are sessile or have longer stalks.

**Seasonal variation:** Probably present all year, recorded in March-October, plurilocular sporangia in May-October and unilocular sporangia in May, July and August.

**Habitat:** Common in shallow water at exposed localities, on boulders and epiphytic on larger algae. Collected by divers to 14.5 m depth.

**References:** Müller (1972), Pedersen (2011), Rosenvinge & Lund (1941).



A: *Ectocarpus fasciculatus*. Dark brown bush-like individuals, lateral branches in upper part close together. On Black Siphon Weed (*Vertebrata fucoides*), Hirsholm, 29.6.1988. Scale 2 cm.

B: *Ectocarpus fasciculatus*. Branch with diffuse growth (cells of unequal length); vegetative cells with ribbon-shaped plastids and many pyrenoids. Scale 10 µm. B-D: Gilleleje, 0.5 m, 29.5.2014.

C: *Ectocarpus fasciculatus*. Plurilocular sporangia. Scale 50 µm.

D: *Ectocarpus fasciculatus*. Main branches and branches which are close together and terminate in false hairs. Scale 100 µm.


## *Ectocarpus penicillatus*

**(C.Agardh) Kjellman**

Artist's Brush Cotton Wool Weed

**Appearance:** Brown to yellow-brown bush-like alga of thin mutually free filaments with branches on all sides, 4-10 cm in height. May also form large, loose cotton-like masses.

**Structure:** Uniseriate filaments with pseudodichotomously branched main branches, with scattered and relatively long lateral branches. The width of branches gradually decreases into a terminal false hair. In very exposed localities the branches may be uniseriate and form fascicles in the upper part of the thallus. Vegetative cells contain few, more or less branched, ribbonshaped plastids with pyrenoids.

**Reproduction:** Plurilocular sporangia typically have a short stalk but are occasionally sessile or have a longer stalk. They are elongate conical, but may be relatively short and wide, 75-150 µm long and 20-30 µm wide. Unilocular sporangia are ellipsoid to ovoid, 40-60 µm long and 25-40 µm wide.

**Seasonal variation:** Present all year, but best developed in April-September. Plurilocular sporangia recorded in April-November and unilocular sporangia in May-June, and August-September.

**Habitat:** Epiphytic on various larger algae. Also drifting as large cotton-like "clouds" in sheltered nutrient-rich localities, typically together with Pylaie's Brown Filaments (*Pylaiella littoralis*). Common in shallow water, collected by divers to 18 m depth and by dredge to 31 m depth.

**Comment:** The species includes the alga which Rosenvinge & Lund (1941) referred to *E. confervoides* f. *penicillatus* according to Kim (2010). Algae mentioned by Rosenvinge & Lund (1941) as *E. confervoides* f. *typica*, f. *arcta* and f. *dasycarpa,* probably also belong to *E. penicillatus*.

**References:** Kim (2010), Rosenvinge & Lund (1941, *E. confervoides* f. *penicillatus*), Wærn (1952, *E. confervoides*).



A: *Ectocarpus penicillatus*. Bush-like alga of thin branched filaments. Jegens Odde, Læsø, 6.5 m, 23.5.1988. Scale 2 cm.

B: *Ectocarpus penicillatus*. Scattered and pseudodichotomous branches (arrow). Many plurilocular sporangia. Scale 50 µm. B-C, E: Bovet, Læsø, drift, 28.4.2016.




C: *Ectocarpus penicillatus*. Vegetative cells with ribbon-shaped plastids, drop-shaped pyrenoids (arrow). Scale 10 µm.

D: *Ectocarpus penicillatus*. Unilocular sporangium. Beach north of Vesterø Havn, Læsø, drift, 5.6.2017. Scale 10 µm.

E: *Ectocarpus penicillatus*. Plurilocular sporangium, being emptied. Scale 10 µm.

# *Ectocarpus siliculosus*

**(Dillwyn) Lyngbye**

Fluffy Cotton Wool Weed

**Appearance:** Brown to yellow-brown bush-like alga of thin mutually free filaments, with branches on all sides, 10-12 cm in height.

**Structure:** Uniseriate filaments are pseudodichotomously branched and gradually decrease in width towards the top. Main branches 40-70 µm in width and in the lower part often covered by rhizoids. Scattered branches on all sides are relatively long and terminate in false hairs.

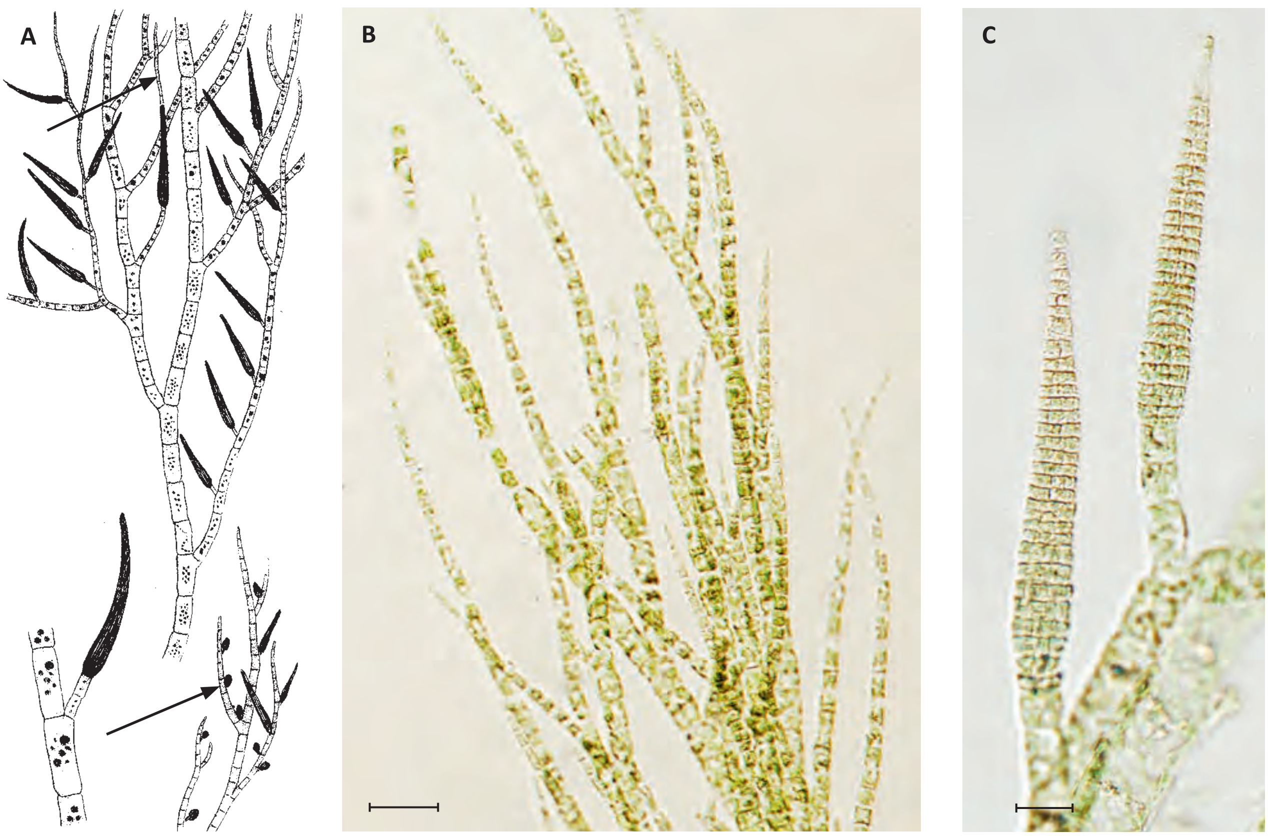
**Reproduction:** Plurilocular sporangia are elongate and develop in the outer part of branches. They are 85-120 µm long and 23-33 µm wide and terminate in a false hair or a hair-like apex.

**Seasonal variation:** Collected in June-July with plurilocular sporangia.

**Habitat:** Epiphytic on various larger algae.

**Comment:** *Ectocarpus siliculosus* is similar to the alga, mentioned as *E. draparnaldioides* by Rosenvinge & Lund (1941, fig. 14D), according to Kim (2010). *Ectocarpus confervoides* f. *siliculosus* and f. *hiemalis* are mentioned by Rosenvinge & Lund (1941) with plurilocular sporangia, which may have a terminal false hair. Therefore, these algae probably also belong in *E. siliculosus*.

**References:** Kim (2010), Lyngbye (1819), Rosenvinge & Lund (1941).




A: *Ectocarpus siliculosus*. Specimens with pseudodichotomous and scattered branches and plurilocular sporangia, one terminating in a false hair (upper arrow); in the lower drawing, unilocular sporangia (lower arrow). After Lyngbye (1819).

B: *Ectocarpus siliculosus*. Apex of narrow branches, terminating in false hairs. Scale 50 µm. B-C: Læsø Trindel, 14.5 m, 4.6.1993.

C: *Ectocarpus siliculosus*. Narrow plurilocular sporangia with few vegetative cells at the apex. Scale 20 µm.

# *Spongonema tomentosum*

**(Hudson) Kützing**

Lamb's Tails

**Appearance:** Thalli resembling brown strings which are branched a few times, 5-7 cm long.

**Structure:** Mutually free uniseriate filaments with scattered branches on all sides. Lateral branches are short and often arise perpendicularly to the main branch. Filaments in longitudinal direction are twisted and may have thin loosely attached rhizoids in the lower parts. Some of the lateral branches are typically hook-shaped and contribute to keeping the filaments together. Filaments are (7-) 8-9.5 (-11) µm in width and often terminate in false hairs. Cylindrical cells are 1.5-2 times as long as wide and contain 1-2 plastids with few pyrenoids.

**Reproduction:** Plurilocular sporangia are elongate ellipsoid and slightly conical. They are sessile on the short branches or on a stalk of 1 or 2 cells. They may also be intercalary in the branches according to Rosenvinge & Lund (1941) and Kuckuck (1960). Unilocular sporangia recorded occasionally, mainly on individuals which also have plurilocular sporangia. Unilocular sporangia are ovoid, sessile or have a short typically unicellular stalk.

**Seasonal variation:** Collected in April-September and December, always with plurilocular sporangia. Unilocular sporangia recorded in March, April and June.

**Habitat:** Epiphytic on Bladder Wrack (*Fucus vesiculosus*) and once observed on Chipolata Weed (*Scytosiphon lomentaria*) and on boulders, 0.5-2 m depth.

**References:** Kornmann & Sahling (1977), Kuckuck (1960), Rosenvinge & Lund (1941, *Ectocarpus tomentosus*), Stegenga & Mol (1983).


A: *Spongonema tomentosum.* Alga of entangled thin filaments, looking like a branched string. At the ferry berth, Vesterø Havn, Læsø, 0.2 m, 2.7.2008. Scale 2 cm.

B: *Spongonema tomentosum.* Entangled thin filaments with short, curved branches. Scale 20 µm. B-E: Northeastern part of Refshaleøen, Copenhagen, 0.2 m, 21.9.2007.

C: *Spongonema tomentosum.* Hook-shaped branch. Scale 10 µm.

D: *Spongonema tomentosum.* Plurilocular sporangium on a stalk of two cells. Scale 10 µm.

E: *Spongonema tomentosum.* Empty plurilocular sporangium on unicellular stalk. Vegetative cells with 1-2 plastids with pyrenoids. Scale 10 µm.




## Family: Scytosiphonaceae

# *Colpomenia peregrina*

**Sauvageau**

Oyster Thief

**Appearance:** Yellow-brown almost spherical, irregular lumpy or sac-shaped hollow thallus, typically, 2-5 cm in width but can be up to 15 cm. Surface compact, not very smooth.

**Structure:** Multi-layered parenchyma surrounds a cavity. The medulla consists of 3-4 cell layers of colourless rounded cells that are smaller outwards. The cortex consists of 1-2 cell layers of small angular cells. Each of them contains a disc-shaped plastid with one pyrenoid. Scattered between the surface cells are small pits with tufts of true brown algal hairs, which arise from pale cells below the cortex. Thalli are attached by rhizoids, which arise from the cortex. Young thalli develop from creeping filaments and are compact before the cavity develops.

**Reproduction:** Plurilocular sporangia form spots (sori) at the surface and may be confluent to form larger areas. Plurilocular sporangia are cylindrical, 20-35 µm in height, uni- or biseriate. Large unicellular ascocysts may occur between the sporangia. Ascocysts are almost colourless when fresh and when preserved in alcohol but become dark brown in dried or formaldehyde-preserved specimens. Culture studies of Oyster Thief (*C. peregrina*) in western Europe showed a direct life history. Swarmers germinated and grew into a filamentous microthallus from which upright thalli developed under specific conditions of temperature and daylength. A crustose stage with unilocular sporangia was observed both in nature and by culture studies in Japan, and sexual reproduction between swarmers from dioecious sac-shaped gametophytes was noted (Kogame & Yamagishi, 1997).

**Seasonal variation:** Collected in January and April-November. Plurilocular sporangia recorded in July-August, October and January.

**Habitat:** On stone and epiphytic on larger algae, 0-3.5 m depth.

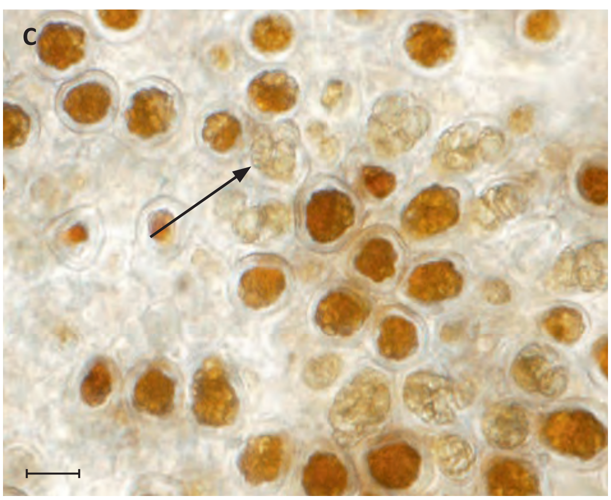
**Resembles:** Appears similar to Punctured Ball Weed (*Leathesia marina*), but that is cartilaginous and smooth with a surface of assimilating filaments, while Oyster Thief (*C. peregrina*) is hollow and parenchymatous with a surface of small angular cells.

**Comment:** First record in Danish waters in the western part of the Limfjord, 1939, other observations in Danish waters only in the Northern Kattegat where it was first observed in 1967.

**References:** Fletcher (1987), Kogame & Yamagishi (1997), Lund (1945), Rosenvinge & Lund (1947).


A: *Colpomenia peregrina* On stone (arrow), dry at low water, together with Chipolata Weed (*Scytosiphon lomentaria*) and Edible Periwinkle (*Littorina littorea*). Tile works, Helligsø, 0 m, 20.7.1996.


B: *Colpomenia peregrina*. On Bladder Wrack (*Fucus vesiculosus*). Hirsholm, 0.5 m, 24.7.1974. Scale 2 cm.




C: *Colpomenia peregrina*. Plurilocular sporangia (arrow) and brown ascosysts, surface view. Scale 10 µm. C-D: Beach south of Vesterø Havn, Læsø, drift, 29.7.2014.


D: *Colpomenia peregrina*. Large pale medullary cells, cortex of small cells with sori of plurilocular sporangia (arrow) and brown ascocysts. Transverse section. Scale 10 µm.

# *Compsonema saxicola*

**(Kuckuck) Kornmann in Kuckuck**

Stone Thread Weed

**Appearance:** Microscopic covering of creeping filaments.

**Structure:** Creeping filaments are more or less confluent and occasionally form a disc in which the basal layer becomes distromatic by longitudinal cell divisions. Upright, short unbranched filaments, unequal in height and mutually free, arise from the basal layer. Vegetative cells contain a parietal lobed plastid with pyrenoid. True brown algal hairs between the upright filaments, also arise from the basal layer.

**Reproduction:** Unilocular sporangia develop from the basal layer. They are spherical to obovate or pyriform, sessile or have a stalk cell. Plurilocular sporangia not known.

**Seasonal variation:** Collected in May and July.

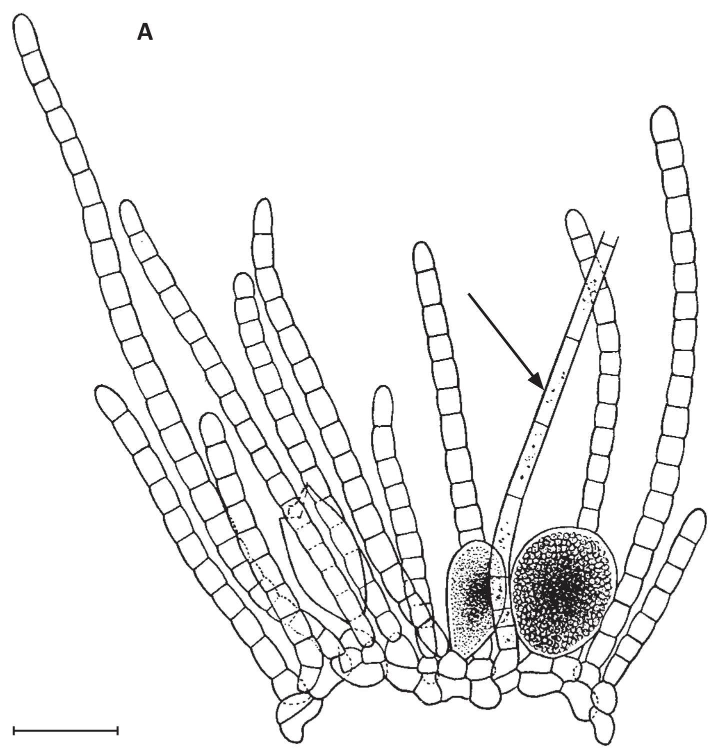
**Habitat:** Collections from Danish waters, 0.2 and 8 m depth. At Helgoland growths of *C. saxicola* on stone in shallow water, with unilocular sporangia in September-December (Kuckuck 1953).

**Comment:** In culture studies of *C. saxicola* from Danish waters, germinated swarmers from unilocular sporangia developed uniseriate filaments (Pedersen, 1981a). Parenchymatous areas were observed after longitudinal cell divisions. Unilocular sporangia formed in these areas and the process continued for several generations.

In other culture studies, uprights arose from creeping filaments. Fletcher (1987) found that they were similar to Leaf Weed (*Petalonia*) or Chipolata Weed (*Scytosiphon*). Pedersen (1981a) referred *C. saxicola* to Scytosiphonaceae. This relationship was confirmed for the type species *C. minutum* (C.Agardh) Kuckuck by Pedersen & Sokhi (1990). In Japan, Kogame & Kawai (1993) found that they resembled Flat Grass Leaf Weed (*Planosiphon zosterifolius*, as *Petalonia zosterifolia*).

Silberfeld et al. (2014) supposed that the genus *Compsonema* was polyphyletic and referred it to Chordariaceae.

**References:** Fletcher (1987), Kogame & Kawai (1993), Kuckuck (1953), Pedersen (1981a), Pedersen & Sokhi (1990), Silberfeld et al. (2014).




A: *Compsonema saxicola.* Creeping filaments, which form a distromatic basal system. Mutually free upright filaments, true brown algal hair (arrow) and unilocular sporangia. After Kuckuck (1953). Scale 50 µm.

# *Petalonia fascia*

**(O.F.Müller) Kuntze**

Broad Leaf Weed

**Appearance:** Flat yellow-brown to dark brown compact unbranched blades, typically ribbon-shaped and occasionally broad ellipsoid, 10-20 (-24) cm in height and 1-4 (-7) cm in width. Blades, which expand from a basal crust and slender stipe, are occasionally twisted or have an undulate margin. Several upright blades often arise from the same basal crust.

**Structure:** Solid parenchyma with a medulla of large colourless cells in 3-6 layers. The cortex consists of 1-3 layers of small angular to rectangular cells, which may form rows in the longitudinal direction of the blade. Each surface cell has a single plastid with one pyrenoid. True brown algal hairs are rare but occasionally occur scattered or in groups, no sheath.

**Reproduction:** Plurilocular sporangia develop from surface cells and gradually cover the entire blade. They are cylindrical, uni- or biseriate, up to 60 µm in height. There are no paraphyses. Upright thalli are gametophytes, which alternate with a crustose sporophyte. Culture studies of the alga from Japan, documented that swarmers from plurilocular sporangia might be sexual, they germinated without or after copulation. In both cases after germination, crustose thalli with unilocular sporangia developed. The swarmers from the unilocular sporangia germinated and developed into upright thalli with plurilocular sporangia or into new crustose thalli with unilocular sporangia (Kogame, 1997). The crustose phase was previously known as *Stragularia clavata* (Harvey in Hooker) Hamel.

**Seasonal variation:** Collected all year with plurilocular sporangia.

**Habitat:** On stone, boulders, Acorn Barnacles (*Semibalanus balanoides*) and Blue Mussel (*Mytilus edulis*). Dense crops in shallow water, 0-1 m depth, few collections by dredge, 3-5 m depth.

**Resembles:** Appears similar to Pointed Brown Tongue (*Punctaria plantaginea*), but that is often rough due to spots with brown algal hairs with sheath, has several plastids per cell and uni- or plurilocular sporangia in sori on the blade.



A: *Petalonia fascia*. Wide ribbon-shaped blades, one of them spotted after partial evacuation of sporangia (arrow). Sheltered side of the eastern harbour jetty, Gilleleje, 0.5 m, 3.5.2008. Scale 2 cm.

B: *Petalonia fascia*. Several narrow thalli from a crustose base. Eastern harbour jetty, Gilleleje, 0.5 m, 6.11.1989. Scale 2 cm.

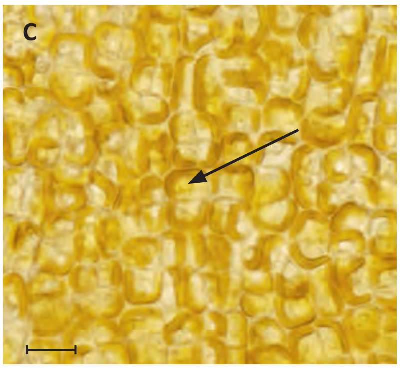
**References:** Fletcher (1978, 1987), Kogame (1997), Kornmann & Sahling (1977), Matsumoto et al. (2014), Rosenvinge & Lund (1947).

## Crustose phase

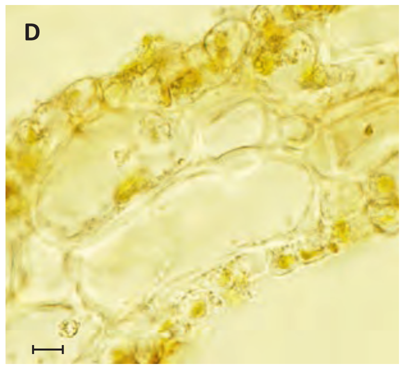
### (previous *Stragularia clavata*)

**Appearance:** A solid crust of circular or confluent filaments, 1-5 cm in width, light to dark brown and firmly attached to the substratum.

**Structure:** Upright filaments are closely connected, but easy to separate in a squash preparation under a coverslip. Upright filaments arise from a monostromatic basal system of branched filaments, which spread over the substratum. The margin is monostromatic but upright filaments develop just inside the margin, where the thalli become pseudoparenchyma-

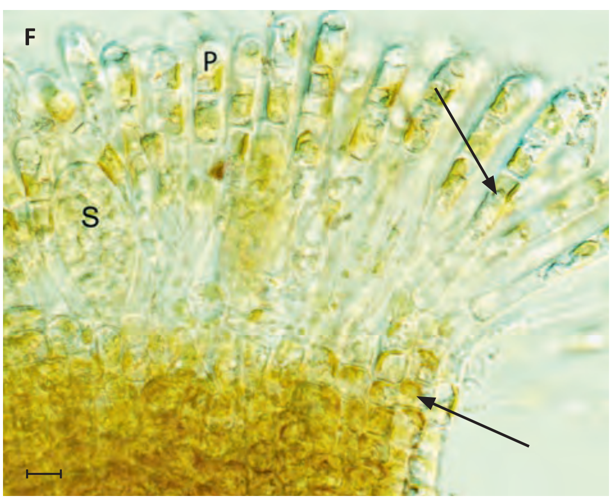



C: *Petalonia fascia*. Surface cells in rows, each with a plate-shaped plastid and one pyrenoid (arrow), surface view. Northeastern part of Refshaleøen, Copenhagen, 0.5 m, 23.2.2009. Scale 10 µm.

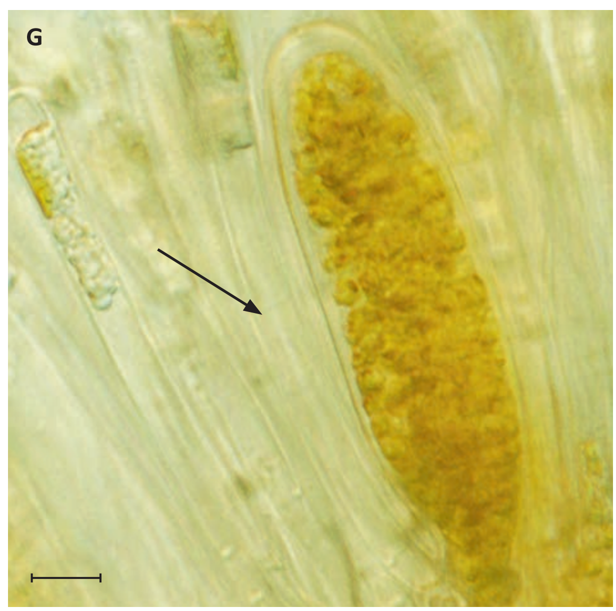



D: *Petalonia fascia*. Medulla of large pale cells and small angular surface cells. Transverse section. On boulder, Vesterø Havn, Læsø, 0.2 m, 19.3.2015. Scale 10 µm.


E: *Petalonia fascia*. Plurilocular sporangia (arrow), transverse section of blade. Beach north of Vesterø Havn, Læsø, 0.5 m, 1.3.2016. Scale 10 µm.




F: *Petalonia fascia*, crustose phase. Closely packed upright filaments, sorus of paraphyses (P) and unilocular sporangium (S). Vegetative cells with one plastid and one pyrenoid (arrows). Scale 10 µm. F-G: On pebble. Beach north of Vesterø Havn, Læsø, water edge, 1.3.2016.




G: *Petalonia fascia,* crustose phase. Mature unilocular sporangium and paraphyses with a long basal cell (arrow). Scale 10 µm.

tous. Filaments are up to 20 cells in height and consist of cylindrical cells, 8-12 µm in height and 5-13 µm in width. The upper end of each cell contains a plate-shaped plastid with one pyrenoid, but this may be difficult to see because the cells often contain grains of assimilating products. True brown algal hairs occasionally occur.

**Reproduction:** Unilocular sporangia occur in extended sori together with multicellular paraphyses. Unilocular sporangia develop from apical cells of the upright filaments. They are obovate or pyriform to elongate ellipsoid, (44-) 50-75 µm in height and 15-23 µm in width. Paraphyses are unbranched and cylindrical to slightly club-shaped. They have 1 (-2) elongated basal cells followed by short cells. The basal cells are c. 5 µm in width and c. 5 times as long as wide. The short cells are c. 13 µm long and 5-9 µm wide. Plurilocular sporangia are mentioned in British material by Fletcher (1987).

**Seasonal variation:** Collected in January-September and November, unilocular sporangia recorded in January-May and September.

**Habitat:** On solid substratum of stone or wood, 0-14 m depth.

**References:** Fletcher (1978, *Ralfsia clavata*, 1987), Kogame (1997), Kornmann & Sahling (1977, *R. clavata*), Matsumoto et al. (2014).

## *Planosiphon zosterifolius*

**(Reinke) McDevit & G.W.Saunders**

Flat Grass Leaf Weed

**Appearance:** Upright ribbon-shaped or linear dark-brown thalli, < 1 (-2) mm in width and to 7-23 (-35) cm in height. Uprights arise from a mat of entangled filaments.

**Structure:** Parenchyma, which consists of a medulla of elongate, rounded cells with a layer of small assimilating cortical cells on each side. Small cavities occur between the innermost medullary cells, but the thalli are still flat. Each assimilating surface cell contains a plate-shaped plastid with one pyrenoid. Some individuals have many true brown algal hairs, individually or in groups.

**Reproduction:** Plurilocular sporangia develop from surface cells, they are cylindrical, uniseriate and 50-60 µm in height. They develop in spots but gradually cover the whole surface. There are no paraphyses. The upright thallus alternates with a microthallus of creeping filaments, from which new uprights arise. Sexual reproduction not known.

**Seasonal variation:** Collected in February-November, plurilocular sporangia recorded in March-September and November.

**Habitat:** On stone and other solid substratum in the lowest part of the littoral zone and at shallow water, few collections by dredge, 2.5-7.5 m depth.

**References:** Fletcher (1987, *Petalonia zosterifolia*), Kogame & Kawai (1993, *P. zosterifolia*), McDevit & Saunders (2017), Rosenvinge & Lund (1947, *P. zosterifolia*).


A: *Planosiphon zosterifolius.* Long narrow ribbon-shaped thalli. On boulder at the light house north of the entrance to Thyborøn Kanal, sheltered side, littoral, 14.8.1979. Leg.: T. Christensen. Scale 2 cm.

## *Scytosiphon lomentaria*

**(Lyngbye) Link**

Chipolata Weed

**Appearance:** Terete, unbranched, yellow-brown to dark brown hollow thalli, 10-40 (70) cm in height and 0.5-3 (-8) mm in width, often with characteristic constrictions. Thalli clearly pointed towards the base, where several uprights arise from a crustose base. Life history comprises the uprights and a microthallus.

**Structure:** Parenchyma with medulla of pale elongated cells in 1-3 layers around the central cavity. This is surrounded by small angular cortical cells, each of which contains a single plate-shaped plastid with one pyrenoid. True brown algal hairs arise from the surface cells, and are scattered, individually or in small groups.

**Reproduction:** Plurilocular sporangia develop from surface cells of the upright thalli. The sporangia are cylindrical and uniseriate, although in older thalli a few longitudinal walls may occur (Rosenvinge & Lund, 1947, fig. 9). Plurilocular sporangia cover the entire surface together with unicellular cylindrical or slightly club-shaped paraphyses when fertile.

**Seasonal variation:** Occurs all year, but best developed with large crops in spring and early summer. Plurilocular sporangia recorded in January, March-September and November.

**Habitat:** On stone, mollusc shells and other solid substrata, rarely epiphytic on larger algae, such as Bladder Wrack (*Fucus vesiculosus*). Forms dense crops in shallow water, 0-1 m depth and are scattered in occurrence at greater depth. Individuals collected by divers to 8 m depth and by dredge at 18 and 27 m depth.

**Resembles:** Young thalli occasionally reminiscent of Thin Sausage Weed (*Asperococcus fistulosus*) and Bootlace Weed (*Chorda filum*), but both of these have several plastids per cell, while Chipolata Weed (*S. lomentaria*) has only one.

**Comment:** Eleven different genetic groups were revealed in a molecular study of *Scytosiphon* from many different area (McDevit & Saunders, 2017). The investigation also comprised morphological studies and it turned out that an alga of the type material for *S. lomentaria* did not have paraphyses. Therefore, Chipolata Weed (*S. lomentaria*) from Danish waters with paraphyses is probably a different species, which requires clarification in future studies.

### Microthallus

**Appearance:** Discs or crustose thalli which are typically confluent, but consist of irregular rounded individuals, c. 1 mm in width (Lund 1966). They are slightly jelly-like, soft, with a greenish margin and a dark central part with furrows and becoming almost black when dry.

**Structure:** Basal system of coherent filaments is typically monostromatic, occasionally consisting of 2 (-3) cell layers. Loosely connected but mutually free, uniseriate, unbranched or sparsely branched upright filaments, 7-8 µm in width and c. 170-250 µm in height arise from the basal system. They fall out in a fan-shape by slight pressure in a slide preparation. In the upper part of the filaments a pair of elongated cells are followed by small barrel-shaped cells. The elongate cells are level with sporangia, and the upper parts of the filaments therefore resemble paraphyses. Vegetative cells contain a plastid with one pyrenoid. True brown algal hairs are lateral or terminal on the upright filaments.

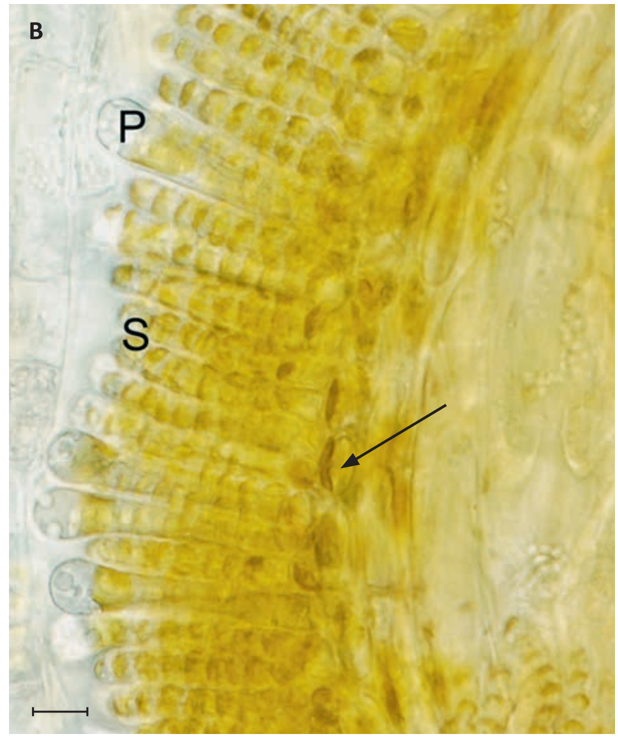
**Reproduction:** Unilocular sporangia are narrow, elongate obovate or club-shaped, 70-100 µm in height and c. 20 µm in width. They may have a unicellular stalk and are lateral on the filaments at the transition area to the upper part, just below the elongated cells.

**Seasonal variation:** The crustose phase is recorded in January, March, May-September and November-December, unilocular sporangia in March, June and October (mainly as *Microspongium gelatinosum* Reinke).

**Habitat:** The crustose phase (as *M. gelatinosum*) is recorded from 0.5-5 m depth.

**Comment:** Upright thalli in direct connection with the crustose phase were observed in Danish waters by Lund (1966). Unilocular sporangia were present and the alga compared with *M. gelatinosum*. A few pluri-

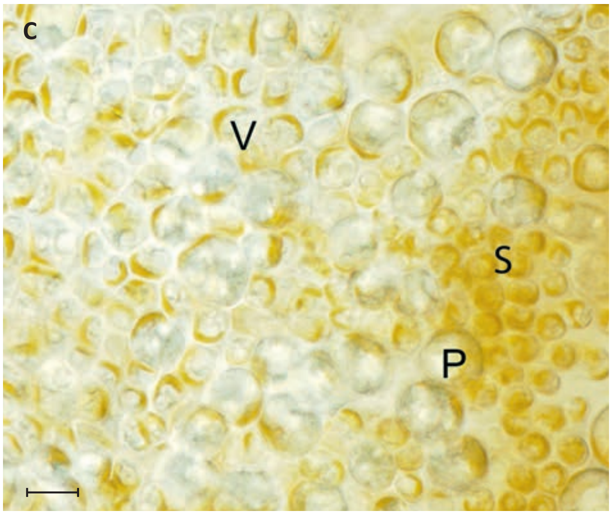

A: *Scytosiphon lomentaria*. Terete, unbranched alga with scattered constrictions. Pramrenden, Langelinie, Copenhagen, 0.5 m, 24.4.1998. Scale 2 cm.



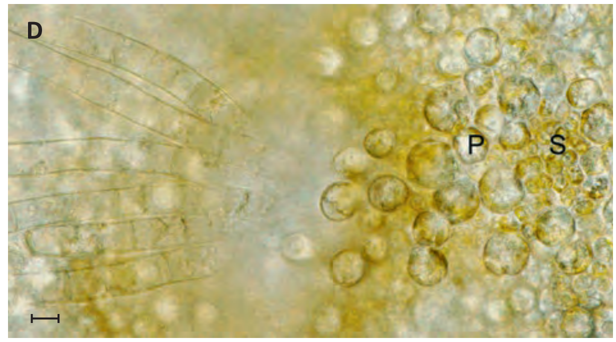

B: *Scytosiphon lomentaria*. Elongate medullary cells, small cortical cells (arrow) plurilocular sporangia (S) and unicellular paraphyses (P). Transverse section of fertile alga. Beach north of Vesterø Havn, Læsø, 0.5 m, 9.5.2014. Scale 10 µm.

locular sporangia were also illustrated (Lund, 1966). Intensive investigations of Chipolata Weed (*S. lomentaria*) in Danish waters were undertaken by Kristiansen (1984), Kristiansen & Pedersen (1979), Kristiansen et al. (1991, 1994) both in nature and by culture studies. These authors suggest that there are temperature and salinity ecotypes in Danish Chipolata Weed (*S. lomentaria*). Culture studies showed that swarmers from plurilocular sporangia on upright thalli germinated and developed into creeping microthalli from which new upright thalli arose (Kristiansen & Pedersen, 1979). The creeping microthallus could consist of uniseriate filaments, had a parenchymatous area ("knot filaments") or was crustose in contact with a solid substratum (Kristiansen & Pedersen, 1979). On a single occasion the crustose thallus developed with unilocular sporangia reminiscent of *M. gelatinosum*. Sexual reproduction was not observed.

*Microspongium gelatinosum* was described with plurilocular sporangia by Reinke (1888a), who extended the description to also include thalli with unilocular sporangia (Reinke, 1889a, b). Kristiansen & Pedersen (1979) argued for the two being different species, which was followed by Fletcher (1987). Unilocular sporangia are reported in the records we know of *M. gelatinosum* from Danish waters, so these specimens probably represent microthalli of Chipolata Weed (*S. lomentaria*). One exception is the plurilocular sporangia on a single branch among the material Lund (1966) recorded as *M. gelatinosum*. The identity of this



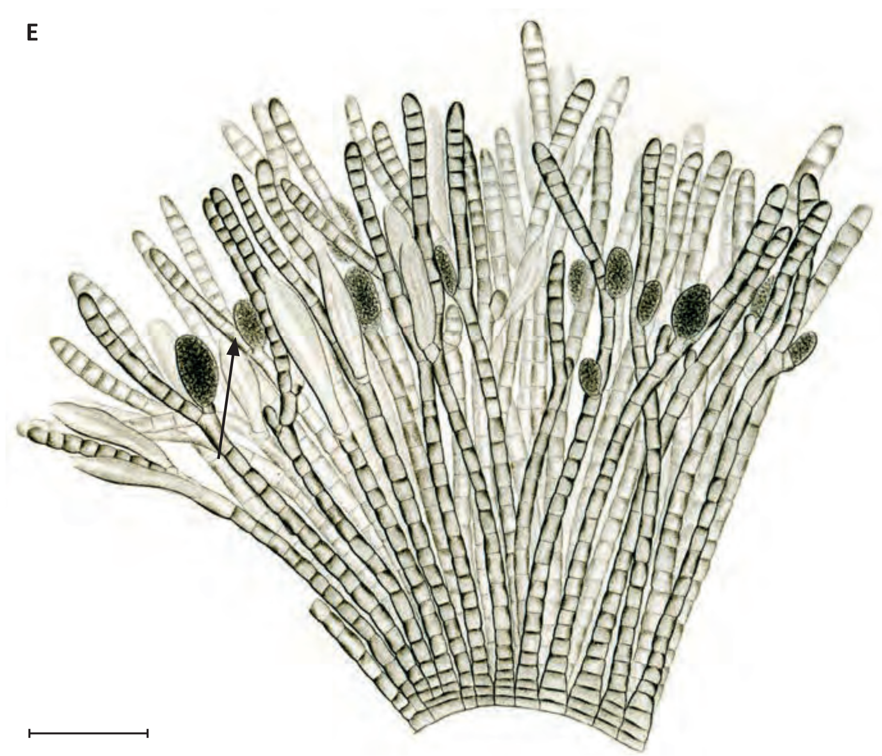

C: *Scytosiphon lomentaria*. Vegetative cells (V) with a plate-shaped plastid, plurilocular sporangia (S) and paraphyses (P), fertile alga surface view. Scale 10 µm. C-D: Beach south of Vesterø Havn, Læsø, drift, 9.7.2013.




D: *Scytosiphon lomentaria*. Group of true brown algal hairs, paraphyses (P) and plurilocular sporangia (S), fertile alga surface view. Scale 10 µm.

alga and possible occurrence of *M. gelatinosum* (with plurilocular sporangia) in Danish waters requires confirmation by future investigations.

**References:** Fletcher (1978, *Microspongium gelatinosum*, 1987, *S. lomentaria* and *M. gelatinosum* phase of *S. lomentaria*), Hoshino et al. (2018), Kristiansen (1981, 1984), Kristiansen & Pedersen (1979), Kristiansen et al. (1991, 1994), Lund (1966), McDevit & Saunders (2017). Pedersen (2011), Reinke (1888a, 1889a, b, *M. gelatinosum*), Rosenvinge & Lund (1947).




E: *Scytosiphon lomentaria,* microthallus. Upright mutually free filaments with unilocular sporangia and empty sporangia walls. The upper part of the upright filaments resembles paraphyses with long basal cell (arrow). Vegetative cells with one plastid. Scale 100 µm. After Reinke (1889b), as *Microspongium gelatinosum*.

## *Sorapion kjellmanii*

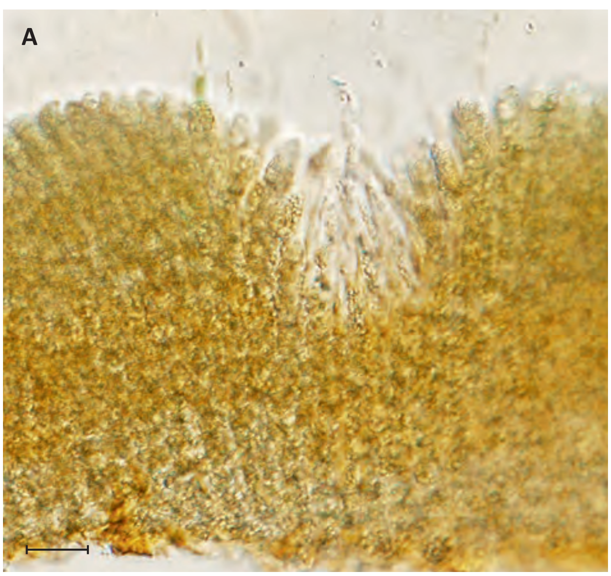
**(Wille) Rosenvinge**

Kjellman's Hair Pit Crust

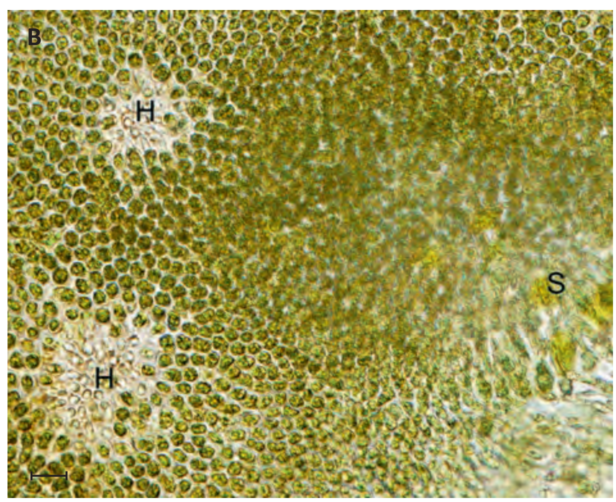
**Appearance:** Dark- to light brown well defined, slightly loose crusts, 0.5-0.75 cm in width.
**Structure:** Upright filaments of 8-10 cylindrical cells, 8-10 µm in width arise from a basal layer. Filaments are loosely connected and have short, scattered branches in the upper part. Vegetative cells contain a plate-shaped plastid. Clusters of true brown algal hairs occur in pits in the crust.
**Reproduction:** Unilocular sporangia are terminal on the upright filaments, they are obovate or pyriform, c. 34 µm long and 15 µm wide.
**Seasonal variation:** Collected in March and August-September, unilocular sporangia recorded in September.
**Habitat:** Epiphytic on Wavy Brown Tongue (*Punctaria tenuissima*) and on stone, 0.5-9.5 m depth.
**Comment:** Culture studies of *S. kjellmanii* from Danish waters by Pedersen (1981b) showed swarmers from unilocular sporangia to germinate and develop into new crustose thalli, plurilocular sporangia developed and were partitioned in four compartments as in *Porterinema fluviatile* (H.C. Porter) Waern. The two were therefore considered synonymous (Pedersen, 1981b).

### *Porterinema*-phase

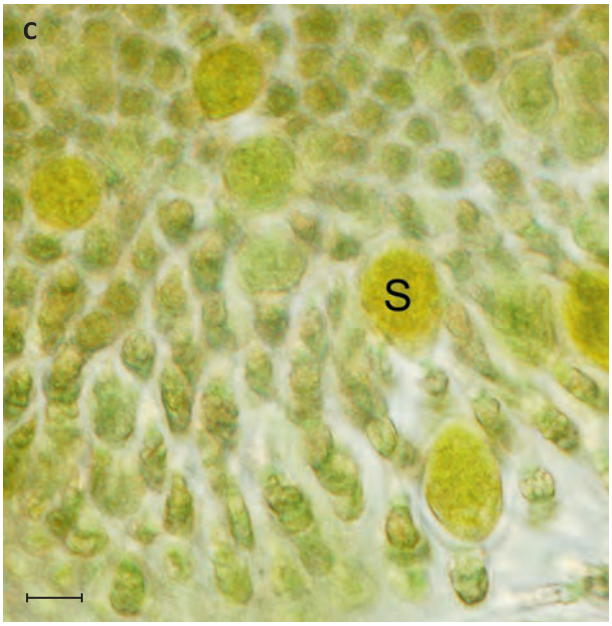
**Structure:** Microscopic creeping filaments, c. 5 µm wide, confluent to a pseudoparenchyma. There are brown algal hairs, which may have a sheath.
**Reproduction:** Plurilocular sporangia are partitioned in four compartments, 4.3-5.6 µm in width. They are intercalary in the creeping filaments or terminal on short upright filaments. The swarmers are released directly from each compartment.
**Seasonal variation:** Collected in May and August, with plurilocular sporangia.
**Habitat:** Epiphytic on Wavy Brown Tongue (*Punctaria tenuissima*) in shallow water.
**References:** Kristiansen (1978), Pedersen (1981b), Wærn (1952, *Porterinema fluviatile*).



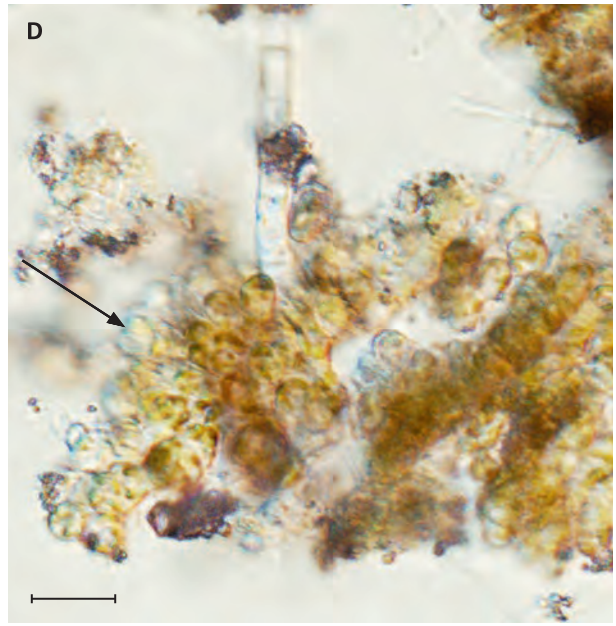

A: *Sorapion kjellmanii*. Crust of closely connected filaments, pit with true brown algal hairs. Longitudinal section. Sjællands Rev, 9.5 m, 10.9.1996. Scale 20 µm.



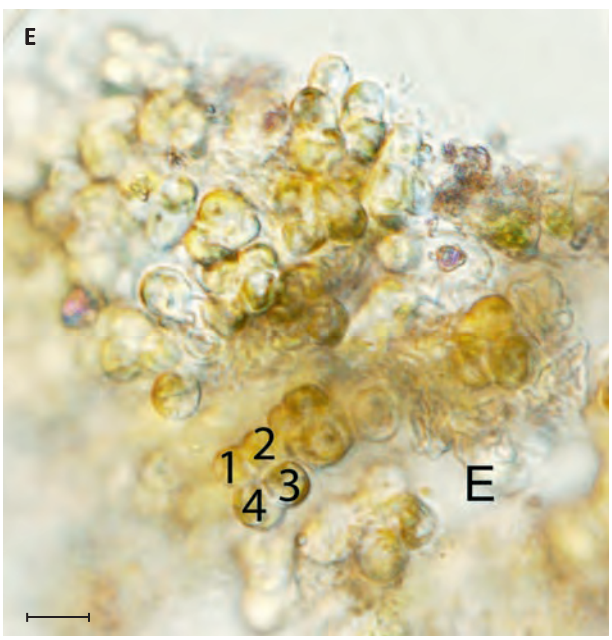

B: *Sorapion kjellmanii*. Two hair pits (H) and an area with unilocular sporangia (S), which are at a slightly higher level than the rest of the crust. Seen from above. Scale 20 µm. B-C: Different focus of same alga. Tangen, 7 m, 15.9.1996.




C: *Sorapion kjellmanii.* Sporangia (S). Scale 10 µm.




D: *Sorapion kjellmanii, Porterinema*-phase. Pseudoparenchyma of small, rounded cells with true brown algal hair and sporangia (arrow). Scale 20 µm. D-F: On pebble, Sydstranden, Dragør 0.2 m, 13.8.2017.




E: *Sorapion kjellmanii, Porterinema*-phase. Sporangium with 4 compartments (1-4) and empty sporangium (E). Seen from above. Scale 10 µm.


F: *Sorapion kjellmanii, Porterinema*-phase. Young brown algal hair with sheath (arrow) and empty sporangia (E). Scale 10 µm.

## *Symphyocarpus strangulans*

**Rosenvinge**

Diamond Dot

**Appearance:** Small brown spots, up to 1 mm in width. Recognisable by individual shining cells (ascocysts) with a hand lens or dissection microscope.

**Structure:** Short thick filaments arise from a monostromatic basal layer of scattered branched filaments, adpressed to the substratum. Upright filaments consisting of short cylindrical cells are sparsely branched and loosely connected. Lower cells are 6-8 µm in height and 16-19 µm in width, while the upper cells are 5-10 µm in height and 9 µm in width. Vegetative cells contain a plate-shaped plastid in the upper part of cell. Large cylindrical ascocysts are scattered and eye-catching with dissection microscope. They have a brown content and are up to 46 µm in height and 19-20 µm in width. They arise from the basal layer or are terminal on few celled upright filaments.

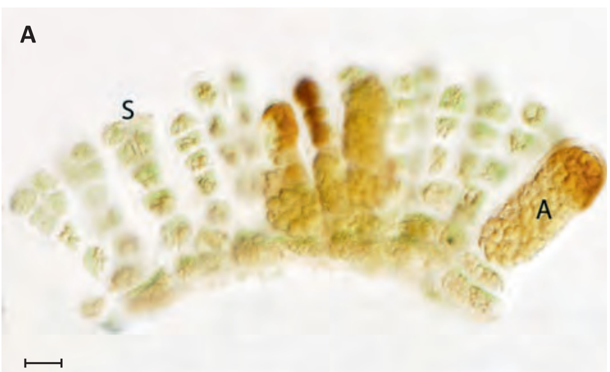
**Reproduction:** Terminal plurilocular sporangia, with compartments in 4 rows. They appear to be partitioned in 4 compartments when seen from above. The sporangia are 9-13 µm in width.

**Seasonal variation:** Collected in January, March and June-November. Plurilocular sporangia recorded in March, June-July and September.

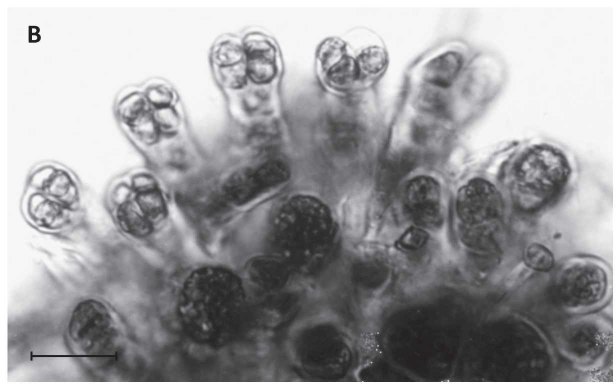
**Habitat:** On small stones, 7-30 m depth.

**Comment:** Culture studies of *Symphyocarpus strangulans* from Greenland showed a direct life history, the swarmers from plurilocular sporangia germinated and developed into crusts similar to the parent (Pedersen, 2011).

**References:** Fletcher (1987), Pedersen (2011).




A: *Symphyocarpus strangulans*. Basal layer with few celled upright filaments, brown ascocysts (A) and plurilocular sporangia (S). Scale 10 µm. A-B: Squash preparation. Schultz's Grund, 7 m, 6.6.1993.




B: *Symphyocarpus strangulans*. Crust with mature plurilocular sporangia. Seen from above. Scale 20 µm.

## Order: Fucales

**Appearance:** Large firm thalli, with a leather-like consistency, developing from a robust basal attachment disc. Fronds are ribbon-shaped, dichotomously branched or much branched with main branch and branches in some cases with small blades. Length of adult thalli varies from c. 10 cm to 2 m or more. Most species in Danish waters have air bladders, which help to keep the algae upright in the water.

**Structure:** Parenchyma with apical growth. Apical cells are pyramid-shaped with 3 or 4 sides and growth is by cells being cut off on several sides. Apical cells are in a small cavity, formed after continued cell divisions in the outer cells. Cortex of small assimilating cells and a medulla of pale cells. Cell divisions continue in the cortex while growth in the medulla occurs by longitudinal stretching of the cells and longitudinal walls simultaneously become thicker and partly gelatinous. Medullary cells therefore appear as if they are at some distance or forming a net. Narrow hyphae-like filaments develop gradually between the medullary cells, particularly in the lower part and contribute to make the thalli strong against the force of water. The main part of the basal disc consists of hyphae-like filaments.

**Reproduction:** Thalli are diploid and have only one generation. Sexual reproduction is oogamous with meiosis immediately before the production of sexual cells. Algae are monoecious or dioecious and have a direct development of upright thalli from the fertilized eggs (zygotes). Sexual organs develop in special branches or branch-apices (receptacles), in which they form in cavities with small exit pores (conceptacles). Receptacles have a knotted appearance because of the content of sexual structures in conceptacles. Antheridia are ellipsoid and terminal on branches in small bushy parts of uniseriate colourless filaments, which arise from the sides and bottom of conceptacles. At maturity, antheridia contain a large number of spermatozoids, typically 64, each with a red eyespot. Egg-cells develop in oogonia, which occur at the walls of the conceptacles, typically on a unicellular stalk, or they are in part embedded in the wall of the conceptacle (*Sargassum*). At maturity, oogonia have 3 wall layers and contain 1, 2, 4 or 8 egg-cells. When eggs are released, the outer wall layer of oogonia remains on the stalk-cell. The second layer ruptures and the inner layer gelatinizes in the water. Conceptacles also contain hair like filaments, which probably produce mucous in the conceptacles, and there may be brown algal hairs particularly at the opening.

Monoecious species sometimes form male and female sexual cells in the same conceptacle, at others in separate conceptacles.

**References:** Christensen (1980), Fritsch (1965).

## Family: Fucaceae

### *Ascophyllum nodosum*

**(Linnaeus) Le Jolis**

Egg Wrack or Knotted Wrack

**Appearance:** Firm, olive-green leather-like thalli, up to 1 m in height. Attached to the substratum with a coarse attachment disc from which several upright thalli may arise. Branches are flattened, 0.5-1 cm in width. Air bladders occur individually in the middle of branches which are without a midrib. Main branches are dichotomously branched with lateral branches from the frond edges and are scattered or arise several together from the same spot. Air bladders are 1-3 cm long and occur at a variable distance along the length of the branches. The first air bladders develop at the age of 2 years, and in consecutive years, a single new air bladder develops at the apex of each branch. The number of air bladders in the main branch, therefore, accounts for the age of the thallus plus the number of years before it produces air bladders. The alga can be several years old, and in the Northern Kattegat 18-year old thalli have been recorded. Occasionally forked air bladders occur in forked branches. The length between the air bladders within a branch indicates the yearly growth.

**Structure:** The construction is as described for the order. Dichotomous branches develop after a bipartition of the apical cell, so it is a genuine dichotomy. Hyphae-like filaments in the medulla are not very well-developed, so Egg Wrack (*A. nodosum*) is not very resistant against the force of the waves and therefore grows in sheltered localities.

**Reproduction:** Dioecious, isomorphic male and female thalli. Receptacles are specialised short branches, shaped like gooseberries or almost spherical on a short stipe. Male thalli are recognizable as orange-red mucilage spots at the openings of mature conceptacle. The colour is caused by the red eyespots of released spermatozoids. In female thalli similar spots are olive-green. There are four eggs in each oogonium. The spermatozoids are attracted chemically by a pheromone from the egg-cells at sexual reproduction.

Receptacles are shed at the end of the reproductive period and leave protruding scars on the branches.
**Seasonal variation:** Receptacles develop in autumn and winter, sexual reproductive structures are released in late winter and spring, and the receptacles which become yellow are shed in May-June.
**Habitat:** On boulders in sheltered places such as the inner side of harbour jetties or between boulders, in shelter from other boulders in front of them. In shallow water from the lowest part of the littoral zone to c. 1 m depth. Egg Wrack (*A. nodosum*) grows attached at Grenå. From there towards the Baltic Sea, only unattached or drifting individuals are known.

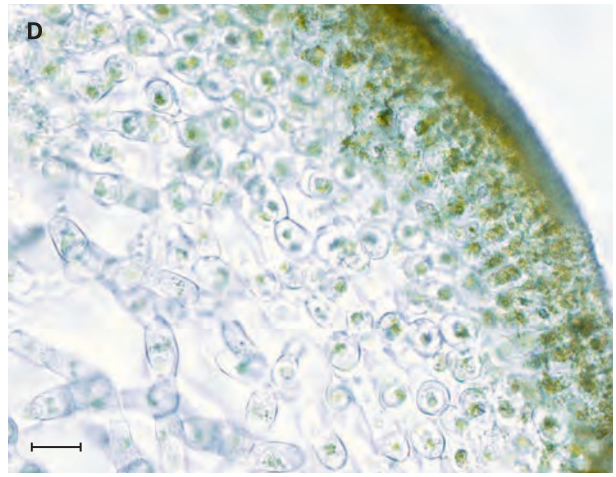
*Ascophyllum nodosum* f. *scorpioides* (Hornemann) Hauck occurs in a few fjords in east Jutland. It is unattached between Eelgrass (*Zostera marina*) and has narrow almost terete slightly curved branches without air bladders. Reproductive structures not known in this form.
**Comment:** In northern localities such as the Faroe Islands, Greenland, Iceland and Norway, Egg Wrack (*A. nodosum*) is used as fodder for sheep and cattle. Sheep may be seen in the littoral grazing directly on the alga. The species is also harvested, dried and ground into a flour, which is blended with fodder or for use as a soil improver, and by the industry for extraction of alginic acid. The ability of individuals


A: *Ascophyllum nodosum*. Main branch with scattered branches, air bladders in the middle of branches, summer. Vesterø Havn, Læsø, 0.5 m, 5.6.2017. Scale 2 cm.


B: *Ascophyllum nodosum*. Mature receptacles, shed in the terminal parts leaving small protruding scars (arrow). A few forked air bladders. Deget, Frederikshavn, water's edge, 8.6.1963. Leg.: T. Christensen. Scale 2 cm.

to regenerate is high, so at harvest, the thalli are cut above the base to let them regenerate.

**References:** Christensen (1980), Fritsch (1965), Müller et al. (1982), Oltmanns (1904, 1905), Pedersen (2011), Rueness (1977).




C: *Ascophyllum nodosum* f. *scorpioides*. Narrow thallus without air bladders. East of Middelfart, 4 m, 10.7.1900. Leg.: Rosenvinge. Scale 2 cm.

D: *Ascophyllum nodosum*. Medulla of cells with thick gelatinized walls and cortex of small assimilating cells. Transverse section. Scale 50 µm. D-E: Sheltered side of northern harbour jetty, Vesterø Havn, Læsø, 0.3 m, 1.3.2016.

E: *Ascophyllum nodosum*. Four egg-cells, released from the conceptacle but kept together in the inner wall-layer of the oogonium. Scale 20 µm.

F: *Ascophyllum nodosum*. Alga on the beach with an air bladder and mature receptacles with orange spots of spermatozoids (arrow). Hirsholm, 4.11.2015. Photo by K.L. Krabbe.

## *Fucus*

Wrack

**Appearance:** Tough leather-like yellow-green to dark brown flattened thalli with dichotomous branches in one plane, up to c. 1 m in height. Secondary scattered branches occasionally occur. Most species have a conspicuous midrib and are attached to the substratum by a robust basal disc.

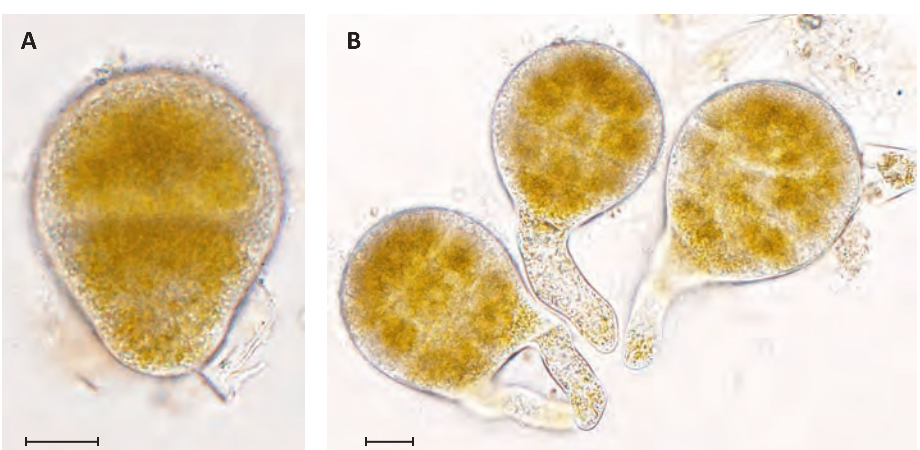
**Structure:** Construction is as described for the order. During initiation of dichotomous divisions of branches the apical cell divides longitudinally, and each of the two new cells develops into a new branch. Small cavities (cryptostomata) are scattered on the surface of the thallus in most species. Cryptostomata contain true brown algal hairs which appear as small whitish tufts.

**Reproduction:** Receptacles develop as the apical part of branches. They more or less resemble vegetative branches in the different species. Following the reproductive process, branches with receptacles degenerate to a branching point where one or both dichotomous branches terminate in a vegetative apex, which continues to grow. Therefore, reproduction may cause a larger part of the thallus to decay. Oogonia contain 8 eggs at maturity. Fertilization takes place outside the thallus. Spermatozoids are chemotactically attracted by a scent (fucoserraten) from the eggs. When the zygotes germinate the first transverse wall is perpendicular to the direction of light. The cell which turns towards the light develops into the upright thallus. The cell which turns away from the light develops a small papilla, which is the initiation of rhizoidal filaments that attach the alga to the substratum and develop into the basal disc. Young individuals are club-shaped with a tuft of true brown algal hairs in a cavity at the apex.

**Comment:** Species identification is sometimes difficult because of considerable morphological variation. This is caused by the influence of ecological factors and by genetic variation within the individual species. Furthermore, hybrids may develop between some of the species. These are known between Spiraled Wrack (*F. spiralis*) and Bladder Wrack (*F. vesiculosus*) and between Two-headed Wrack (*F. distichus*, as *F. evanescens* C.Agardh) and Serrated Wrack (*F. serratus*) (Billard et al., 2005a, b, Coyer et al., 2002a, b, c).

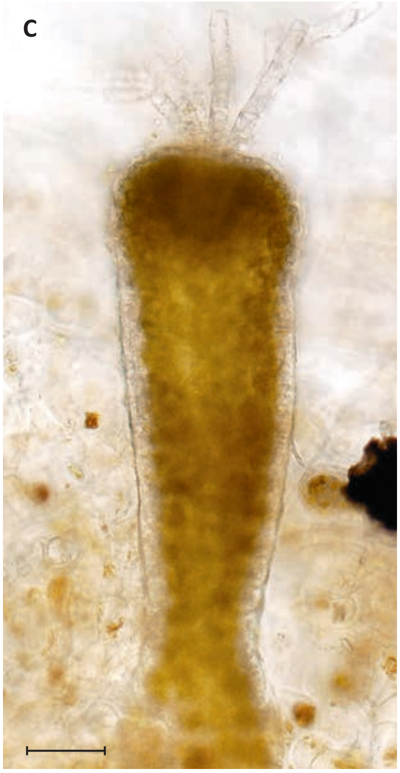
In the Northern Kattegat, The North Sea and Skagerrak species of Wrack (*Fucus*) are an important habitat-forming element in the algal zonation in the littoral and in the shallow subtidal. In the inner districts towards the Baltic Sea, the variations in water level are irregular and longer periods of low water occur, which causes the Wrack (*Fucus*) there to be always sublittoral.

**References:** Andersson et al. (1994), Billard et al. (2005a, b), Christensen (1980), Coyer et al. (2002a, b, c), Fritsch (1965), Moss (1967), Müller & Gassmann (1978).



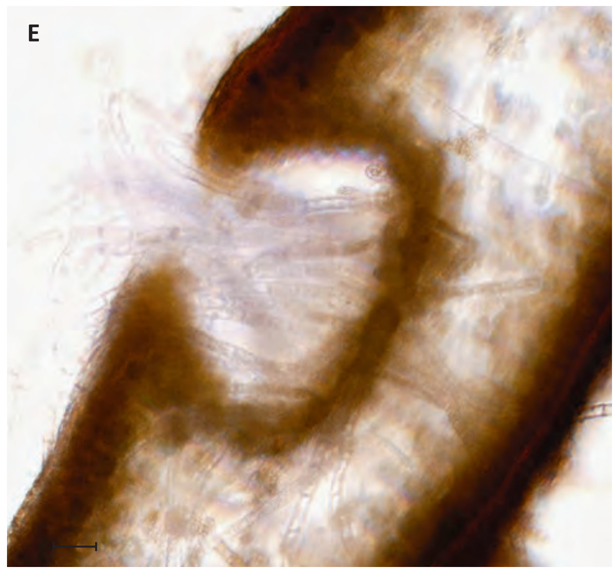

A: *Fucus*. Germling of two cells. Scale 20 µm. A, B: In crude culture of Spiraled Wrack (*Fucus spiralis*). Initiated from collection at the beach north of Vesterø Havn, Læsø, 0.2 m, 2.9.2017. The mature receptacles were left in a petri-dish with sea water 5.9.2017 and photographed 8.9.2017.

B: *Fucus*. Germlings of several cells with 1-2 rhizoids. Scale 20 µm.





D: *Fucus*. Young thalli with hairs in cryptostomata (arrow). Beach north of Vesterø Havn, Læsø, 0.1 m, 26.7.2017. Scale 1 cm.




C: *Fucus*. Young alga with true brown algal hairs at the apex. Scale 10 µm. On Pointed Brown Tongue (*Punctaria plantaginea*), beach south of Vesterø Havn, Læsø, drift, 3.6.2017.

E: *Fucus*. Cryptostomata with true brown algal hairs. Transverse section of Bladder Wrack (*Fucus vesiculosus*). Beach north of Vesterø Havn, Læsø, 0.2 m, 2.9.2017. Scale 50 µm.

**Identification key to species of *Fucus***

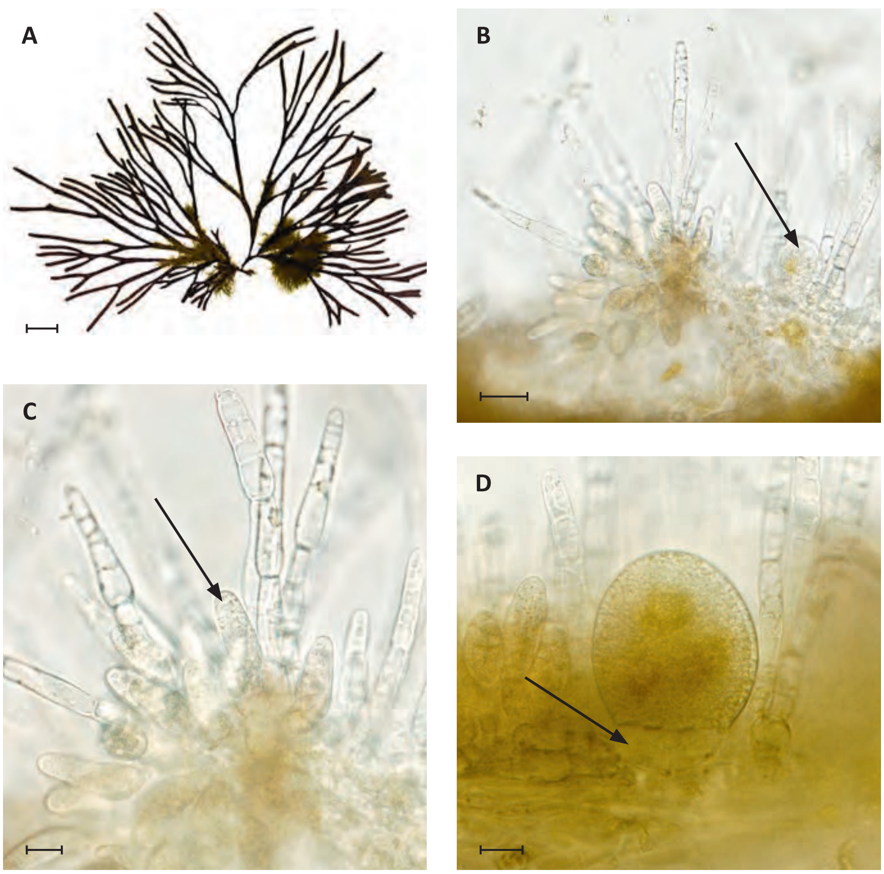
| | | |
|---|---|---|
| 1a. | With air bladders in pairs | *F. vesiculosus* |
| 1b. | Without air bladders | 2 |
| 2a. | Dentate margin, receptacles flat, dioecious | *F. serratus* |
| 2b. | Margin regular, receptacles thick and contain mucilage | 3 |
| 3a. | Branches typically slightly twisted as in a spiral, receptacles short, 1-2 cm long with a vegetative margin, monoecious | *F. spiralis* |
| 3b. | Branches not twisted, receptacles 2-5 cm long | 4 |
| 4a. | Diffuse midrib, narrow branches often with caecostomata (small cavities below the surface of thallus, apparent in transparent light), fertile in March-April, monoecious | *F. distichus* |
| 4b. | Conspicuous midrib, without caecostomata, dioecious | *F. vesiculosus* |

# *Fucus distichus*

**Linnaeus**

Two-headed Wrack

**Appearance:** Thalli with narrow branches, 20-25 (-28) cm in height and 0.3-10 mm in width. Branches with regular margin, without air bladders. Midrib not conspicuous and absent in the terminal branches. Small spherical cavities below the surface (caecostomata), visible in transparent light as small points which appear brighter than the rest of the branches. No cryptostomata. Receptacles are long and narrow, 3-5 (-6) cm long and 5-6 mm wide, typically slightly wider than vegetative branches.
**Structure:** Construction is as described for the order and genus.
**Reproduction:** Monoecious with antheridia and oogonia in the same conceptacles.
**Seasonal variation:** Perennial, fertile in spring, mature receptacles recorded in February-July.
**Habitat:** On boulders often in harbours with nutrient rich water, among Bladder Wrack (*F. vesiculosus*), 0.5-1.5 m depth.
**Comment:** A northern species, the first attached alga found in Danish waters was collected at Charlottenlund, the Sound in 1948. The algal herbarium, Natural History Museum of Denmark documents the spread and distribution with collections from Skagerrak 1996, Skagen 1978, Frederikshavn 1968-1975 (later looked for in vain), the Southern part of Kattegat 1968, Samsø-area 1984, and in 1989 from the Middle part of Kattegat, Little Belt, the Great Belt, the Western part of the Baltic Sea and the Archipelago south of Funen.
**References:** Kristiansen (1972, *F. distichus* ssp. *edentatus*), Lund (1949, *F. edentatus*), Nielsen (2008, *F. evanescens*), Powell (1957, *F. distichus* subsp. *edentatus*), Rice & Chapman (1985), Thomsen et al. (2005, *F. evanescens*).




A: *Fucus distichus*. Narrow dichotomously branched alga without conspicuous midrib, long receptacles. Bush-like epiphytic Pylaie's Brown Filaments (*Pylaiella littoralis*) on the lower part of the thallus. Outer part of Margretheholms Havn, Copenhagen 0.5 m, 15.4.2004. Scale 2 cm.

B: *Fucus distichus*. Part of conceptacles, many colourless hairs, filaments with antheridia and a young oogonium (arrow). Scale 50 µm. B-D: Outer part of Margretheholms Havn, Copenhagen, 0.5 m, 22.2.2008.

C: *Fucus distichus*. Antheridium (arrow), the eyespots of the spermatozoids visible as dark points. Scale 20 µm.

D: *Fucus distichus*. Young oogonium on stalk-cell (arrow). Scale 20 µm.

## *Fucus serratus*

**Linnaeus**

Serrated Wrack

**Appearance:** Flat dichotomously branched thalli. The branches have midrib, a dentate margin, but no air bladders, up to 40-60 cm in height and branches 0.75-5 cm in width.

**Structure:** The construction is as described for the order and genus.

**Reproduction:** The alga is dioecious. Receptacles, which develop in the terminal part of branches, are similar to vegetative branches apart from their knotted appearance.

**Seasonal variation:** Perennial. Receptacles collected in January-September and in November. Antheridia recorded in January-March, June, August-September, November and oogonia in March-April.

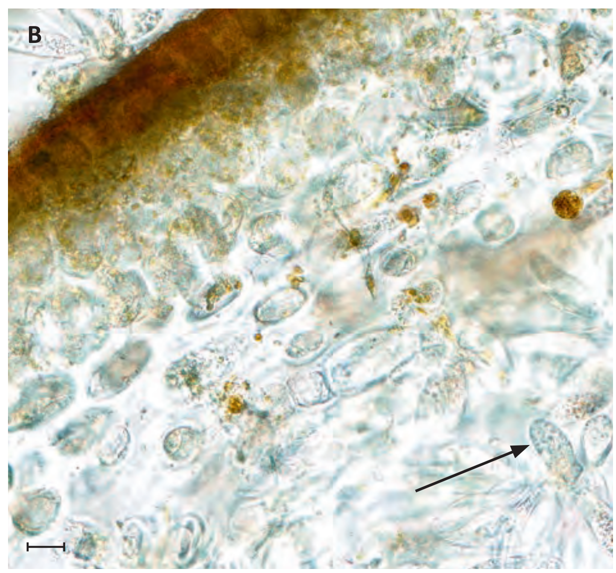
**Habitat:** On stone, sublittoral in Danish waters. The upper distributional border of Serrated Wrack (*F. serratus*) in the Northern Kattegat is used to define the upper border of the sublittoral zone. Collected by divers to 10.5 m depth.

**Resembles:** Forms hybrids with Two-headed Wrack (*F. distichus*) whose appearance is intermediate between the two species, with dichotomous narrow branches without or with tiny dentation, a faint midrib and are dioecious. They are probably similar to the alga mentioned as *F. serratus* f. *elongata* by Lund (1949).

**Comment:** Comparison of collections from the beginning and the end of the 19th century indicates a reduction in depth as well as geographical distribution (Nielsen, 1998).

**References:** Coyer et al. (2002a, b, c), Lund (1949), Nielsen (1998).

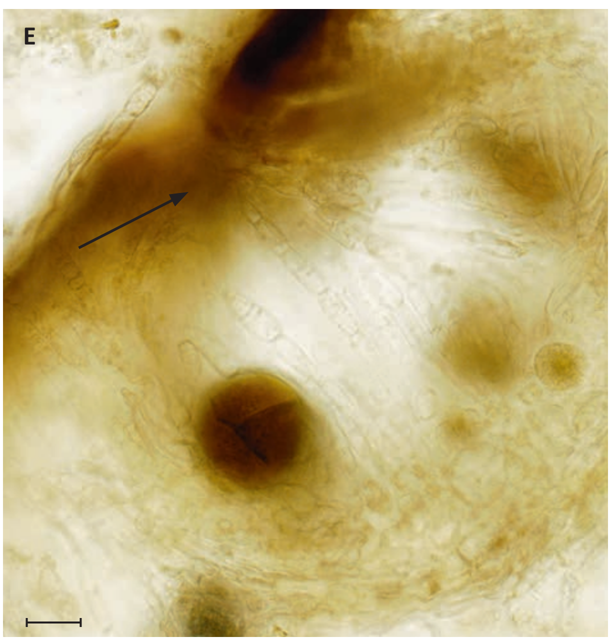

A: *Fucus serratus*. Dichotomously branched dentate alga, spread on a garden table which is 1 m in diameter. Western side of Nordre Rønner, Læsø, 4 m, 19.8.2005.



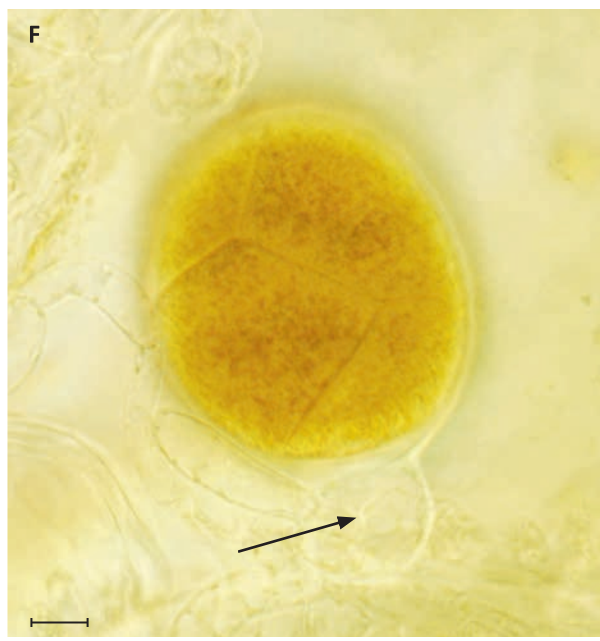

B: *Fucus serratus*. Part of male receptacle, with antheridium (arrow), Transverse section. Scale 50 µm. B, D: Aarhus, 0.5 m, 22.1.2015. Leg.: K.L. Krabbe.


C: *Fucus serratus*. Receptacles of male gametophyte with orange-yellow spots of released spermatozoids. Hirsholm, drift, November 2014. Photo by K.L. Krabbe.


D: *Fucus serratus*. Branch with young, mature and empty antheridia, red eyespots of the spermatozoids visible. Scale 10 µm.




E: *Fucus serratus*. Female conceptacle with colourless hairs and young oogonia, exit tube of the conceptacle (arrow). Transverse section. Scale 50 µm. E, F: Hirsholm, 14.4.2015.




F: *Fucus serratus*. Oogonium on stalk-cell (arrow). Scale 20 µm.

## *Fucus spiralis*

**Linnaeus**

Spiraled Wrack

**Appearance:** Thalli have a regular margin and a conspicuous midrib but are without air bladders, 5-25 cm in height. Branches have a tendency to be twisted, particularly in the upper part. Receptacles are short and swollen to almost spherical, occasionally forked. They are 1-2 cm in width and have a small vegetative margin (comb or rim).

**Structure:** Construction is as described for the order and genus.

**Reproduction:** Monoecious with antheridia and oogonia in the same conceptacle.

**Seasonal variation:** Perennial, young receptacles recorded in March-April and mature receptacles in May-October.

**Habitat:** On stone and boulders in not too exposed localities in the upper part of the littoral zone. Spiraled Wrack (*F. spiralis*) forms a belt above Bladder Wrack (*F. vesiculosus*). It can resist desiccation, but not for an extended time. Low water in spring combined with warm sunny weather cause much damage to the alga in upper part of the littoral zone. Low water in spring therefore determines the upper limit for this species.

**Resembles:** Distinguished from Bladder Wrack (*F. vesiculosus*) without air bladders by the monoecious conceptacles, the rim on the receptacles and the twisted fronds.

**References:** Billard et al. (2005a, b).


A: *Fucus spiralis.* Dichotomous twisted branches; many receptacles with a vegetative rim (arrow) and many whitish tufts of hairs from the conceptacles. Aarhus Havn, upper part of littoral zone, 15.6.2016. Photo by K.L. Krabbe.


B: *Fucus spiralis.* Conceptacle with many colourless filaments, small antheridia (arrow) and dark young and mature oogonia. Scale 50 µm. B-D: Beach north of Vesterø Havn, Læsø, on pebbles at the water edge, 9.7.2013.



C: *Fucus spiralis.* Colourless filaments with antheridia. Scale 20 µm.

D: *Fucus spiralis.* 8 released eggs still kept together in the innermost wall of the oogonium. Scale 20 µm.

## *Fucus vesiculosus*

**Linnaeus**

Bladder Wrack

**Appearance:** Thalli yellow-brown to dark olive-brown, typically with pairs of air bladders and up to c. 60 cm in height and branches, 0.5-2 cm in width. Branches with regular margin and a conspicuous midrib. Attached to the substratum by a robust basal disc. Morphological variation comprises thalli with wide branches and relatively short distance between the branching points and narrow thalli with short or long distances between branching points. Air bladders sometimes occur individually, or 3 next to each other or missing. Pairwise air bladders are close after each other in some individual while there is a relatively long distance between them in others. Secondary branches may occur particularly in regenerating tissues after damage.

A form completely without air bladders is f. *mytilii* (Nieburg) Mathieson & Dawes, which occurs in the Wadden Sea. It grow loosely but attached by the byssus filaments of Blue Mussel (*Mytilus edulis*). Another special form without air bladders is f. *filiformis* (C.Agardh) Kjellman, which is a few centimetres in height and uniform branches, 0.5-1 mm in width. It occurs unattached in the wet part of salt meadows in the Southern Sealand and the archipelago of Smålandshavet, between Sealand and Møn. Sexual reproduction is unknown in these forms.

**Structure:** Construction is as described for the order and genus.

**Reproduction:** The alga is dioecious with ellipsoid rounded or slightly pointed somewhat swollen receptacles.

**Seasonal variation:** Perennial, living for probably 2-3 years in Danish waters. The alga has well developed receptacles all year (Hunding 2021).

**Habitat:** On stone and boulders. Bladder Wrack (*F. vesiculosus*) forms a belt in the lower part of the littoral zone in Skagerrak and the Northern Kattegat where it is replaced by Serrated Wrack (*F. serratus*) in the upper sublittoral zone. In the inner districts of Danish waters towards the Baltic Sea is it always sublittoral, forms a dense crop just below the water surface, and has a scattered distribution at greater depth.

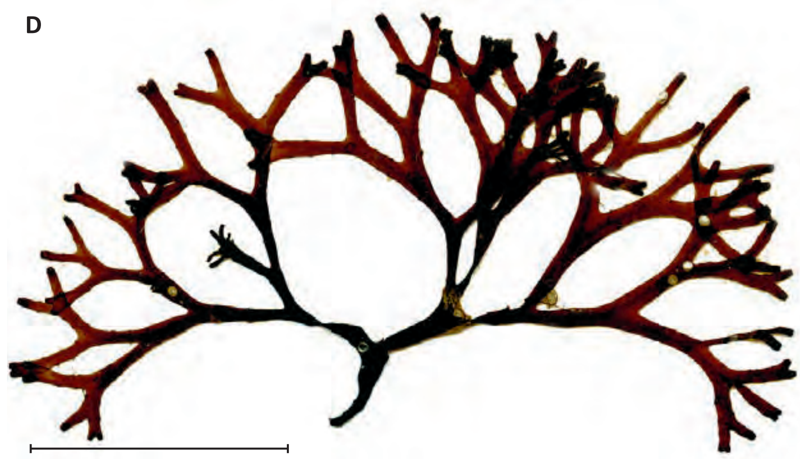
**References:** Billard et al. (2005a, b), Carlson (1991), Hunding (2021), Kalvas & Kautsky (1993), Nienburg (1925, 1932), Parusel (1991), Svedelius (1901).

A

B

A: *Fucus vesiculosus.* Dichotomous flat branches with pairwise air bladders. Lower branches with receptacles (arrow). Beach north of Vesterø Havn, Læsø, 0.5 m, 26.7.2017. Scale 5 cm.

B: *Fucus vesiculosus.* Dichotomous flat branches with pairwise air bladders very close to each other. Kobberhage, drift, 25.8.2017. Leg.: K.L. Krabbe. Scale 5 cm.


C: *Fucus vesiculosus*. Narrow dichotomously branched alga without air bladders, f. *mytilii*. Fanø, Nordby, drift, 24.6.1913. Scale 2 cm.

D: *Fucus vesiculosus*. Very tiny f. *filiformis*. Nyord, Møn, 0.6 m, 21.6.2001. Scale 2 cm.

E: *Fucus vesiculosus*. Small filaments with terminal antheridia; pressed out of male conceptacles. Scale 20 µm. E-F: Gilleleje, 0.5 m, 29.5.2014.

F: *Fucus vesiculosus*. Part of female conceptacle with colourless filaments and oogonia. Scale 50 µm.

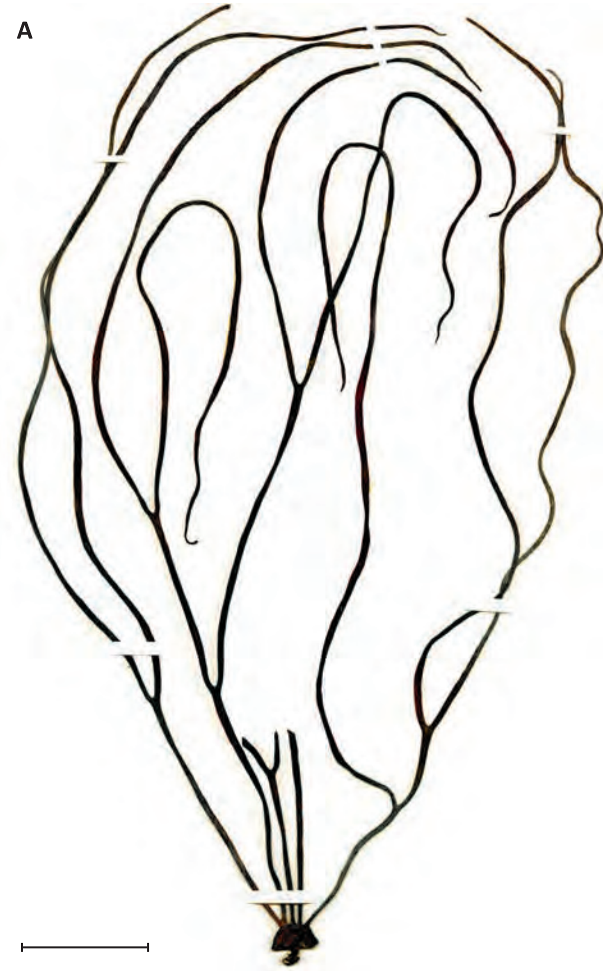

## Family: Himanthaliaceae

# *Himanthalia elongata*

**(Linnaeus) S.F.Gray**

Thong Weed

**Appearance:** The vegetative part of the alga is obconical, 2-5 cm in width. The upper side may be slightly bowl-shaped in old individuals and they are yellow-brown to dark brown. Receptacles resemble narrow dichotomously branched straps and are the major part of the thallus. They arise from the central area of the flat side of the conical vegetative part and are up to 2 m in height and 1-1.5 cm in width.
**Habitat:** Does not grow attached in Danish waters, but sometimes occurs as drift on the West coast of Jutland, on shores of Skagerrak and very occasionally on beaches in the Northern Kattegat. It is frequent in the littoral of wave exposed rocky shores in the North Atlantic.
**Comment:** Drift receptacles often occur without the vegetative conical part.
**References:** Kornmann & Sahling (1977), Kristiansen (2014), Nielsen (1982a, b), Rosenvinge (1905).




A: *Himanthalia elongata.* Long dichotomously branched receptacles from the central part of the small vegetative thallus. Kandestederne, drift, 10.7.1960. Leg.: J. Andersen. Scale 5 cm.

## Family: Sargassaceae

# *Halidrys siliquosa*

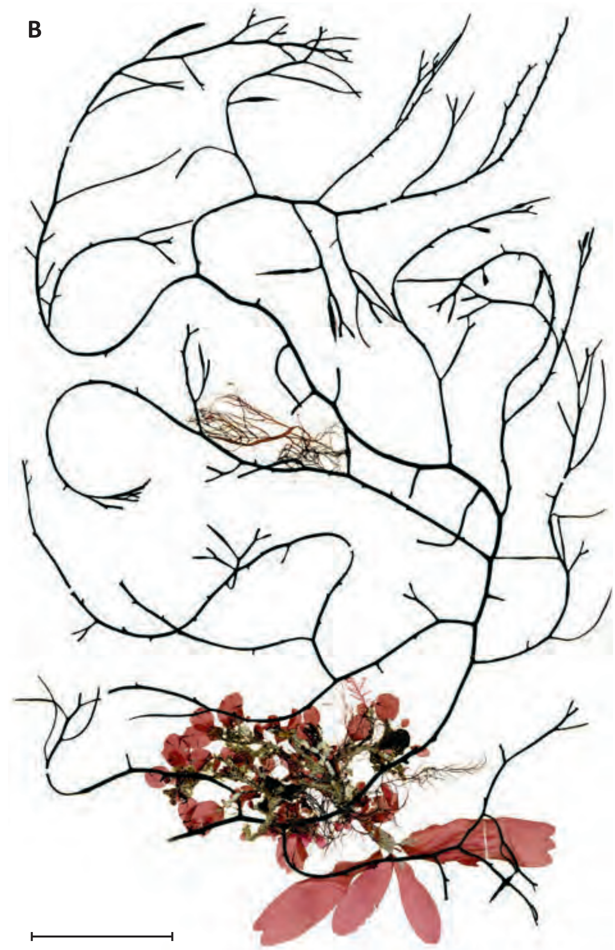
**(Linnaeus) Lyngbye**

Brown Sea Oak

**Appearance:** Tough much branched olive-brown to dark brown bush-like thallus, up to 2 m in height. Branches are leathery, terete to slightly flattened, 1-5 mm in width with scattered distichous branches. Elongate air bladders with internal transverse walls are characteristic, 1-5 cm in height and 2-6 mm in width, with 3-10 seriate compartments. Air bladders are frequent and develop at irregular intervals intercalary in short branches. Base of thallus is compact and conical, up to 5-7 cm in height and in the lower broadest part 3-5 cm in width. Several upright fronds may arise from the upper end of the conical base. Young individuals have flat elongate branches resembling blades. When dry, the alga becomes very dark to almost black.

A form, with terete branches that resembles Clawed Fork Weed (*Furcellaria lumbricalis*) occurs in the


A: *Halidrys siliquosa.* Much branched frond with air bladders (right arrow) and thinner receptacles (left arrow). Briseis Flak, 9 m, 25.3.1992. Scale 5 cm.




B: *Halidrys siliquosa.* Part of a large frond with open branch angles, few branches and few air bladders. Red algal epiphytes: Dulse (*Palmaria palmata*), Sea Oak (*Phycodrys rubens*) and Purple Claw Weed (*Cystoclonium purpureum*). Tønneberg Banke, 15 m, 10.6.1990. Scale 5 cm.

archipelago of Smålandshavet, between Sealand and Møn. It is not attached but the lower part is buried in sand. It is yellow-brown when fresh.

**Structure:** The construction is as described for the order.

**Reproduction:** Monoecious gametophytes. Receptacles are small elongate branches which develop near the apex, are only slightly wider than the vegetative branches and recognizable on the rough surface. Oogonia and antheridia occur in the same conceptacle. Each oogonium contains a single egg-cell.

**Seasonal variation:** Perennial with the largest growth of new shoots in spring and early summer. Receptacles develop in autumn-winter. Young receptacles recorded in October-November, mature receptacles in January-March and may still be present in April-May. Receptacles decay and leave small pin-like structures on the branches when reproduction is finished. Each year, a series of the pin-like structures are left, so by counting these, it may be possible to estimate the age of the thallus, according to Moss & Lacey (1963). Very young thalli with only flat branches, appearing as blades, are observed July-August.

C: *Halidrys siliquosa.* Conical base of old thallus, 2.5 cm in height and 3.5 cm in width, with basal parts of several uprights. Briseis Flak, 9 m, 24.8.2013. Photo by O. Lund.

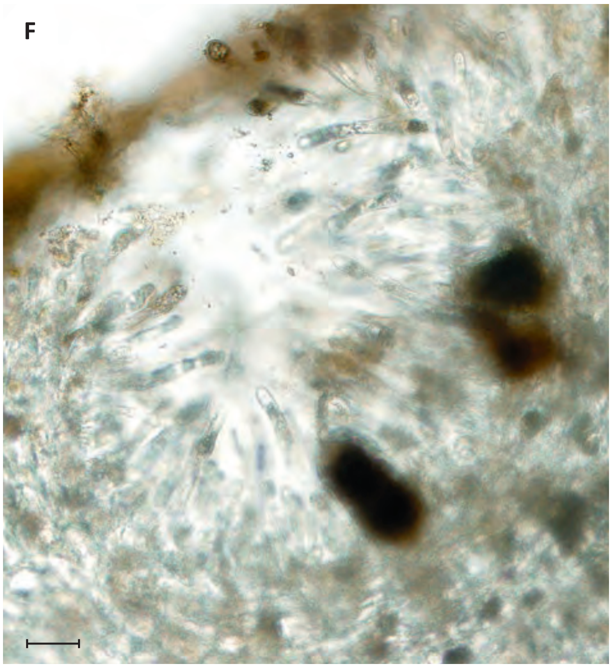
E: *Halidrys siliquosa.* Special form, reminiscent of Clawed Fork Weed (*Furcellaria lumbricalis*). Keldernæs, Lolland, the archipelago of Smålandshavet, between Sealand and Møn, 0.5 m, 9.8.1944. Leg.: S. Lund. Scale 2 cm.

D: *Halidrys siliquosa.* Young individual, only long flat branches like blades. Store Middelgrund, 11 m, 25.8.1993. Scale 2 cm.

**Habitat:** On stone, collected by divers, 2-19 m depth. In older collections by dredge from greater depth, of which a single small slightly decayed alga was from 30 m depth, but this might have been drift.

**Comment:** In the archipelago of Smålandshavet, between Sealand and Møn, only the delicate form, which is reminiscent of Clawed Fork Weed (*Furcellaria lumbricalis*) occurs.

**References:** Fritsch (1965), Moss & Elliot (1957), Moss & Lacey (1963), Nielsen (1985), Wernberg et al. (2000).



F: *Halidrys siliquosa*. Conceptacles with almost mature dark oogonia. Beach north of Vesterø Havn, Læsø, drift, 12.12.2014. Scale 20 µm.

G: *Halidrys siliquosa*. Very young alga, 1 mm in height. Per Nilen, 12 m, 27.8.2013. Photo by S. Lundsteen.

## *Sargassum muticum*

**(Yendo) Fensholt**

Wire Weed

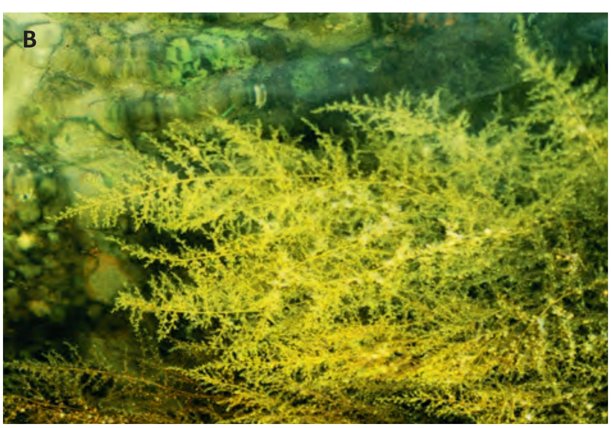
**Appearance:** Large, much branched, yellow-brown fronds, which become more than 2 m in height. Dark brown main axes, 5-10 cm in height, arise from a tough basal attachment disc. Narrow spatula-shaped blades, c. 2 cm in height and several long fronds arise from the main axis. Long fronds are repeatedly branched with main branches and scattered branches on all sides. Delicately dentate bladelets, 1-2 cm in height, are scattered on the branches on all sides together with many small air bladders terminal on short branches. Air bladders are almost spherical or egg-shaped, c. 1 mm in width.

**Structure:** The construction is as described for the order.

**Reproduction:** Fronds are monoecious with more or less terete receptacles that are a few centimetres long. Antheridia develop in male conceptacles and oogonia in female conceptacles. Oogonia contain a single egg-cell. Zygotes germinate immediately, while still attached to the receptacle. Drifting branches with fertilized eggs or germlings are thus very effective units for the spread of the species because the germlings may fall out into the water and settle on solid substratum. Germlings soon become ovoid and divide with many longitudinal and transverse walls. Numerous rhizoids, which attach the alga to the substratum, develop from the narrow end of the germling, and the upright thallus develops from the broad end.

**Seasonal variation**: The main axis is perennial with over-wintering blades. The long shoots are annual, initiated in September-October, with the largest growth

in May-July, receptacles form in late summer, and the annual branches decay and are shed in autumn.
**Habitat:** On small stones in gravelly sand, on boulders and epiphytic on other algae, 0.3-6 m depth.
**Comment:** Invasive species, first observation in Danish waters in the western part of the Limfjord, 1984. With large dispersal potential and the fast growth rate of the relatively large summer frond, Wire Weed (*S. muticum*) has rapidly become a dominant species at several localities in the Limfjord and a strong competitor with the already established algae. The species has also spread to other districts in Danish waters and forms vigorous vegetation at several localities in the Northern Kattegat. It is found attached at the har-



A: *Sargassum muticum*. On small stones on a sandy bottom. A-B: Tile works, Helligsø, 0.5 m, 20.7.1996.

B: *Sargassum muticum*. Air bladders hold the large frond up in the water so it stretches along the water surface.

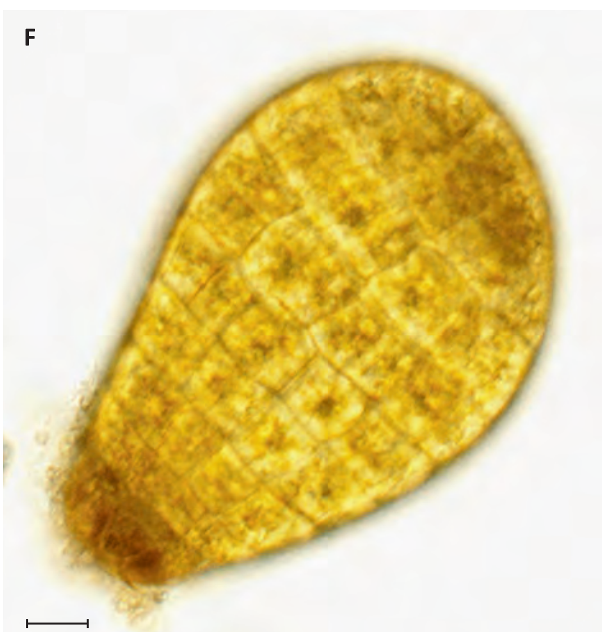
C: *Sargassum muticum*. Basal stem with relatively dark overwintering blades. Upright annual main branch (arrow) has branches with minor blades and many air bladders. Rønbjerg, 0.5 m, 10.5.1993. Leg.: L. Mathiesen. Scale 2 cm.

bour of Aarhus and as drift on shores of North Sealand.

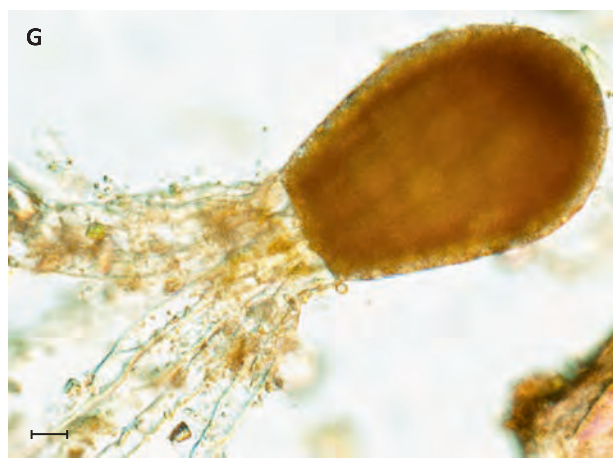
**References:** Christensen (1984), Fletcher (1975a, b, 1980), Oak (2010), Stæhr et al. (2000), Thomsen et al. (2007), Wernberg et al. (2000), Wernberg-Møller et al. (1998).


D: *Sargassum muticum*. Small winter alga with relatively long, wide blades. Venø Færgehavn, Kleppen, 0.5 m, 16.1.1996. Leg.: L. Mathiesen. Scale 2 cm.


E: *Sargassum muticum*. Part of frond with narrow blades (upper arrow), air bladders and receptacles (lower arrow), in late summer. Scale 2 cm. E-G: Vesterø Havn, Læsø, 0.5 m, 12.8.2015.




F: *Sargassum muticum*. Young ovoid germling with small buds for rhizoids in the narrow end. Scale 20 µm.




G: *Sargassum muticum*. Germling with rhizoids. Scale 20 µm.

**Order: Laminariales · Family: Alariaceae**

# *Alaria esculenta*

**(Linnaeus) Greville**

Dabberlocks

**Appearance:** Elongate large blade with approximately parallel sides and narrow to triangular lower part arising from a terete stipe. In continuation of the stipe the blade has a conspicuous solid midrib. The frond is yellow-brown and might become several metres in height and 10-20 cm in width. The upper part of blade is commonly decayed, and at the apex only the midrib remains. The lower part of the stipe has a short, root-like holdfast (haptera) for attachment of the thallus. Spatula-shaped blades (sporophylls), up to 20 cm in height and 3-4 cm in width, occur along the stipe.

**Reproduction:** Unilocular sporangia, together with paraphyses form a covering on both sides of the sporophylls.

**Habitat:** Does not grow attached in Danish waters, but now and then occurs as drift at the shores of West Jutland, Skagerrak and the Western part of the Limfjord. Common in the upper part of the sublittoral at wave exposed rocky shores in the North Atlantic.

**References:** Kristiansen (2014), Nielsen (1982a), Rosenvinge (1905).


A: *Alaria esculenta*. Elongate blades with conspicuous midrib, terete stipe with haptera at the base. A couple of young sporophylls on the stipes. Uggerby Strand, drift.3.5.1981. Scale 2 cm.

## Family: Chordaceae

# *Chorda filum*

**(Linnaeus) Stackhouse**

Mermaids Tresses or Bootlace Weed

**Appearance:** Long, terete, unbranched yellow-brown to dark brown alga, which appears as cords in the water. Typically, 0.5-1.5 m in height and 0.5-3 mm in width, but may be up to 3-4 m in height. Upright thalli arise from a small attachment disc. The cord decreases slightly in width towards the top into a very narrow constriction, 10-20 cm below the apex. Young thalli are covered by colourless hairs. Older thalli are hollow. Strangely-shaped specimens, which in the area of the thalli at the water surface are twisted and blown up, occasionally occur in late summer. Fertile thalli are covered by paraphyses and unilocular sporangia apart from a short stipe, which is a few centimetres in height.
**Structure:** Parenchyma with an intercalary growth zone at the constriction, 10-20 cm below the apex. The central cavity is surrounded by a medulla of 4-10 layers of pale elongate cells with thick walls. The innermost part of the medulla has narrow longitudinal filaments and transverse hyphae-like filaments of cylindrical cells which may form internal transverse walls. Towards the surface the elongate cells are broader and surrounded by two layers of small cortical cells with plastids. Cortical cells continue to divide both in longitudinal and transverse directions along with the stretching of medullary cells. Unicellular paraphyses and true brown algal hairs arise from the outer cortical cells. Paraphyses are unicellular, club-shaped and contain several elongate plastids. The attachment disc is formed by downward-growing rhizoids.
**Reproduction:** Unilocular sporangia are elongate ellipsoid, develop from cortical cells and appear between the paraphyses. Swarmers from unilocular sporangia germinate and develop into microscopic uniseriate filaments, which are dioecious male and female gametophytes with oogamous reproduction. Male gametophytes are thinner and more branched than female gametophytes. Sexual male cells have flagella (spermatozoids) and develop in small elongate ellipsoid antheridia at the apex of branches in the male gametophytes. Club-shaped oogonia form at branch apices of female gametophytes with a single egg-cell in each. The egg remains in the oogonium at maturity but grows so the upper part breaks through the oogonium wall. The eggs are fertilised after chemical attraction of spermatozoids (Müller et al., 1985). The zygote germinates and develops a new upright sporophyte.
**Seasonal variation:** Summer alga, which appears in spring and decays late in the year. Over-wintering as gametophytes or in rare instances as upright thalli. Collected in April-November and a few decaying individuals in January (March). Unilocular sporangia recorded in summer and autumn.

A

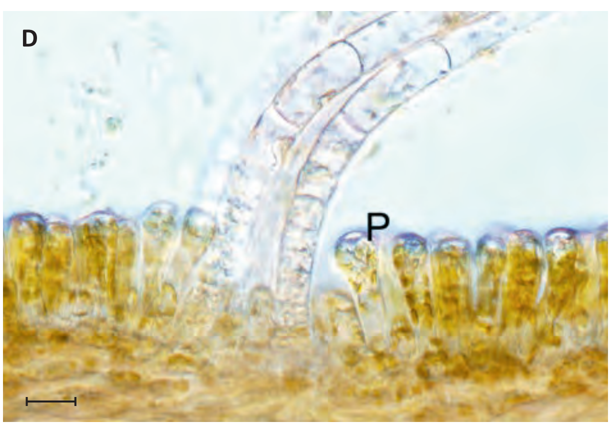
A: *Chorda filum*. Long unbranched terete algae appearing as cords, constriction slightly below the apex (arrow). Deget, Frederikshavn, shallow water, 18.7.1963. Scale 2 cm. Leg.: C. Hansen.

**Habitat:** On pebbles and mollusc shells on sandy bottoms, sparsely on boulders where it may occur epiphytic on coarse algae, also on the rhizomes and leaves of Eelgrass (*Zostera marina*). Typically in shallow water and collected by divers to 15 m depth. Collected by dredge at Bornholm, 20 m depth and in The North Sea, 31 m depth.

**References:** Kylin (1918, 1933), Maier & Müller (1986), Müller et al. (1985), Rosenvinge & Lund (1947), Sasaki & Kawai (2007), South & Burrows (1967).


B: *Chorda filum*. Part of older alga with swollen and slightly twisted area (arrow). Quintus, Holmen, Copenhagen, 0.5 m, 23.9.1999. Scale 2 cm.


C: *Chorda filum*. Cavity (C), thick-walled medullary cells and cortex of small assimilating cells. Surface covered by club-shaped paraphyses and unilocular sporangia. Transverse section. Beach north of Vesterø Havn, Læsø, 0.5 m, 23.6.2013. Scale 50 µm.




D: *Chorda filum*. True brown algal hairs and club-shaped paraphyses (P) with plastids. Scale 20 µm. D-E: Horneks Odde, Læsø, 0.5 m, 24.9.2017.


E: *Chorda filum*. Unilocular sporangia (S) between paraphyses (P). Scale 20 µm.

## Family: Laminariaceae

Kelps (*Laminaria* spp.) and Sugar Kelp (*Saccharina latissima*) are perennial. They are the largest algae in Danish waters and the dominating element in Danish kelp-forests. Leathery frond consists of a blade and a terete stipe with short branches (haptera)close together in the lower end to form a holdfast which attaches the frond to the substratum. The algae are very smooth and become slimy when picked. The identification of young algae to species is uncertain the first and second year, as all species have an elongate blade and a cylindrical, smooth stipe. Species-specific characters develop later.

Kelps occur in arctic and temperate areas in the Northern Hemisphere, where they are frequent along rocky shores. This particularly concerns Forest Kelp (*L. hyperborea*), which forms kelp forests of large tough thalli with long thick stipes on exposed shores and in the shallow subtidal in the North Atlantic among other places including the Faroe Islands and along the west coast of Norway. At low water the upper part of the stipes and blades are typically visible above the water in many localities. In Denmark Forest Kelp (*L. hyperborea*) is smaller than in the North Atlantic and has relatively short stipes. It grows in the sublittoral on stone reefs and occurs as drift at the beaches of the North Sea, Skagerrak and occasionally the Western part of the Limfjord. Sugar Kelp (*Saccharina latissima*) and Oar Weed (*L. digitata*) occur near the water's edge in the Northern Kattegat, but in the Baltic Sea with brackish water, they are submerged and only occur at greater depth.

Kelps grow all year, but with the largest increase in the thallus in winter and spring. They have an intercalary growth zone at the transition area between the stipe and the blade, which every year forms a new blade. This develops between the stipe and the old blade, which is pushed up and in time torn away. Between the old and the new blade there is a narrow area, especially noticeable in Forest Kelp (*L. hyperborea*) and Sugar Kelp (*S. latissima*), while the transition area in Oar Weed (*L. digitata*) is less pronounced. In early summer kelps with both the old and a young blade are frequent. It is unusual to find such individuals with more than these two blades, but it may happen in very sheltered localities. The blades therefore are seldom more than one year old, and the youngest part is next to the stipe. Contrary to this the stipes can be several years old. They grow both longitudinally and in transverse direction, with the oldest part in the centre and at the base. The growth zone contributes to the longitudinal growth of the stipe, and near the surface there is a layer of actively dividing cells which contribute to the width. As the growth does not happen with the same speed all year, annual growth rings are formed. Small cells develop with the slowest growth while larger cells form during rapid growth in spring. Annual rings are visible in transparent light in cross-sections of the stipes, and best seen in the basal part of Forest Kelp (*L. hyperborea*). Longitudinal sections in the lower part of Forest Kelp (*L. hyperborea*), reveal that the haptera develop in whorls, and each of them corresponds to an annual ring (Kain, 1963). After some training, is it thus possible to estimate the age of an alga by counting the number of haptera-whorls and annual rings. Forest Kelp (*L. hyperborea*), 7-8 years old, have been collected in the Northern Kattegat.

**Structure:** Parenchymatous thallus has a surface of small assimilating cells with many disc-shaped plastids. The small surface cells continue to divide, and in the growth zone, tangential divisions contribute to the growth in thickness. Longitudinal growth in the inner part of the thallus takes place by stretching. Cells just below the surface layer become larger both in height and width. Cells towards the centre stretch and become pointed. The elongated cells divide by transverse walls, and the longitudinal walls become wider. Simultaneously, thin hyphae-like filaments arise from the cells. Medullary cells in the centre have very wide longitudinal walls. They stretch so much that the original width is only present in the transverse walls and cells termed trumpet cells. The hyphae weave the medullary cells together and contribute to the strength of the thallus. The surface cells continue to divide far up the blade so the area increases. Growth in thickness of stipes takes place in a cell layer below the surface cells. The three species found in Denmark typically have mucilage ducts immediately below the growth layer. In Oar Weed (*L. digitata*) and Sugar Kelp (*S. latissima*) this is only in the blade, while Forest Kelp (*L. hyperborea*) also has mucilage ducts in the stipe. Mucilage ducts develop as small cavities between the cells. There are small groups of cells on the inner surface of the thallus which probably produce the mucilage. Alginate is exuded together with the mucilage.

**Reproduction:** The life history, is known from culture studies. Upright fronds are the sporophytic generation (macrothallus). At maturity a dense cover of unilocular sporangia and club-shaped unicellular paraphyses form large spots (sori) on the surface of both sides of the blades. Unilocular sporangia appear as small spindle-shaped sacs, which after meiosis contain many swarmers. Swarmers germinate and develop microscopic, few celled filamentous microthalli, which are male and female gametophytes with oogamous reproduction. Sexual cells develop in antheridia and unicellular oogonia. Mature egg-cells emit a scent (lamoxirene), which causes the antheridia to release the spermatozoids, which are then attracted by the eggs. The fertilized eggs germinate and develop into new sporophytes. Young sporophytes soon develop stipe and blade which are monostromatic in very young thalli.

Laboratory experiments have shown that red light prohibits the development of sexual cells in the microthalli. Therefore, it is possible to keep vegetative gametophytes in culture and control the development of sexual cells by adjustment of the light (Lüning, 1990).

Old blades of Forest Kelp (*L. hyperborea*) and Sugar Kelp (*S. latissima*) have irregular dark brown spots of sori in winter. Blades typically have holes of the same size and shape as the sori, after the release of swarmers. The seasonality of Oar Weed (*L. digitata*) is less stable, the sori are inconspicuous and olive-green, and occur in late summer and autumn.

**Comment:** There is tradition for eating *Saccharina japonica* (Areschoug) C.E.Lane, C.Mayes, Druehl & G.W.Saunders (previous *L. japonica* Areschoug) in Japan and China. This species, which is similar to Sugar Kelp (*S. latissima*), is called kombu in Japan, and hai dai in China. In both these countries many thousands of tons are consumed every year, so the species is economically important. The alga is collected from shores and also cultured at sea, where it grows attached to rope or net with large meshes and are kept at a suitable depth by floats and anchors. Sea temperatures in China are too high in summer for growth of *S. japonica*, but microthalli are maintained in laboratories, where the gametophytes develop under artificial light and at suitably low temperatures. When sea temperature in autumn is sufficiently low, the young sporophytes are moved into the sea, where they grow large. Previously, porous clay pots with nutrients were placed between the sporophytes and the nutrients leaked out over time. This procedure is no longer economic. Today a nutrient solution is regularly spread over the sea crop from boats to fertilize the crop.

*Laminaria* is used in Western countries for the extraction of alginic acid. The salts, alginates are used as stabilisers and emulsifiers in cosmetics, food and pharmacy (alginate E number = E 401). In Europe *Laminaria* is harvested off the coast of Brittany, France, Ireland, at the west coast of Norway and in Iceland (Briand, 1991). There is a long tradition for collecting in Brittany (Arzel 1987). In Iceland the harvest of Oar Weed (*L. digitata*) began in 1975 and has increased with up to 5200 tons wet weight per year, and the harvest of Forest Kelp (*L. hyperborea*) began in 2009 with up to 1350 tons wet weight per year (Karl Gunnarsson, personal information). In Denmark and on the Faroe Islands (Bruhn et al., 2016, Marinho et al., 2015, Mols-Mortensen et al., 2017) culturing at sea began with Sugar Kelp (*S. latissima*). Previously, drift algae and particularly the large brown algae were collected and used as fertilisers in farms.

**References:** Arzel (1987), Briand (1991), Bruhn et al. (2016), Christensen (1966, 1980), Kain (1963), Lane et al. (2006), Lüning (1990), Lüning & Müller (1978), Maier & Müller (1986), Marinho et al. (2015), Mols-Mortensen et al. (2017), Müller & Gassmann (1980), Müller et al. (1985), Rosenvinge & Lund (1947).

# *Laminaria*

Kelps

**Identification key to species of *Laminaria***

| | | |
|---|---|---|
| 1a. | Stipe slightly conical and rough in older individuals, typically with mucilage ducts, not flattened in upper part. Haptera in whorls in longitudinal rows. Typical blades are extended in a broad fan-shape, the lower part frequently heart-shaped. Narrow transition between old and new blades | *L. hyperborea* |
| 1b. | Stipe cylindrical and smooth, without mucilage ducts, commonly flattened in the upper part. Haptera arise displaced from each other. Typical blades have approximately parallel sides and extend from an acute angle at the base. Gradual transition between old and new blades | *L. digitata* |

## *Laminaria digitata*

**(Hudson) J.V.Lamouroux**

Oar Weed

**Appearance:** Brown, yellow-brown or olive-green alga, the blade regular and smooth, split in several narrow parts, the stipe smooth and flexible cylindrical but often flattened in the upper end. Haptera arise in no particular order, are close together, relatively long or short and more or less branched. The part of the stipe where the haptera occur is short and may be slightly bulbous. There is an even transition from the old to the young blades. Morphological variation is large. Some individuals have relatively long stipes, blades with approximately parallel sides, split in many narrow lobes and with a small triangular base. Such individuals are often up to 1 m in height and 20-30 (-40) cm in width. Thalli of this morphology may be extremely large and occur as drift on the shores of Skagerrak or attached to stone reefs in the Northern Kattegat or in the northern part of Great Belt. An alga which was collected at Broen, Great Belt, 12 m depth, 10.9.1991, had a 51 cm long stipe, and the blade was 229 cm in height and 59 cm in width. Other individuals have short stipes, widely extended blades with a broad, more or less heart-shaped base. In some thalli the blade is slightly bow- or hood-shaped (cucul-

A

A: *Laminaria digitata.* Blade with roughly parallel sides, narrow lobes and base with an acute angle. Skiveren, drift, 14.6.1991. Scale 5 cm.

B

C

D

E

F

B: *Laminaria digitata*. Blade with parallel sides, narrow lobes and a broad base. Grey spots of hydroids. Tangen, 7 m, 15.9.1996. Scale 5 cm.

C: *Laminaria digitata*. Blade with parallel sides, a broad base, not split into lobes. Sjællands Rev, 16 m, 10.9.1996. Scale 5 cm.

D: *Laminaria digitata*. Large alga, old and new blades with an even transition area between them (arrow), upper, old part with many grey hydroids. Lysegrund, 10.5 m, 19.1.1997. Scale 5 cm.

E: *Laminaria digitata*. Young alga, blade not split. Old narrow blade, above the younger broad heart-shaped and brighter blade, which is bowl-shaped and therefore slightly folded. Short stipe. Briseis Flak, 13 m, 7.6.1990. Scale 5 cm.

F: *Laminaria digitata*. Small alga from a wave exposed locality. Exposed side of the northern harbour jetty, Frederikshavn, 0.5 m, 6.6.2002. Scale 2 cm.

late) almost without splitting. Small narrow relatively tough individuals are found in shallow wave exposed water. The alga becomes bright olive-green after drying.

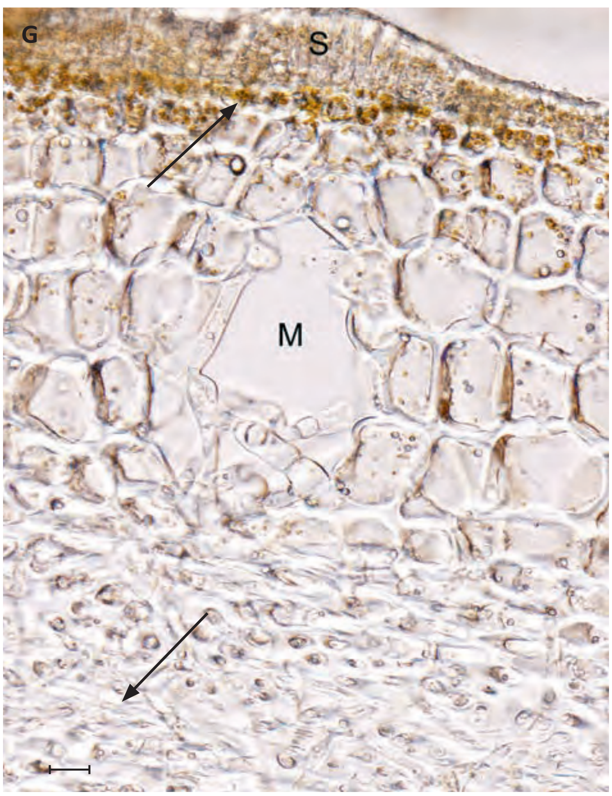
**Structure and reproduction:** Construction and reproduction is as described for the family.

**Seasonal variation:** Perennial, new blades develop in winter, (October), December-January, and old blades are still present in spring to early June. Unilocular sporangia recorded in late summer to May.

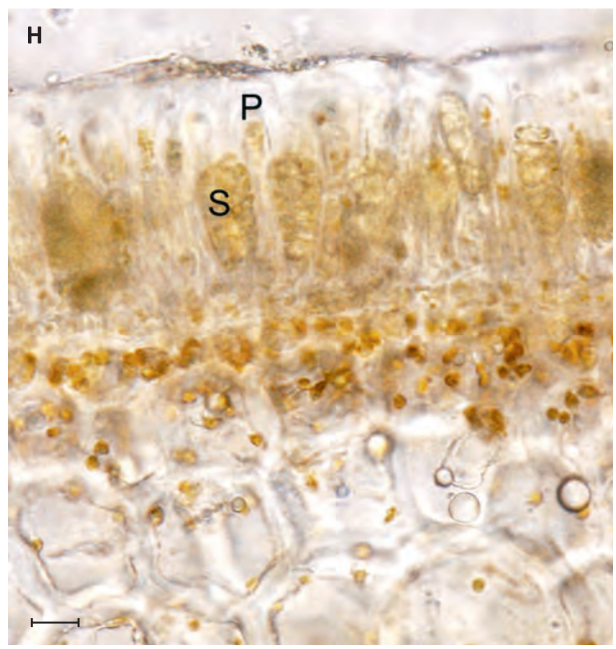
**Habitat:** On stone and small individuals can be epiphytic on other algae. Collected in the Northern Kattegat from 0.5 m depth and by divers to 18 m depth. In the algal herbarium, Natural History Museum of Denmark, the innermost collection towards the Baltic Sea is from the area around Møn, collected by dredge, 7.5 and 11.5 m depth, 1894. In the Sound there is a single alga collected by divers, at Hornbæk, 3 m depth, and two older collections by dredge at Knollen, south of Saltholm, 9.5 m depth, and at Tårbæk Rev, 12 m depth.

**Resembles:** Because of the morphological variation, it is often difficult to distinguish Oar Weed (*L. digitata*) from Forest Kelp (*L. hyperborea*). It is possible to use benzidin which gives a different colour reaction with the two species (Jensen & Haug, 1952). However, this is problematic because the chemical is considered carcinogenic. Furthermore, the solution is not stable, so it has to be prepared immediately before use. Molecular studies were used by Erting et al. (2004) to distinguish species in Danish waters.

**References:** Erting et al. (2004), Jensen & Haug (1952), Rosenvinge & Lund (1947).




G: *Laminaria digitata*. Sporangial sorus (S), monostromatic cortex of small cells (upper arrow). Mucilage duct (M) between large cells, medullary thick walled cells and narrow hyphae (lower arrow). Transverse section. Scale 20 µm. G-H: Beach south of Vesterø Havn, Læsø, drift, 28.11.2017.




H: *Laminaria digitata*. Sporangial sorus, unilocular sporangia (S), paraphyses (P). Transverse section. Scale 20 µm.

## *Laminaria hyperborea*

**(Gunnerus) Foslie**

Forest Kelp, Northern Kelp or Cuvie

**Appearance:** Brown to dark brown alga with a smooth blade, split in several elongate lobes and a stiff terete, slightly conical stipe which has a rough texture. In the Northern Kattegat the blades are typically up to 40-60 (-90) cm in height and the stipes up to 20 (-28) cm long, in Skagerrak the blades may be up to 70 cm in height and the stipes up to 60 cm long (Rosenvinge & Lund, 1947). The bases of blades are typically broad and heart-shaped, and the blades have a uniform height and width or are slightly wider than high. The stipe gradually decreases in width from the base towards the blade. It is fragile and typically snaps when bent. Branches of the holdfast occur in whorls and are short and tough. A new whorl develops each year with new branches just above branches of the year before. Between new and old blades there is a characteristic narrow area. Dried herbarium specimens are brown to dark brown.

**Structure and reproduction:** Construction and reproduction is as described for the family.

**Seasonal variation:** New blades are initiated at the end of December. In spring, thalli appear with both old and new blades. Thalli with the two generations of blades can be observed as late as June-August.

**Habitat:** On stone, collected by divers to 21.5 m depth, and by dredge in the North Sea to 34 m depth. In the Northern Kattegat the uppermost individuals occur at 3-4 m depth. The innermost record towards the Baltic Sea is at Store Middelgrund.

**Resembles:** Sometimes similar to Oar Weed (*L. digitata*), see comment for that species.

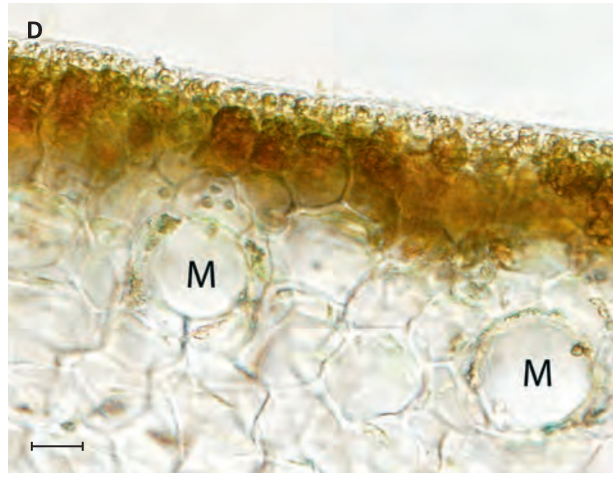
**Comment:** Investigations at Helgoland showed that short days (daylength less than 12 hours) together with the temperature below 15°C were the physical factors that triggered the start of growth in new blades. It was also found that deposited carbon and nutrients were transported from the old to the new blade at this stage.

**References:** Erting et al. (2004), Kain (1963), Lane et al. (2006), Lüning (1990), Lüning & Müller (1978), Rosenvinge & Lund (1947).

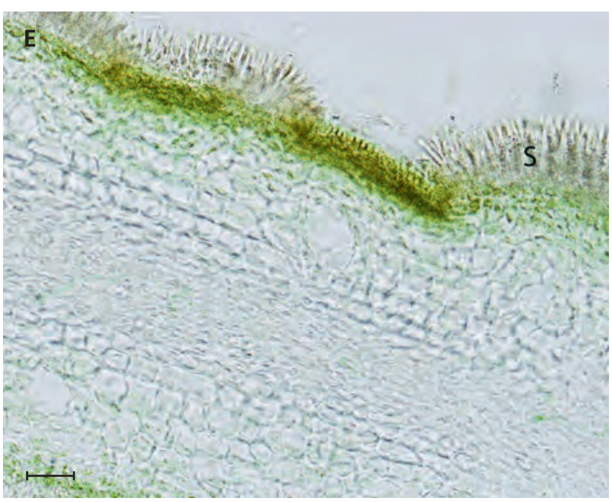

A: *Laminaria hyperborea*. Large alga, old blade with broad base. New blade just started (arrow). Læsø Trindel, 10.5 m, 1.2.1996. Scale 5 cm.


B: *Laminaria hyperborea*. Narrow transition area (arrow) between the old and new blades. Kims Top, 15 m, 4.2.1996. Scale 2 cm.

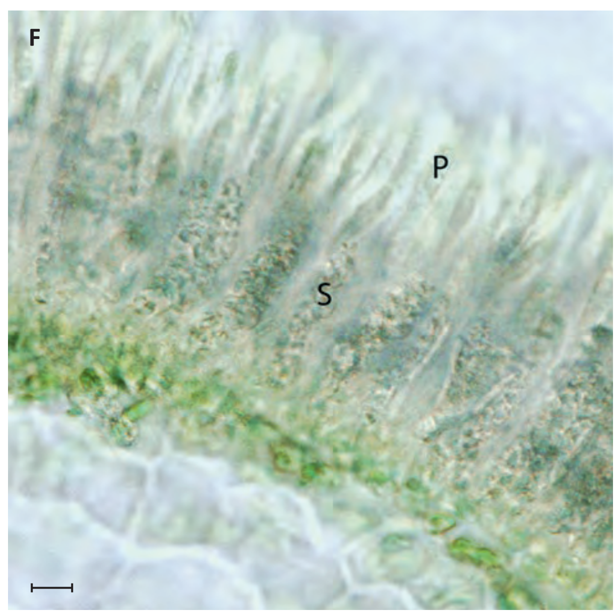

C: *Laminaria hyperborea.* Lower part of stipe with rows of haptera branches. Tønneberg Banke, 14.5 m, 16.1.1997. Scale 2 cm.




D: *Laminaria hyperborea.* Mucilage ducts, appear as round holes (M) in the medulla below the surface of assimilating cells. Transverse section of blade. Læsø Trindel, 14.5 m, 4.6.1993. Scale 20 µm.




E: *Laminaria hyperborea.* Blade with sporangial sori (S), Transverse section. Scale 50 µm. E-F: Store Middelgrund, 5.5 m, 14.1.1997.




F: *Laminaria hyperborea.* Sorus of unilocular sporangia (S) and paraphyses (P) Transverse section. Scale 10 µm.

## *Saccharina latissima*

**(Linnaeus) C.E.Lane, C.Mayes, Druehl & G.W.Saunders**

Sugar Kelp

**Appearance:** Elongate olive-brown to yellow-brown leather-like blades, undivided with approximately parallel sides. The lower part is narrow triangular, rounded or broad heart-shaped. Consistency and size of the blade varies according to the locality. It is typically uneven, curly with a ruffled margin and a narrow, even middle part, blades typically, 1-2 m in height and 10-20 (-30) cm in width. Largest individuals in Danish waters were collected in the Northern Kattegat at Tønneberg Banke, 15 m, 30.5.1992, when one blade was 340 cm in height and 29 cm in width, the stipe in this individual was 10 cm in height. In the northern part of the Sound, blades up to 238 cm in height were recorded by Rosenvinge & Lund (1947). The stipe is cylindrical


A: *Saccharina latissima*. Terete stipe and relatively thick haptera, elongate curly blade with triangular base. Læsø Trindel, 11 m, 4.6.1989. Scale 2 cm.

B: *Saccharina latissima*. Terete stipe and thin haptera, elongate curly blade with broad base. Broen, Great Belt, 17 m, 11.9.1991. Scale 2 cm.

C: *Saccharina latissima*. Narrow area between old and a small new blade. Beach north of Vesterø Havn, Læsø, drift, 6.12.2018. Scale 5 cm.

D: *Saccharina latissima*. Dark brown sorus (lower arrow), and hole after spore release and decay of sorus (upper arrow). Per Nilen, 8 m, 6.6.1989. Scale 2 cm.

and smooth, commonly relatively short, but the length varies, 4-40 cm in height. Haptera are relatively long and in irregular whorls. At the most exposed localities, as Hirtshals outside the lighthouse, blades are coarse, tough and narrow with a triangular base. In more sheltered localities, as Frederikshavn, blades are curly and broad at the base. On stone reefs in deep water at Bornholm the blades are relatively broad and almost transparent and membranous. There is a narrow transition area between old and new blades.

**Structure and reproduction:** Construction and reproduction are as described for the family.

**Seasonal variation:** Perennial with growth of new blades in winter. New blades apparent in December and spring, a few may still be present in July or slightly later. On stone reefs in deep water near Bornholm, thalli have been collected with three generations of blades. Sporangia, which form dark brown sori on both side of the blades, are recorded in December-April and June-October.

**Habitat:** On boulders, and small, young individuals also on gravel or epiphytic on other algae. In Skagerrak and the Northern Kattegat Sugar Kelp (*S. latissima*) occurs at 0.5-21 m depth. In the Sound, south of Elsinore, it only occurs at or below 5 m depth and on stone reefs at Bornholm, collected by divers, 15-21 m depth and by dredge, 30 m depth.

**Comment**: In other localities such as Helgoland, the blades are reasonably even.

**References:** Kristiansen (2014), Nielsen, M. et al. (2016), Rosenvinge & Lund (1947, *Laminaria saccharina*).

## Order: Ralfsiales · Family: Lithodermataceae

### *Pseudolithoderma*

Brown Rock Crusts

**Appearance:** Compact yellow-brown or very dark brown crustose algae. They form small spots or extended coverings on rocks.

**Structure**: Sparsely branched, very closely packed filaments arise from a monostromatic basal layer. Vegetative cells have several disc-shaped plastids, apparently without pyrenoids.

**Reproduction:** Uni- and plurilocular sporangia are terminal on upright filaments and form extended sori without paraphyses.

**Comment:** Species identification is only reliable when fertile in winter. In Danish waters, *Pseudolithoderma extensum* is common, and there is a single collection of *P. rosenvingei*. It is expected that a thorough investigation may reveal more species, including *P. subextensum* (Waern) S. Lund, which is described from the Swedish part of the Baltic Sea. This species is, among other characters characterised by true brown algal hairs.

**Comment:** It is uncertain as to which order the family Lithodermataceae belongs. Silberfeld et al. (2014) referred it to the Sphacelariales, referring to McCauley & Wehr (2007), although these authors recommended that a precise placement should await an investigation of more crustose algae.

**References:** Fletcher (1987), McCauley & Wehr (2007), Silberfeld et al. (2014), Wærn (1949, 1952, *Lithoderma*).

**Identification key to species of *Pseudolithoderma***

| | | |
|---|---|---|
| 1a. | Upright filaments have short broad cells at the base and are separable by pressure. Many plastids in vegetative cells. Sporangia are four-partitioned by longitudinal walls | *P. rosenvingei* |
| 1b. | Upright filaments closely packed and not easy to separate. 2-4 plastids per cell, although difficult to observe. Plurilocular sporangia cylindrical, partitioned by oblique walls | *P. extensum* |

# *Pseudolithoderma extensum*

**(P.Crouan & H.Crouan) S.Lund**

Spreading Brown Rock Crust

**Appearance:** Brown to dark brown slightly matt crusts with an irregular outline and a leather-like consistency. They become 5-10 cm in width and are firmly attached to the substratum.

**Structure:** Monostromatic layer of branched filaments, completely covers the substratum. Upright filaments arise from the basal layer, are very closely packed, up to c. 20 cells in height and occasionally dichotomously branched. Cells are cylindrical, the basal ones short, approximate 0.5 times as long as wide, and become slightly longer towards the upper end, 8-13 µm in width and about as long as wide. Each cell contains 2-4 small disc-shaped plastids, but they are often difficult to see because the cells also contain grains of different assimilation products. The surface of the crust is covered by a thick wall. No brown algal hairs.

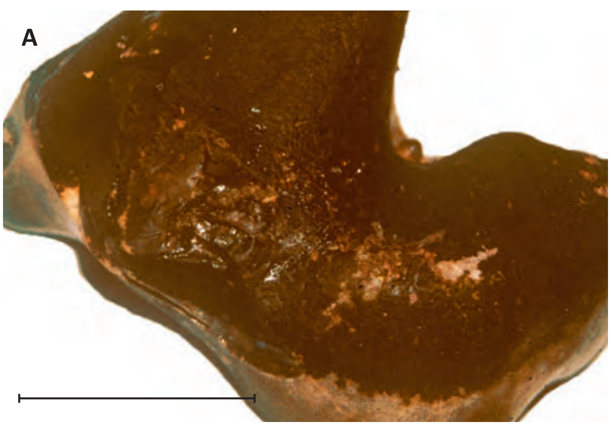
**Reproduction:** Plurilocular sporangia form sori in a large area on the surface of the crust. They develop from apical cells of the upright filaments and are closely packed. They are cylindrical or elongate ellipsoid, 25-33 µm in height and 8.5-11 µm in width. The compartments of a sporangium are separated by characteristic oblique walls. Large ascocysts with a brown content may occasionally occur between the sporangia. Unilocular sporangia may occur and add a dark brown colour to the crusts as opposed to crusts with plurilocular sporangia which are light brown. Unilocular sporangia are broad ellipsoid or spherical, 25-37 µm in height and 10-18 µm in width.

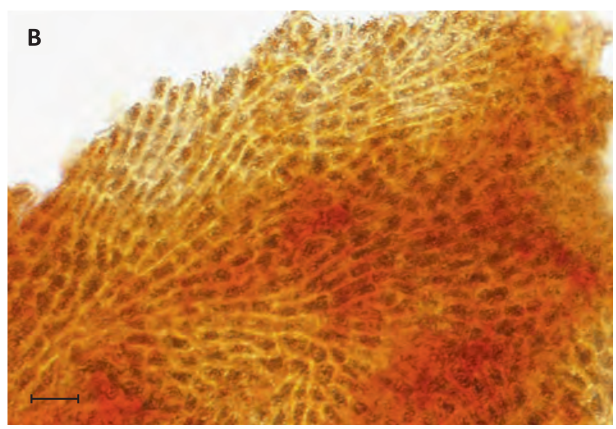
**Seasonal variation:** Perennial, plurilocular sporangia recorded in January-March and unilocular sporangia in January.

**Habitat:** On stones and boulders, 4-25 m depth.

**Comment:** Culture studies of the alga from Helgoland showed an alternation between gametophytes, which had plurilocular sporangia and sporophytes with unilocular sporangia (Peters, 1989).

**References:** Fletcher (1987), Lund (1938, *Lithoderma fatiscens*), Peters (1989), Wærn (1952, *L. extensum*).




A: *Pseudolithoderma extensum*. Brown leather-like cover on stone. Ryggen, Great Belt, 13.5 m, 5.3.1997. Scale 5 cm.

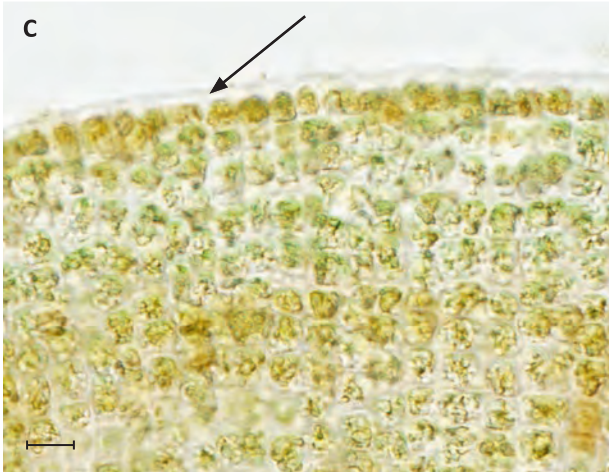
B: *Pseudolithoderma extensum*. Basal layer of radiating filaments, seen from below. Scale 20 µm. B, E-F: Store Middelgrund, 9.5 m, 14.1.1997.

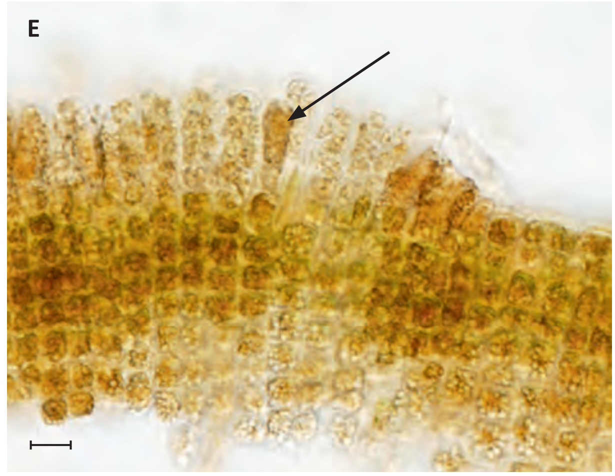
C: *Pseudolithoderma extensum*. Upright filaments closely packed, and surface covered by a thick wall (arrow). Longitudinal section. Scale 10 µm. C-D: Herthas Flak, 20 m, 2.2.1996.

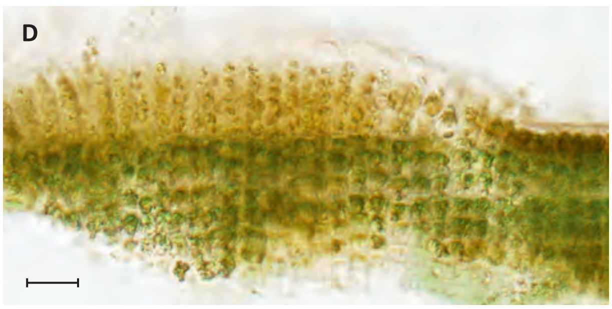
D: *Pseudolithoderma extensum*. Sporangial sorus of plurilocular sporangia. Longitudinal section. Scale 20 µm.

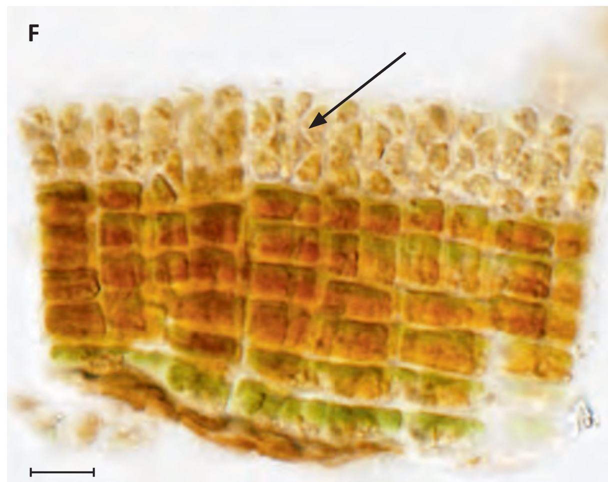
E: *Pseudolithoderma extensum*. Sorus with ascocyst (arrow). Longitudinal section. Scale 10 µm.

F: *Pseudolithoderma extensum*. Plurilocular sporangia, the compartments separated by oblique walls (arrow). Longitudinal section. Scale 10 µm.




## *Pseudolithoderma rosenvingei*

**(Waern) S.Lund**

Rosenvingea's Brown Rock Crust

**Appearance:** Compact crusts firmly attached to the substratum.

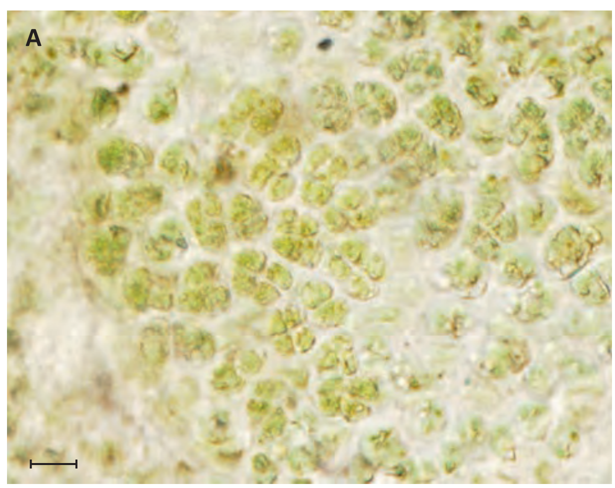
**Structure:** Basal layer of radiating filaments, from which upright filaments arise. These are sparsely branched and separate with pressure. Filaments have relatively short and wide cells at the base (Wærn, 1952). Vegetative cells contain 7-8 or more plastids.

**Reproduction:** Sporangia are terminal on the upright filaments. They appear partitioned in four compartments by longitudinal walls.

**Seasonal variation:** Collected in January with sporangia.

**Habitat:** Only a single collection from Danish waters, 7 m depth.

**References:** Wærn (1952, *Lithoderma rosenvingei*).



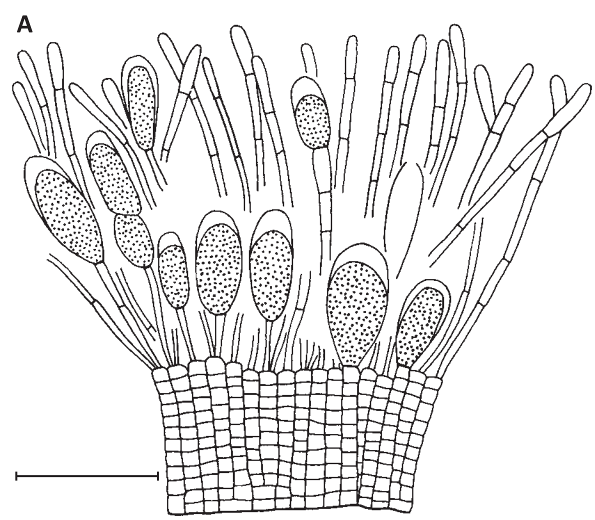

A: *Pseudolithoderma rosenvingei*. Brown crust with sporangia in four parts, seen from above. Schultz's Grund, 7 m, 18.1.1997. Scale 10 µm.

## Family: Ralfsiaceae

# *Ralfsia lucida*

**S.Lund**

**Appearance:** Crustose alga, of which the older crusts are confluent, irregular and cover an area of several $cm^2$. They are yellow-brown to olive-green and become almost black when dry with a shiny surface. Crusts are closely adpressed to the substratum, 40-120 (-225) µm in width. Young crusts are circular in outline, 1-2.5 mm in width.
**Structure:** Upright filaments arise from a basal cell layer and are close together, occasionally with dichotomous divisions and consisting of 8-20 (-35) cells, 5-8 µm in width and 0.5-1 times as long as wide. Thickness varies, the widest cells are at the base or just below a dichotomous division. The uppermost cells contain an elongate plate-shaped plastid. True brown algal hairs develop from apical cells but are rare.
**Reproduction:** Unilocular sporangia together with multicellular paraphyses form an extended sorus on top of the upright filaments. Sporangia are obovate, ovoid or short club-shaped, 38-60 µm in height and 16-21 µm in width. They may form from apical cells of the upright filaments, which may be interpreted as the lower cells of paraphyses, or the sporangia are higher up and develop from cells in the paraphyses, in which case they might be lateral and occur 2 or 3 closely after each other, or terminal. Paraphyses have thin walls surrounded by a mucilaginous substance. They are cylindrical or slightly club-shaped, 80-150 µm in height and 5-6.5 µm in width. They consist of 3-5 cells, of which the lowest 1-(2) are relatively long and colourless, while the upper ones contain an elongate plate-shaped plastid. The cell wall of the lowest thin-walled cells rupture by longitudinal growth and appears as a small collar at the base of the cell. Similar may happens at the base of sporangia. Plurilocular sporangia not observed.
**Seasonal variation:** Collected in December-April, mature unilocular sporangia recorded in February-March.
**Habitat:** Collected on stone and boulders, 0-1 m depth.
**Comment:** *Ralfsia lucida* is described on algae from Denmark (Lund, 1967). It differs from *Pseudoralfsia verrucosa* by not having ascending but upright filaments The paraphyses with a long basal cell and sporangia which are lateral or apical on paraphyses are characters reminiscent of microthalli in species of Scytosiphonaceae. A more natural taxonomic placement of the species must await new investigations.
**References:** Lund (1967).




A: *Ralfsia lucida*. Basal system of closely packed upright filaments, with paraphyses and unilocular sporangia on top. Elsinore. Scale 50 µm. After Lund (1967).

## Family: Pseudoralfsiaceae

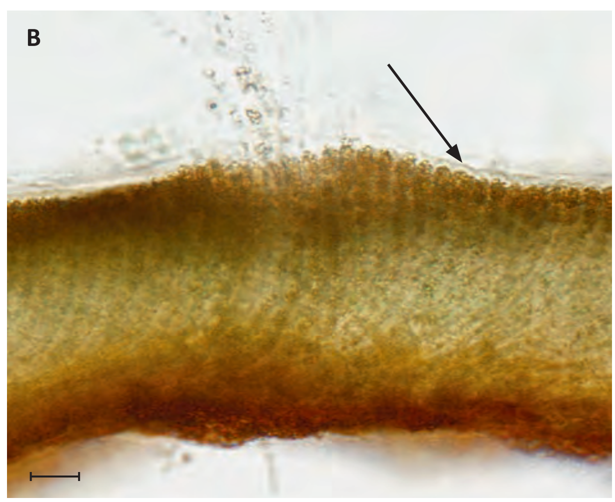
# *Pseudoralfsia verrucosa*

**(Areschoug) Parente, Fletcher & G.W.Saunders**
**Recent synonym:** *Ralfsia verrucosa* (Areschoug) Areschough in Fries
Brown Limpet Paint

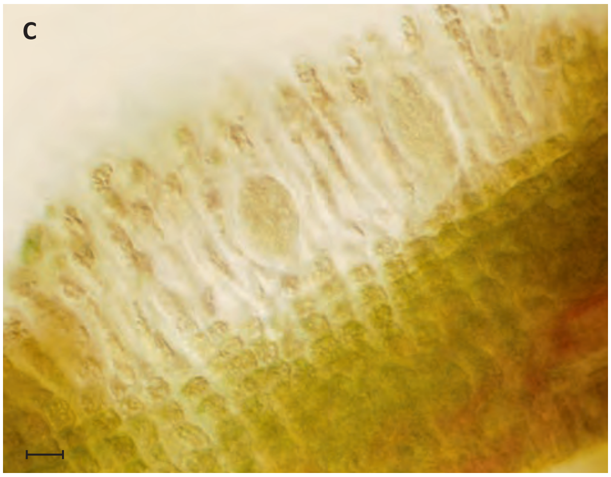
**Appearance:** Dark brown, glossy and very compact leather-like crusts, that are circular and up to c. 5 cm in width, but frequently confluent into irregular spots. They might have yellow-brown growing edges. Crusts are firmly adpressed to the substratum apart from wart-like swellings in the middle part, and the margin which may be slightly loosely attached. The central part of old crusts might be vaulted and worn away so only the ring-shaped peripheral part remains.
**Structure:** Basal layer of confluent branched filaments, stretches along the substratum. Ascending filaments bend upwards from the basal layer, making the basal layer appear polystromatic. Upright filaments consist of many cylindrical cells, 8-12 µm in width, and uniform in width and height, or typically slightly shorter than wide. The cells contain a plate-shaped plastid, apparently without pyrenoid. The plastid typically occurs in the upper part of the cell. Upper cells are covered by a relatively thick outer wall. True brown algal hairs occasional present.

**Reproduction:** Unilocular sporangia together with multicellular paraphyses form sori, which arch slightly above the surface of the vegetative thallus. Unilocular sporangia are terminal on upright filaments, sometimes on a few celled stalk. They are obovate, 31-35 µm in height and 14-14.5 µm in width. Paraphyses may curve slightly over the sporangia, and they consist of cylindrical cells, of which the lower one is approximately the same height as the following cells. Plurilocular sporangia observed once in Danish waters, and sori apparently lacked paraphyses. Plurilocular sporangia are uniseriate, 5.7-5.9 µm in width and 35.5 µm in height.
**Seasonal variation:** Perennial, collected in January, March-November. Uni- and plurilocular sporangia recorded in September.
**Habitat:** On stone, boulders and mollusc shells, most collections from shallow water in the littoral to 2 m depth. Collected by divers to 10 m depth and by dredge at Hanstholm Rev, The North Sea, 23 m depth.
**Resembles:** Different from other brown crusts in Danish waters by the solid construction and the ascending filaments.
**References:** Fletcher (1978, 1987), Kylin (1947). Parente et al. (2021).

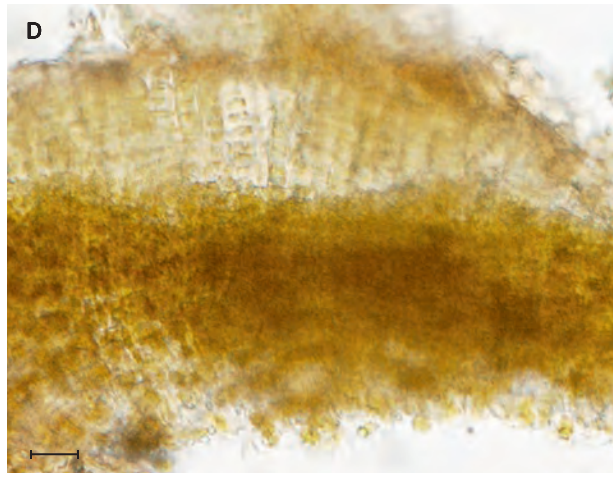

A: *Pseudoralfsia verrucosa*. Circular or confluent uneven crusts on small stone. The match = 5 cm. West of Nordre Rønner, Læsø, 2 m, 19.8.2005.




B: *Pseudoralfsia verrucosa*. Crust of ascending filaments, true brown algal hairs and surface covered by a thick wall (arrow). Saltholm, 0.2 m, 17.7.1997. Scale 20 µm.




C: *Pseudoralfsia verrucosa*. Sorus of unilocular sporangia and paraphyses of relatively short cells. Halskov Rev, 10 m, 25.9.1997. Scale 10 µm.




D: *Pseudoralfsia verrucosa*. Sorus of plurilocular sporangia. On shell of Sand Gaper (*Mya arenaria*), beach north of Vesterø Havn, Læsø, 0.5 m, 1.9.2014. Scale 20 µm.

**Order: Sporochnales · Family: Sporochnaceae**

## *Sporochnus pedunculatus*

**(Hudson) C.Agardh**

Woolly Seed Weed

**Appearance:** Yellow-brown bush-like alga of terete compact branches up to 20 cm in height. An axial branch extends the length of the thallus with a single order of scattered branches. These arise with open branch angles, on all sides or biseriate, are uniform in width and each has a terminal tuft of brown hair-like filaments. Short branchlets with restricted growth occur laterally on branches and are dark with a terminal tuft of brown hair-like filaments. Thalli occur individually or a few together from a small attachment disc.

**Structure:** The central part of branches consists of colourless filaments with relatively long cylindrical cells. The cortex consists of small cells with few disc-shaped plastids. Branches terminate in a tuft of hair-like filaments. These arise from a growth zone which also contributes to the longitudinal growth of the branches (trichothallic growth). Hair-like filaments consist of uniseriate unbranched cylindrical cells with many disc-shaped plastids. The short branchlets arise from surface cells near the apex of the long branches. The branchlets also have trichothallic growth and a terminal tuft of hair-like filaments.

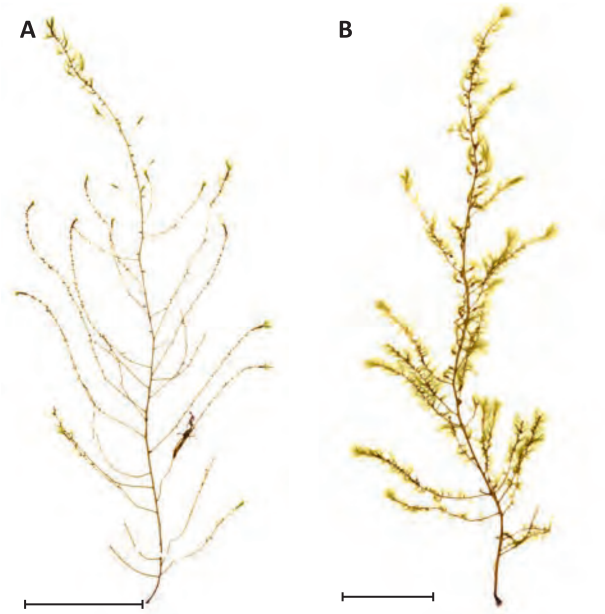
**Reproduction:** Sori of unilocular sporangia and paraphyses develop at the surface of the branchlets and may eventually elongate on the carrying branch. Sporangia are ovoid or ellipsoid. They develop from the lower cells of the club-shaped paraphyses or between them. The paraphyses consist of a few cylindrical cells and a large vesicular apical cell, and they may have small branches.

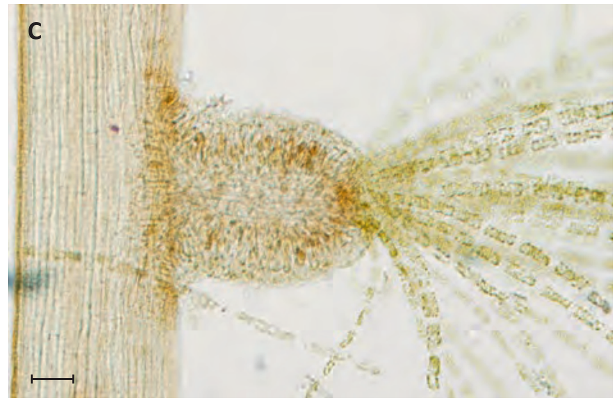
**Seasonal variation:** Collected in July-September with unilocular sporangia.

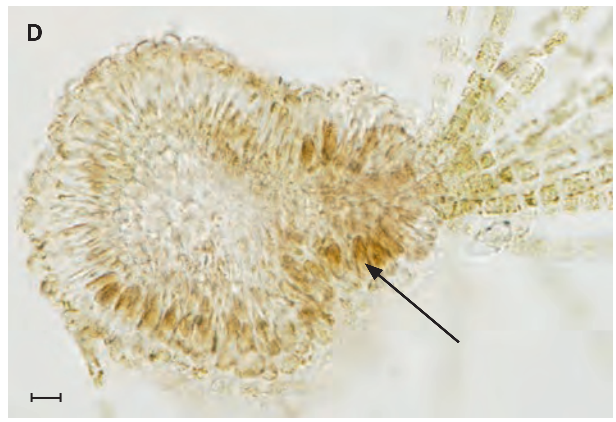
**Habitat:** On small stone or gravel. Collected by divers in the Northern Kattegat, 12-21 m depth and by dredge in the North Sea, 24-38 m depth.

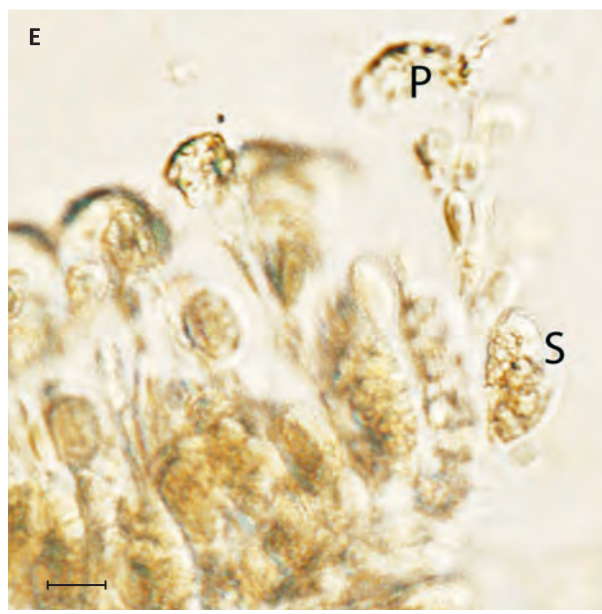
**Comment:** Culture studies in France showed that the life history comprised a microthallus of uniseriate creeping filaments.

**References:** Fletcher (1987), Rosenvinge & Lund (1943).




A: *Sporochnus pedunculatus.* Main branch, long branches, branchlets and terminal tufts of hair-like filaments. Herthas Flak, 20 m, 28.8.1993. Scale 2 cm.

B: *Sporochnus pedunculatus.* Small alga with many hair-like tufts. Tønneberg Banke, 15 m, 17.8.1993. Scale 1 cm.

C: *Sporochnus pedunculatus.* Branchlet with terminal hair-like filaments, many disc-shaped plastids per cell. Scale 50 µm. C-E: Per Nilen, 12 m, 27.8.2013.

D: *Sporochnus pedunculatus.* Branchlet with sorus of paraphyses and unilocular sporangia (arrow), the sorus also cover part of the supporting branch. Transverse section of branch. Scale 20 µm.

E: *Sporochnus pedunculatus.* Part of sorus. Paraphysis with a large apical cell (P), small branches, and at the base a unilocular sporangium (S). Scale 10 µm.

## Order: Tilopteridales · Family: Cutleriaceae

# *Cutleria multifida*

**(Turner) Greville**

Cutler's Many Cleft Weed

**Appearance:** Upright thallus is yellow-brown with a fan-shaped outline. The thallus is repeatedly irregularly split in ribbon-liked sections, with upper parts gradually narrower than the lower ones. Individual parts, 3-5 mm in width with parallel sides, the lowest part of thallus almost triangular. The upper margin terminates in a fringe or tuft of narrow filaments. Thalli attached in Danish waters, are 2-3 (-10) cm in height, while drift thalli are up to 10 (-20) cm in height. The uprights arise from a felt-like disc-shaped base.

Life history comprises upright gametophytes and a small crustose sporophyte. The crust, also known as the *Aglaozonia*-phase, is yellow-brown and appears as a small membrane. It is circular or slightly irregular with a wavy margin, up to 5 cm in width and loosely attached to the substratum.

**Structure:** Uprights have a layer of quadrangular or rectangular cortical cells with many disc-shaped plastids without pyrenoids. Below the surface, cells are larger with fewer plastids. The innermost cells are elongate and colourless. The cortical cells in the lower part of the thallus are irregularly arranged. The cortical cells near the apex form distinct rows which terminate in uniseriate filaments. There is an intercalary growth zone at the base of the filaments. Each of the filaments corresponds to two cell rows in the thallus and like these cells, contain many disc-shaped plastids per cell. Cells below the growth zone stretch and divide both longitudinally and transversely. There are true brown algal hairs, scattered or in small groups on both sides of the thallus.

Crusts grow from the outer edge and have a monostromatic margin. The thallus soon becomes polystromatic by cell divisions behind the marginal area. There are true brown algal hairs which are scattered at the surface. They develop early from surface cells, but gradually as the thallus become thicker they appear as if they originated in a small groove. Many few-celled rhizoids develop from the underside of the thallus. They are branched or unbranched and have a small attachment pad.

**Reproduction:** Upright thalli are dioecious gametophytes with oogamous reproduction. Sexual structures occur in sori with true brown algal hairs on both sides of the thallus. Male gametophytes have small uprights of uniseriate slightly curved branches with lateral or apical antheridia. These are cylindrical, (49-) 57-62 (-64) µm long and 9-12 µm wide, multiseriate with up to 16 levels and up to 8 compartments at each level, and with a single spermatozoid per compartment. Oogonia are short cylindrical to broad ellipsoid, 49-62 µm long and c. 31 µm wide. They are lateral or apical on few-celled stalks. There are 4-5 cell levels in height, biseriate or with up to 4 cells in each level. Crustose sporophytes form unilocular sporangia as a cover on the surface. The sporangia are c. 30 µm in height and approximately half as wide.

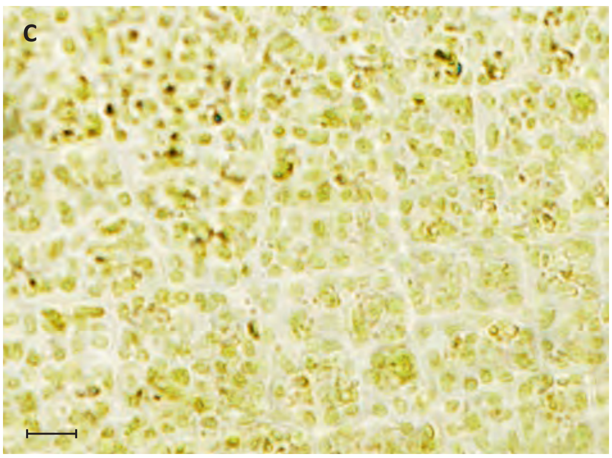
Culture studies of the alga from European waters showed sexual reproduction, in which spermatozoids were chemically attracted by egg-cells. Zygotes germinated and developed into the crustose phase (Müller, 1974). It was also found that the sequence of generations was not always regular, and female gametes might develop directly into the crustose phase. Variations also occurred in the development of spores from the crustose phase (Fletcher, 1987).

**Seasonal variation:** Upright thalli collected in May-August and October. Antheridia and oogonia recorded in August and October. Crustose phase is collected in January and April-October, sporangia recorded in June-July and September-October.

**Habitat:** Uprights recorded on stone, the crustose thalli on stone, gravel, mollusc shells and epiphytic on larger algae.

**References:** Coppejans (1983), Fletcher (1987), Lund (1950), Müller (1974), Nielsen (1982b).







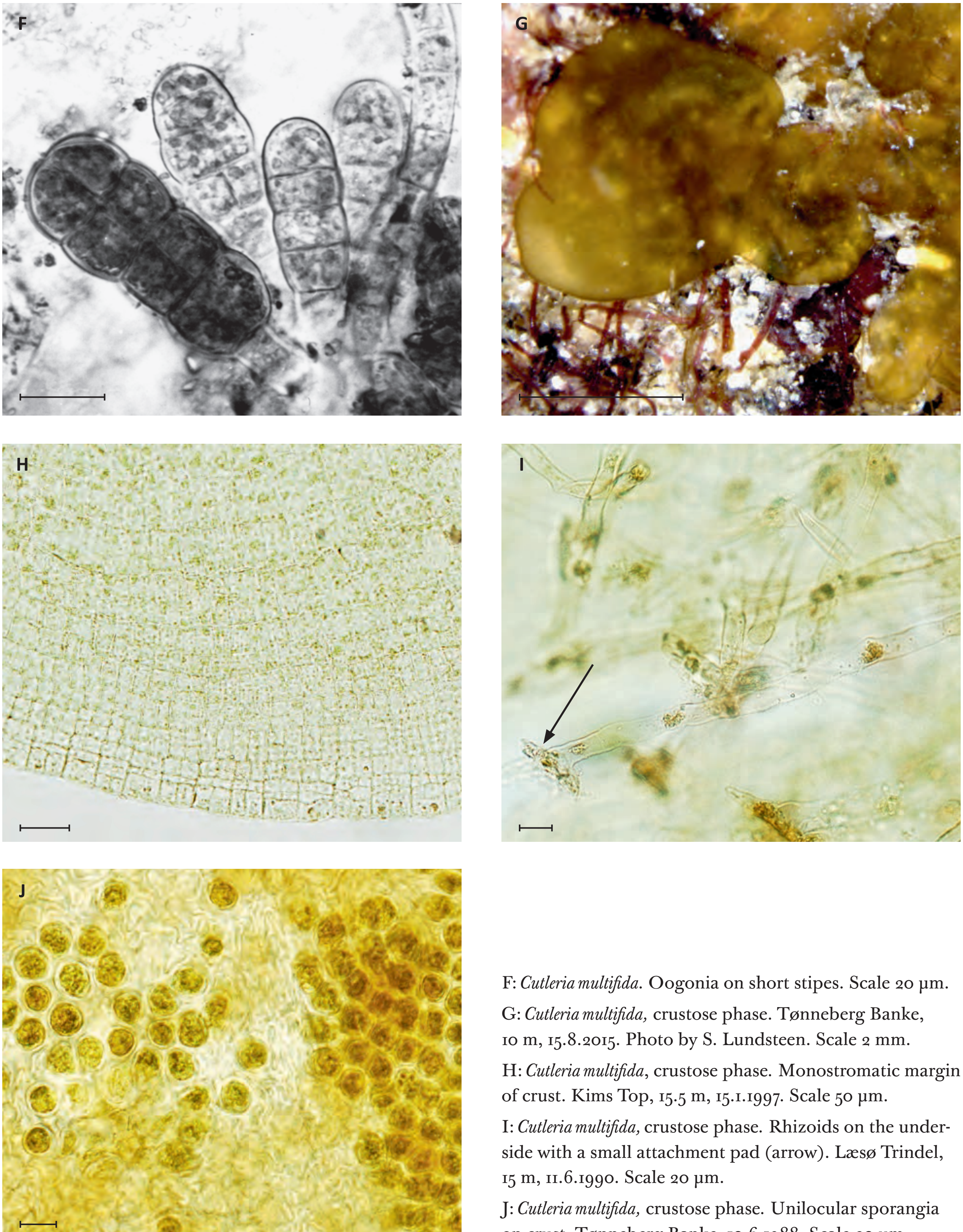

A: *Cutleria multifida.* Fan-shaped and split alga with hair-like filaments at the apices. The beach northwest of Råbjerg Kirke, drift, 22.8.1959. Leg.: T. Christensen. Scale 2 cm.

B: *Cutleria multifida.* Apical part of uniseriate filaments with growth zone of short cells (arrow). Scale 20 µm. B-D: Tønneberg Banke, 15 m, 20.8.1991.

C: *Cutleria multifida.* Surface cells with many disc-shaped plastids. Scale 10 µm.

D: *Cutleria multifida.* Sorus of oogonia and few true brown algal hairs. Scale 20 µm.

E: *Cutleria multifida.* Antheridia. Scale 20 µm. E-F: Kærsgård Strand, drift, 10.10.1976.




F: *Cutleria multifida*. Oogonia on short stipes. Scale 20 μm.

G: *Cutleria multifida,* crustose phase. Tønneberg Banke, 10 m, 15.8.2015. Photo by S. Lundsteen. Scale 2 mm.

H: *Cutleria multifida*, crustose phase. Monostromatic margin of crust. Kims Top, 15.5 m, 15.1.1997. Scale 50 μm.

I: *Cutleria multifida,* crustose phase. Rhizoids on the underside with a small attachment pad (arrow). Læsø Trindel, 15 m, 11.6.1990. Scale 20 μm.

J: *Cutleria multifida,* crustose phase. Unilocular sporangia on crust. Tønneberg Banke, 10.6.1988. Scale 20 μm.

## Family: Halosiphonaceae

# *Halosiphon tomentosus*

**(Lyngbye) Jaasund**

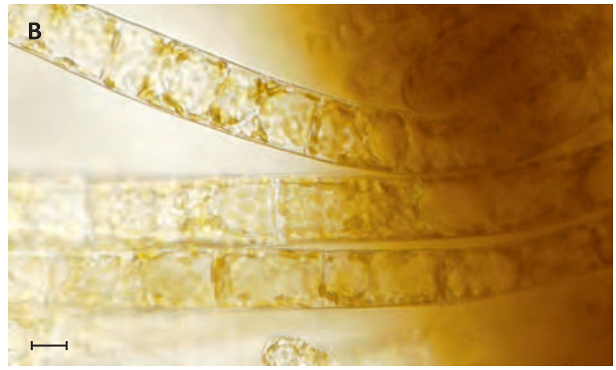
Furry Rope Weed

**Appearance:** Terete thallus reminiscent of a furry string, typically c. 50 cm in height and 2-3 mm in width in Danish waters but can be 135 cm in height. Surface is covered with brown hair-like filaments, 0.7-1 cm in height, except the lowest stipe-like part which lacks filaments. The thallus arise from a disc-shaped base, from which several uprights may occur.

**Structure:** Parenchyma with diffuse growth. Medulla consists of long cylindrical, colourless cells that become shorter and thinner towards the surface. Monostromatic cortex of small angular cells with disc-shaped plastids. Brown hair-like filaments (assimilators) arise from cortical cells. They are uniseriate, unbranched and consist of cylindrical cells with many disc-shaped plastids. Between the assimilators are unicellular cylindrical paraphyses, which have a rounded apex.

**Reproduction:** Unilocular elongate ovoid sporangia develop between the paraphyses. They are slightly shorter than the paraphyses. There is an alternation with a microthallus of small, uniseriate branched filaments, which are monoecious gametophytes with oogamous reproduction. Spermatozoids are chemotactically attracted by egg-cells during sexual reproduction (Maier, 1984).

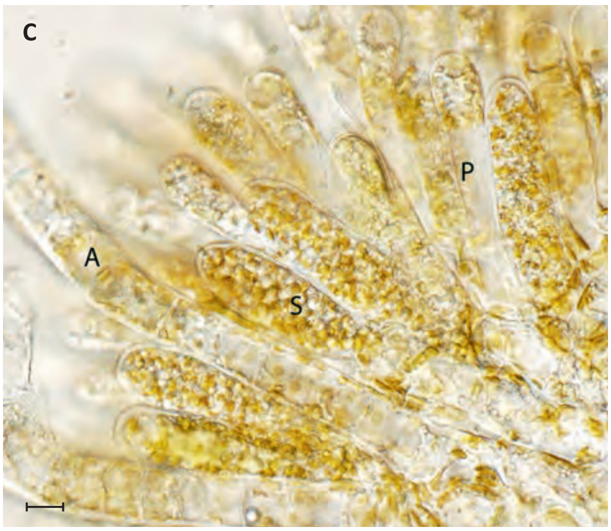
**Seasonal variation:** Occur in spring, collected from end of March to the beginning of July. Sporangia




B: *Halosiphon tomentosus.* Assimilators of cylindrical cells with many disc-shaped plastids. Scale 10 µm. B-D: Gilleleje, 0.5 m, 29.5.2014.


A: *Halosiphon tomentosus.* Rope-like alga surrounded by brown hair-like filaments (assimilators). Lynetteløbet, Copenhagen, 0.5 m, 24.4.1998. Scale 2 cm.

recorded in May-July. Probably wintering as inconspicuous branched filaments.
**Habitat:** On stone from 0.5 m depth, collected by divers to 19 m depth and in older collections by dredge to 35 m depth. The largest and most vigorous individuals grow in shallow waters, whereas at greater depth the alga is tiny and relatively short.
**Resembles:** Decaying individuals without assimilators are reminiscent of Bootlace Weed (*Chorda filum*). They can be distinguished on the paraphyses, which are cylindrical in Furry Rope Weed (*H. tomentosus*) and club-shaped in Bootlace Weed (*C. filum*).
**References:** Jaasund (1965), Kornmann & Sahling (1977, *Chorda tomentosa*), Maier (1984, *C. tomentosa*), Maier & Müller (1986, *C. tomentosa*), Peters (1998), Rosenvinge & Lund (1947, *C. tomentosa*), Sasaki & Kawai (2007), Sundene (1963, *C. tomentosa*).



C: *Halosiphon tomentosus*. Assimilator (A), unilocular sporangium (S) and paraphysis (P). Scale 10 µm.

D: *Halosiphon tomentosus*. Cylindrical paraphysis (P) and unilocular sporangium (S). Scale 10 µm.

## Family: Tilopteridaceae

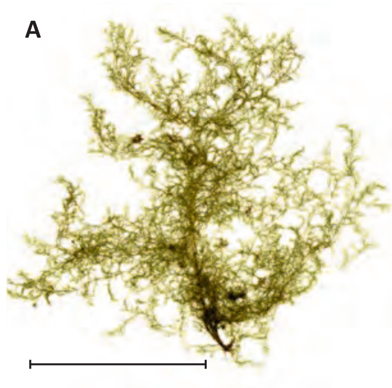
# *Haplospora globosa*

**Kjellman**
Sporethread

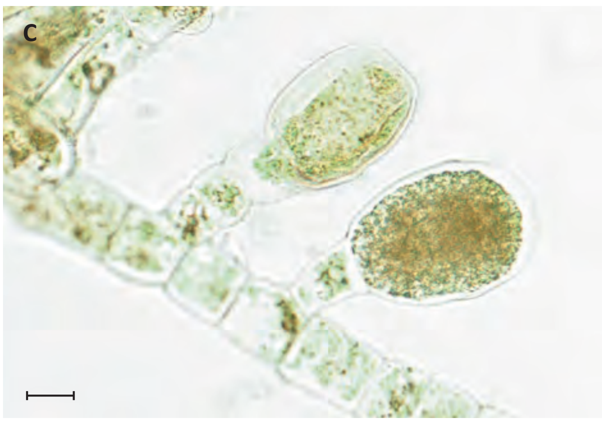
**Appearance:** Delicate, branched, brown bush-like alga with distinct main branch, scattered branches and occasionally with opposite branches. Both a sporophyte and a gametophyte generation occur. The sporophyte generation is up to 23 cm in height and relatively evenly branched. The gametophyte generation is up to 12 cm in height and densely branched with short, recurved branches.

**Structure:** Main branches have scattered branches, which may be unilateral or occasionally opposite. When present, the opposite branches turn in the same direction so the angle between them differs from 180°. Youngest branches are uniseriate with diffuse growth. They gradually decrease in width and terminate in hair-like apices (false hairs). In older branches there are intercalary growth zones, where the cells are shorter than in areas without growth. Oldest parts of the branches have many longitudinal walls and sometimes also secondary transverse walls. Attachment rhizoids arise from the lower part of the main

A: *Haplospora globosa*. Gametophyte with short branches curving backwards. Vejrø, 8 m, 9.4.1989. Scale 2 cm.
B: *Haplospora globosa*. Sporophyte with strait branches. Vejrø, 4.5 m, 26.3.1992. Scale 2 cm.








C: *Haplospora globosa*. Sporophyte, monosporangia on short branches. Store Middelgrund, 15 m, 9.6.1993. Scale 20 μm.


D: *Haplospora globosa*. Gametophyte with intercalary, spherical oogonium (O) and antheridia (A). Scale 20 μm. D-E: Vejrø, 10 m, 9.4.1989.


E: *Haplospora globosa*. Intercalary oogonium next to a vegetative cell. Branches with antheridia. Scale 20 μm.

branches. Vegetative cells contain many disc-shaped plastids. Sporophytes have main branches, 90-110 µm in width, and well-developed cells up to 2 times as long as wide. Gametophytes have main branches up to 120 µm in width, and well-developed cells up to 1.5 times as long as wide.

**Reproduction:** Monosporangia occur in the sporophyte and are apical on unicellular or few celled branches or lateral and sessile, occasionally intercalary or in series in the branches. Mature monosporangia are spherical, 80-105 µm in width, with 4 nuclei. Gametophytes are monoecious. Oogonia are intercalary in branches, almost spherical, 65-82 µm in width, and contain a single nucleus. They develop from a single vegetative cell or after a longitudinal cell division, after which oogonia form in one or both cells. Antheridia are intercalary in short branches, or a whole branch develop into antheridia. They are elongate, 40-175 µm long and 25-40 µm wide and consist of a single layer of small cells surrounding a cavity in the branches.

**Seasonal variation:** Collected in March-June. Sporophytes with monosporangia recorded in April-June, and gametophytes with oogonia and antheridia in April-May.

**Habitat:** On stone and epiphytic on larger red algae, 1.5-22 m depth, collected by divers to 16 m depth and by dredge at greater depth.

**Comment:** Culture studies of Sporethread (*H. globosa*) from Canada, Oslofjord and Helgoland showed a life history in which the sporophyte and the gametophyte alternated irregularly and without sexual reproduction. New sporophytes developed from oogonia, and antheridia had no function, or occasionally also developed into sporophytes. Only sporophytes are known in the nature at Helgoland and gametophytes only formed in a few atypical cases in culture (Kuhlenkamp & Müller, 1985). There are no culture studies of Sporethread (*H. globosa*) from Danish waters. The life history with two generations without sexual reproduction is considered a reduction, which has developed even further in Winged Thread Weed (*Tilopteris mertensii*). The terms used here are based on the morphology.

**References:** Kuhlenkamp & Hooper (1995), Kuhlenkamp & Müller (1985), Kuhlenkamp et al. (1993), Rosenvinge & Lund (1941).

## *Tilopteris mertensii*

**(Turner) Kützing**

Winged Thread Weed

**Appearance:** Filamentous brown bush-like alga, which has main branches with opposite branches in a single plane. Thalli are 2-10 cm in height.

**Structure:** Conspicuous main branch with branches in one plane. Most branches are opposite, but scattered branches occasionally occur. Branches have a terminal false hair. Youngest branches are uniseriate with diffuse growth and short cells. Later, the cells become slightly longer than wide. In the lower part of main branches and the oldest branches there are many longitudinal walls. The main branch is up to 150 µm in width. Vegetative cells contain many disc-shaped plastids.

**Reproduction:** Dark brown unilocular monosporangia are almost spherical and 60 µm in width. They are intercalary in branches and individually or in series of two after each other, seldom 3-4 in a row. Oogonia are also mentioned in literature, but antheridia are not recorded in the alga from Danish waters.

**Seasonal variation:** Collected in March-July, monosporangia recorded in July.

**Habitat:** On mollusc shells, pebbles and on Spider Crab (*Macropodia rostrata*), 2-11 m depth and a single collection by dredge, 25 m depth.

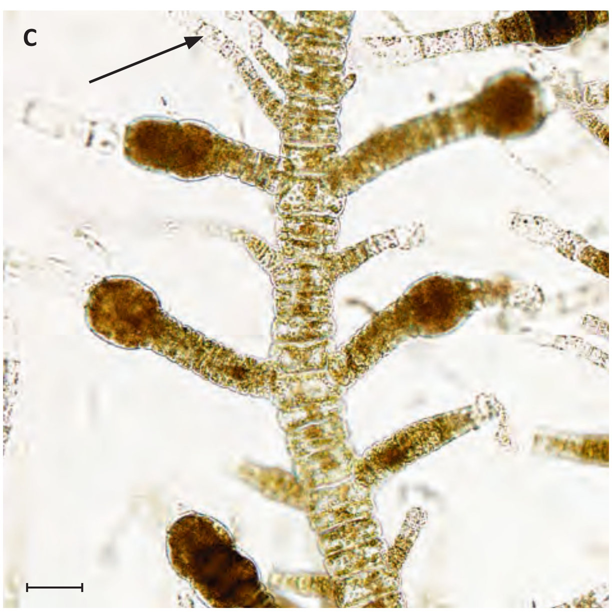
**Comment:** Sexual reproduction never observed. Culture studies of Winged Thread Weed (*T. mertensii*) from Canada and Helgoland showed a direct life history (Kuhlenkamp & Müller, 1985). Spores from oogonia which were not fertilized germinated to new upright thalli, similar to the previous generation. Single antheridia were observed but not fertilization. According to Kuhlenkamp & Müller (1985) the life history is reduced compared with the life history of Sporethread (*Haplospora globosa*), because only gametophytes occur in Winged Thread Weed (*T. mertensii*).

**References:** Kuhlenkamp (1989), Kuhlenkamp & Hooper (1995), Kuhlenkamp & Müller (1985), Moestrup et al. (1975), Rosenvinge & Lund (1941), South (1972).

A: *Tilopteris mertensii*. Small bushy alga, distinct main branch with short opposite branches in a single plane. Trestensrev, Frederikshavn, 5 m, 16.6.1977. Scale 1 cm.

B: *Tilopteris mertensii*. Main branch with opposite branches, diffuse growth and a few longitudinal walls (arrow). Scale 200 µm.

B-D: Læsø Trindel, 8 m, 8.6.1991.



C: *Tilopteris mertensii*. Monosporangia in branches, individual or two in a series. Short branches terminate in false hairs (arrow). Scale 50 µm.

D: *Tilopteris mertensii*. Monosporangia in branch. Scale 20 µm.

# Identification key to genera of Phaeophyceae – Brown algae

## In a few cases identification go to species

| | | |
|---|---|---|
| 1a. | Thallus upright or consists of creeping filaments | 2 |
| 1b. | Thallus a crust, a disc or irregular masses to spherical | 75 |
| 2a. | Macroscopic algae | 3 |
| 2b. | Microscopic algae or only a few millimetres | 92 |
| 3a. | Thallus completely or partly in one plane | 4 |
| 3b. | Thallus terete, unbranched or branched | 19 |
| 4a. | Thallus thin ribbon-shaped or with ribbon-shaped sections | 5 |
| 4b. | Thallus thick, like leather | 10 |
| 5a. | Unbranched ribbon | 6 |
| 5b. | Branched or a divided blade | 9 |
| 6a. | Thallus smooth, surface covered by plurilocular sporangia. One plastid per cell | 7 |
| 6b. | Thallus not smooth, surface with brown algal hairs with sheath. Several disc-shaped plastids per cell | 8 |
| 7a. | Up to 4 cm wide, compact ribbon-shaped blades. Disc-shaped base | *Petalonia* |
| 7b. | 1 mm wide, ribbon-shaped or linear blades, with central cavities. Base of entangled filaments | *Planosiphon* |
| 8a. | Up to 1 (-3) cm wide ribbon-shaped compact blades | *Punctaria* |
| 8b. | Narrow, 2 mm wide, ribbon-shaped, hollow alga | *Asperococcus ensiformis* |
| 9a. | Thallus fan-shaped repeatedly split in sections which become narrower towards the apex and terminate in a tuft of hair-like filaments | *Cutleria* |
| 9b. | Thallus regularly dichotomously branched | *Dictyota* |
| 10a.(4) | Thallus consists of a stipe with an undivided or split blade | 11 |
| 10b. | Thallus branched and not separated into a stipe and blade | 14 |
| 11a. | Blade with a distinct midrib. The stipe may have blades with sporangia | *Alaria* |
| 11b. | Blade without midrib | 12 |
| 12a. | Blade split in elongate lobes | *Laminaria* |
| 12b. | Blade entire | 13 |

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| 13a. | Blade elongate, often ruffled | *Saccharina* |
| 13b. | Blade rounded, smooth and may be bowl-shaped | *Laminaria digitata* |
| 14a.(10) | Dichotomous branches | 15 |
| 14b. | Main axis with branches | 16 |
| 15a. | Up to 1-2 m long, strap-like branches c. 1.5 cm wide, without midrib. Arising from an obconical base, a few cm in height | *Himanthalia* |
| 15b. | Thallus broad ribbon-like, arising from a small basal attachment disc. Frequently with midrib | *Fucus* |
| 16a. | With air bladders | 17 |
| 16b. | Without air bladders, old fronds with spines at edges and a dark brown colour. Young fronds (April-June) covered by brown hair-like filaments | *Desmarestia aculeata* |
| 17a. | Elongate air bladders with internal transverse walls. Thallus olive-brown to dark brown | *Halidrys* |
| 17b. | Air bladders without internal transverse walls | 18 |
| 18a. | Air bladders in the middle of branches. Thallus olive-green | *Ascophyllum* |
| 18b. | Air bladders apical on short branches | *Sargassum* |
| 19a(3) | Thallus unbranched apart from uniseriate assimilating hairs-like filaments or short branches | 20 |
| 19b. | Thallus branched | 34 |
| 20a. | Large algae, typically on stone or other inorganic substrata, seldom epiphytic | 21 |
| 20b. | Epiphytic on other algae, 1 mm to a few cm in height. Forms tufts, which occur scattered or so dense that the host alga appears shaggy | 26 |
| 21a. | Thallus up to 0.5-1.5 m long and 0.5-3 mm wide, shape as a long cord or string | 22 |
| 21b. | Thallus short or delicate | 23 |
| 22a. | Surface shaggy of uniseriate assimilating filaments, which appear as brown hairs. Between the hairs are unicellular cylindrical paraphyses and unilocular sporangia. Diffuse growth. May-June | *Halosiphon* |
| 22b. | Surface smooth, covered by unicellular club-shaped paraphyses, unilocular sporangia and true brown algal hairs. Intercalary growth zone, at a short distance from the apex, gives the thallus a characteristic constriction. June-December | *Chorda* |

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| 23a. | The surface of the thallus covered with large sac-shaped cells, 61-86 µm in height and 43 (-63) µm in width each with several disc-shaped plastids in the outer part | *Delamarea* |
| 23b. | The surface of the thallus consists of smaller cells | 24 |
| 24a. | Plurilocular sporangia develop from special small branch systems on the surface of the thallus and occur like sori which become confluent | *Coelocladia* |
| 24b. | Sporangia develop from surface cells without special branch systems | 25 |
| 25a. | Thallus hollow, typically with constrictions at irregular intervals. The surface of the thallus even and at maturity completely covered by plurilocular sporangia, unicellular paraphyses and true brown algal hairs. One plastid per cell | *Scytosiphon* |
| 25b. | Thallus hollow without constrictions. Surface of thallus with spots of unilocular, seldom plurilocular sporangia, few-celled uniseriate paraphyses and brown algal hairs with sheath. Several disc-shaped plastids per cell | *Asperococcus* |
| 26a.(20) | Uniseriate filaments | 27 |
| 26b. | Parenchymatous filaments | 31 |
| 27a. | Filaments have basal growth and form tufts on host alga | 28 |
| 27b. | Filaments are scattered or form a hairy cover on the host alga | 29 |
| 28a. | Filaments, 0.5-2 cm in height, of cylindrical cells, arise from small knots together with multicellular paraphyses and unilocular sporangia. No brown algal hairs. Typical on *Fucus* spp. | *Elachista* |
| 28b. | Filaments, up to 0.2 cm in height, narrow at the base and the apex (spindle-shaped), most cells barrel-shaped. No paraphyses but true brown algal hairs | *Myriactula* |
| 29a. | Brown algal hairs with sheath at the apex and scattered on the thallus. Many plastids per cell. Plurilocular sporangia conical or elongate ellipsoid, protrude from the surface | *Punctaria tenuissima* |
| 29b. | Filaments without true brown algal hairs | 30 |
| 30a. | Filaments, 7-16 µm in width. All cells gradually become plurilocular sporangia after longitudinal divisions in vegetative cells | *Leptonematella* |
| 30b. | Filaments, 20-40 µm in width. Plurilocular sporangia form belts around the filaments. On leaves of *Zostera marina* | *Halothrix* |
| 31a.(26) | Brown algal hairs with or without sheath | 32 |
| 31b. | Without hairs. Few cm in height and may be slightly club-shaped | *Pogotrichum* |

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| 32a. | Tufts on host alga, up to 1.5 cm in height. Short, more or less confluent branches, which are protruding as the uni- and plurilocular sporangia, scattered on the surface of the thallus. Common on *Scytosiphon* | *Myriotrichia* |
| 32b. | Scattered unbranched threads on host alga, individually or a few from the same base. Sporangia develop from vegetative surface cells and occur scattered among these | 33 |
| 33a. | Brown algal hairs with sheath | *Trachynema* |
| 33b. | True brown algal hairs without sheath | *Litosiphon* |
| 34a.(19) | Coarse bush-like, constructed as a parenchyma or syntagma | 35 |
| 34b. | Fine bush-like, the youngest or all branches are uniseriate, but may by entangled. Older branches sometimes with cortex or a plain parenchyma after formation of longitudinal cell divisions | 62 |
| 35a. | Main branch, 1 mm or more in width, not very smooth or slimy. Branches with spines along the margins | *Desmarestia aculeata* |
| 35b. | More delicate or very smooth, branches without spines | 36 |
| 36a. | Parenchyma with segments of cells which are uniform in height, cortex of small cells may occur | 37 |
| 36b. | Not segmented | 46 |
| 37a. | Delicate alga, uniseriate at base, higher up the cells are longitudinally divided, the alga becomes segmented and the width increase. Plurilocular sporangia in fascicles at the base or sessile on the segmented part of the thallus | *Giraudya* |
| 37b. | The filamentous thalli even in width or widest at base. Filaments stiff, so branches appear bristly, when lifted out of the water | 38 |
| 38a. | Main branches with short, branches in whorls so the alga looks like a dark brown pipe-cleaner | *Cladostephus* |
| 38b. | Branches not in whorls. Parenchyma of even width, with apical cell, much larger than other cells | 39 |
| 39a. | Algae feather-like with rhizoidal cortex | 40 |
| 39b. | Algae irregularly branched or feather-like without rhizoidal cortex | 41 |
| 40a. | Coarse stiff alga, main branches completely covered by cortex | *Chaetopteris* |
| 40b. | More delicate, flexible alga, rhizoidal cortex only covers area between the branches, while the middle part of the main branches lacks cortex | *Battersia plumigera* |

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| 41a. | Tuft, matt or sparsely branched alga. A few mm to 1 cm in height | 42 |
| 41b. | Large stiff bush-like alga, appearing as if cut because many branches end in the same height | *Halopteris* |
| 42a. | Upright tufts | 43 |
| 42b. | Confluent crusts with sparsely branched uprights | 44 |
| 43a. | Segments divided by longitudinal walls, secondary transverse walls rare, but may occur in the lower part of the alga. Propagules frequent | *Sphacelaria* |
| 43b. | Segments divided by longitudinal and secondary transverse walls. No propagules | *Battersia arctica* |
| 44a. | Segments divided by 2-5 longitudinal walls, many secondary transverse walls and many pericysts. Branches 33-50 µm in width | *Protohalopteris* |
| 44b. | Segments divided by a few longitudinal walls, no pericysts, or they are insignificant. Branches < 33 µm in width | 45 |
| 45a. | Segments divided by 1-2 (-3) longitudinal walls, only a few secondary transverse walls. No pericysts. There are many stolons and basal discs of confluent stolons | *Sphacelorbus* |
| 45b. | Segments divided by 1-4 longitudinal walls, many secondary transverse walls, pericysts are insignificant. Basal discs are thick, only few stolons | *Sphaceloderma* |
| 46a.[36] | Branches, including branchlets on all sides with terminal tufts of brown filaments | *Sporochnus* |
| 46b. | Branches do not terminate in tufts of brown filaments | 47 |
| 47a. | With opposite branches | 48 |
| 47b. | Dichotomously branched or with scattered branches | 50 |
| 48a. | Scattered and a few opposite branches. Unilocular sporangia and true brown algal hairs in sori, which form dark whorls on the branches | *Striaria* |
| 48b. | Many opposite branches, without dark whorls | 49 |
| 49a. | Branching rich, regularly opposite, short distance between branching points | *Desmarestia viridis* |
| 49b. | Branching sparse, main branch with long opposite branches, relatively long distance between branching points | *Arthrocladia* |
| 50a. | Parenchyma with cortex of small cells. Much branched on all sides | 51 |
| 50b. | Syntagma | 52 |
| 51a. | Branches terminate in an apical cell | *Dictyosiphon* |
| 51b. | Branches terminate in a true brown algal hair | *Stictyosiphon* |

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| 52a. | Main branch with relatively short branches. Brown algal hair with an unusual long basal cell. Plurilocular sporangia have a lumpy rounded shape | *Halonema* |
| 52b. | True brown algal hairs without long basal cell | 53 |
| 53a. | Thallus with scattered branches, often very smooth. Surface consists of assimilating filaments and true brown algal hairs | 54 |
| 53b. | Thallus pseudodichotomously branched, not very smooth | 60 |
| 54a. | Thallus, 1-7 cm in height, appears shaggy because the assimilating filaments are loosely connected | *Myriocladia* |
| 54b. | Thallus with an even surface | 55 |
| 55a. | Thallus gelatinous and very smooth | 57 |
| 55b. | Thallus smooth with a solid consistency, branching open with long, nearly unbranched branches | 56 |
| 56a. | Thallus dark brown, almost black, branches even in width. Main branch with one generation of long branches, a small second generation branch is sometimes present near the top. Apex blunt | *Chordaria* |
| 56b. | Thallus yellow-brown, branches gradually pointed and terminate in a true brown algal hair (trichothallic growth) | *Acrothrix* |
| 57a. | Small thallus, sparsely and scattered branched or unbranched with soft branches. Plurilocular sporangia from the outer cells in assimilating filaments. On *Zostera marina* | *Cladosiphon* |
| 57b. | Larger algae with scattered branches on all sides | 58 |
| 58a. | Much and repeatedly branched algae, branches even in width and arise at 90° branch angles. The large apical cells of the assimilating filaments are swollen, like a balloon, or spherical | *Sphaerotrichia* |
| 58b. | Much branched with distinct main branch and branches | 59 |
| 59a. | Assimilating filaments increase in width towards the apex. Occur in summer and late summer | *Mesogloia* |
| 59b. | Assimilating filaments even in width. Common in spring and early summer | *Eudesme* |
| 60a.(53) | Syntagma with 4-6 central filaments, visible in transverse section or at the apex, relatively large assimilating filaments or paraphyses all over the surface | *Halorhiza*, *Stilophora* |
| 60b. | Syntagma with one central filament, visible in transverse section or at the apex | 61 |

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| 61a. | In the upper part there are whorls of protruding primary assimilating filaments, 7-9 cells long. Further down the surface is covered by small cortical cells | *Spermatochnus* |
| 61b. | Surface covered by confluent 1-2 cells long assimilating filaments of short, rounded cells | *Stilopsis* |
| 62a.(34) | Thallus resembles string and consists of entangled, uniseriate branched filaments, (7-) 8-9.5 (-11) µm in width. Hook-shaped branches occur. Often epiphytic on *Fucus vesiculosus* | *Spongonema* |
| 62b. | Filaments not much entangled no hook-shaped branches | 63 |
| 63a. | Uniseriate except a few scattered cells which may be longitudinal divided | 64 |
| 63b. | In part a parenchyma (multiseriate) | 72 |
| 64a. | With true brown algal hairs at the apex, growth continues from the cell below the hair (sympodial growth) | 65 |
| 64b. | Without true brown algal hairs, branches often terminate in long pale cells (false hairs) | 67 |
| 65a. | Vegetative cells with many disc-shaped plastids | 66 |
| 65b. | Vegetative cells with ribbon-shaped plastids | *Kuckuckia* |
| 66a. | Plurilocular sporangia elongate ovoid, in dense stands or conical sori | *Botrytella* |
| 66b. | Sori of plurilocular sporangia are irregularly cylindrical or club-shaped. Each sorus appears as a single sporangium, but is a complex of small sporangia, each with separate aperture | *Polytretus* |
| 67a. | Filaments sparsely branched with perpendicular branch angles. Main branches, 30-56 µm in width. Many disc-shaped plastids. Only monosporangia, which are lateral, often on a stipe cell, from which several monosporangia may arise | *Acinetospora* |
| 67b. | Much branched, branch angles not perpendicular, no monosporangia | 68 |
| 68a. | Vegetative cells with ribbon-shaped plastids. Scattered branches on all sides | *Ectocarpus* |
| 68b. | Vegetative cells with disc-shaped plastids | 69 |
| 69a. | Uni- or plurilocular sporangia in intercalary series in branches. Opposite branches occur. Longitudinal divisions of scattered cells occur. Common in the littoral and upper part of the sublittoral | *Pylaiella* |
| 69b. | Sporangia lateral, sessile or on short stalks | 70 |

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| 70a. | Intercalary growth, localised in growth zones, often below an apical false hair | 71 |
| 70b. | Diffuse growth | *Hincksia* |
| 71a. | Filaments < 21 µm in width | *Hincksia ovata* var. *intermedia* |
| 71b. | Filaments >21 µm width | *Feldmannia* |
| 72a.[(63)] | Regular opposite branching | 73 |
| 72b. | With scattered branches | 74 |
| 73a. | Main branch prominent with opposite distichous branches, so shoots are flat. Branches terminate in false hairs | *Tilopteris* |
| 73b. | Opposite branches or sporangia develop after longitudinal divisions of a cell in the main branch, which is divided into 3 cells, of which the central cell is visible between the opposite branches or sporangia. Branches attenuate towards the apex | *Isthmoplea* |
| 74a. | Short, backwards curved branches. Plurilocular sporangia (antheridia) are intercalary and like a tube around a central cavity of the branches. Intercalary monosporangia (oogonia) occur singly or in pairs, often following a longitudinal division of a vegetative cell | *Haplospora* (gametophyte) |
| 74b. | Branches not particularly backwards curved. Monosporangia terminal on short branches | *Haplospora* (sporophyte) |
| 75a.[(1)] | Thallus irregularly lumpy or spherical | 76 |
| 75b. | More or less extended crusts or discs | 77 |
| 76a. | Solid smooth syntagma, up to 3-5 cm in width, older thalli become hollow | *Leathesia* |
| 76b. | Irregular parenchymatous bladder, 2-5 (-15) cm in width | *Colpomenia* |
| 77a. | Crustose algae on stones | 78 |
| 77b. | Microscopic to 1 mm large disc-shaped or irregular algae, mainly epiphytes, but may occur on other hard substrata | 88 |
| 78a. | Crusts of clearly radiating filaments of seriate cells | 79 |
| 78b. | Crusts or discs with basal layer and upright filaments | 80 |
| 79a. | Thin membranous yellow-brown c. circular alga, loosely attached to the substratum with rhizoids | *Cutleria* (*Aglaozonia*-phase) |
| 79b. | Coarse dark brown crusts, firmly attached to the substratum | Sphacelariales (basal crusts) |

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| 80a. | Tough crusts, with closely connected upright filaments, which consist of many cells | 81 |
| 80b. | Upright filaments, easily separated by light pressure, or consist of few cells | 82 |
| 81a. | Basal layer with ascending filaments. Vegetative cells with 1 plastid. Sporangial sori of unilocular sporangia and paraphyses | *Pseudoralfsia* |
| 81b. | Basal layer with upright filaments. Vegetative cells with several plastids. Sporangial sori without paraphyses, ascocysts may occur between the sporangia | *Pseudolithoderma* |
| 82a. | Upright filaments with 8-10 cylindrical cells. True brown algal hairs in pits | *Sorapion* |
| 82b. | No pits with true brown algal hairs | 83 |
| 83a. | With ascocysts | 84 |
| 83b. | Without ascocysts | 85 |
| 84a. | Crust, up to 1 mm in width. Ascocysts prominent on the basal layer or apical on 1-2 cells long upright filaments | *Symphyocarpus* |
| 84b. | Upright filaments of up to 30 cells. Ascocysts are terminal or intercalary in filaments | *Petroderma* |
| 85a. | Terminal sporangia form extended sori without paraphyses. Filaments continue growth through emptied sporangia, so remnants of sporangia walls may occur on the filaments | *Petroderma* |
| 85b. | Sporangia and paraphyses form sori on the surface of the crust, or sporangia are lateral at elongate intercalary cells in the filaments | 86 |
| 86a. | The upper part of upright filaments has a couple of elongate intercalary cells followed by short barrel-shaped cells. True brown algal hairs occur apical or lateral on the filaments. Unilocular sporangia are lateral on the filaments at the transition to the upper part | *Scytosiphon* microthallus |
| 86b. | Upright filaments without elongate intercalary cells. Paraphyses often have 1-2 long cells at the base | 87 |
| 87a. | Unilocular sporangia arise from the upper cells of the upright filaments at the base of the paraphyses | *Petalonia* microthallus |
| 87b. | Unilocular sporangia are terminal on the upright filaments and lateral on paraphyses | *Ralfsia lucida* |
| 88a.[77] | Vegetative cells with several disc-shaped plastids | 89 |
| 88b. | Vegetative cells with one or a few disc-shaped or lobed plastids | 90 |

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| 89a. | Pseudoparenchyma or basal disc with forked marginal cells, mutually free upright filaments and brown algal hairs with sheath | *Hecatonema* |
| 89b. | Pseudoparenchyma, true brown algal hairs with a long cell below the growth zone. Plurilocular sporangia have a lumpy rounded shape | *Phaeostroma* |
| 90a. | Basal system monostromatic with upright uniseriate filaments, vegetative cells each with 1-3 plastids | 91 |
| 90b. | Basal system in part distromatic with closely connected upright uniseriate filaments and plurilocular sporangia, ascocysts may occur between the sporangia. A single lobed plastid per cell. Terminal brown algal hairs with sheath and plurilocular sporangia may occur on the upright filaments | *Phycocelis* |
| 91a. | Plurilocular sporangia and brown algal hairs with sheath occur on the central cells, and prominent ascocysts may occur. On *Zostera marina* and *Ulva fenestrata* | *Myrionema* |
| 91b. | Unilocular sporangia are spherical or pyriform, sessile or on a stalk cell at the creeping filaments. No hairs. Plurilocular sporangia are uniseriate, but rare. On *Dumontia* | *Ulonema* |
| 92a.[2] | With large unilocular almost spherical or ellipsoid sporangia on creeping filaments and mutually free upright uniseriate filaments | 93 |
| 92b. | Without large unilocular sporangia on creeping filaments | 94 |
| 93a. | Vegetative cells with a lobed plastid. The creeping filaments are confluent and form a basal system, in part distromatic. True brown algal hairs. Without plurilocular sporangia | *Compsonema* |
| 93b. | Vegetative cells with several plastids. Upright filaments may terminate in a tuft of uniseriate plurilocular sporangia | *Myriotrichia* |
| 94a. | Syntagma or parenchyma | 95 |
| 94b. | Uniseriate filaments | 96 |
| 95a. | Multiaxial syntagma with surface of assimilating filaments and true brown algal hairs. Elongate plurilocular sporangia at the base of the assimilating filaments | *Microcoryne* |
| 95b. | Thallus uniseriate at the base, higher up are the cells longitudinal divided so the thallus become a parenchyma of segments of cells, uniform in height | *Giraudya* |
| 96a. | With creeping and upright mutually free filaments | 97 |
| 96b. | Filaments are endophytic, endozoic or adpressed to the substratum | 101 |

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| 97a. | Yellow-brown cover at shaded places in the salt-dust zone. Upright filaments, 6-8 µm in width, often with unilateral branches | *Pilinia* |
| 97b. | Does not grow in the salt-dust zone | 98 |
| 98a. | Tuft of unbranched filaments with basal growth. Cells mainly barrel-shaped and contain many disc-shaped plastids. With true brown algal hairs | *Myriactula* |
| 98b. | Not a tuft of unbranched filaments | 99 |
| 99a. | Semi-spherical epiphytes of closely packed filaments, cylindrical cells, 5.5-9.5 µm wide and 2-8 times as long as wide, true brown algal hairs. Uniseriate plurilocular sporangia apical or lateral on the filaments | *Microspongium globosum* |
| 99b. | Felty cover of sparsely branched filaments. Cylindrical cells, 5-8 µm in width and up to 4 times as long as wide | 100 |
| 100a. | Vegetative cells with bilobed plastid and a large pyrenoid. Plurilocular sporangia on creeping or upright filaments. Sporangia often multiseriate and may be branched. Brown algal hairs with sheath occur. Epiphytic or on solid substratum | *Protectocarpus* |
| 100b. | Vegetative cells with 2 short ribbon-shaped plastids. Plurilocular sporangia are uniseriate and terminal or lateral, perpendicular protruding on the upright filaments. No hair. Epiphytic | *Laminariocolax tomentosoides* |
| 101a.[(96)] | Filaments confluent to pseudoparenchyma, completely or in part attached to the substratum or endophytic in the outer cell walls of host algae | 102 |
| 101b. | Endophytic or endozoic with mutually free filaments | 103 |
| 102a. | Filaments, 6-9 µm in width. Sporangia resemble vegetative cells or only slightly larger, often confluent in larger area, no hairs | *Mikrosyphar polysiphoniae* |
| 102b. | Filaments, c. 5 µm in width. Plurilocular sporangia separated in 4 compartments, scattered on creeping filaments or terminal on short upright branches. Brown algal hairs with sheath may occur | *Sorapion* (*Porterinema*-phase) |
| 103a. | In walls of hydroids, few plastids in each cell. Plurilocular sporangia are irregularly rounded, intercalary or terminal | *Endodictyon* |
| 103b. | Endophytic filaments | 104 |
| 104a. | Unilocular sporangia grow out of the host from endophytic filaments or are sessile on free branches which terminate in false hairs. Endophytic in *Desmarestia viridis* | *Herponema* |
| 104b. | Grow inside the substratum, except the brown algal hairs with or without sheath and sporangia, which may have a stalk. These structures are outside the host | 105 |

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| 105a. | Form small, pinhead-size crater-like penetrations with sporangia and true brown algal hairs in the surface of *Laminaria* and *Saccharina* | *Laminariocolax aecidioides* |
| 105b. | No crater-like penetrations in the surface of host algae | 106 |
| 106a. | Vegetative cells with 1-2 plastids. Sporangia not much different from vegetative cells. With true brown algal hairs. Endophytic in *Porphyra* | *Mikrosyphar porphyrae* |
| 106b. | Upright sporangia, not similar to vegetative cells | 107 |
| 107a. | Brown algal hair with very long basal cell. Plurilocular sporangia multiseriate with a lumpy rounded shape in *Chorda filum, Leptosiphonia* and *Vertebrata* | *Phaeostroma* (*Streblonema aequale*) |
| 107b. | True brown algal hairs or brown algal hairs with sheath, without a long basal cell | 108 |
| 108a. | Creeping filaments with short upright filaments, true brown algal hairs and ovoid unilocular sporangia. Plurilocular sporangia may occur. Between the assimilating filaments of *Mesogloia vermiculata* | *Litosiphon laminariae* microthallus (*Streblonema danicum*) |
| 108b. | Plurilocular sporangia on upright filaments, no unilocular sporangia | 109 |
| 109a. | Plurilocular sporangia are ovoid, sessile on creeping filaments or with a unicellular stalk. True brown algal hairs. Endophytic in *Ceramium*, *Cystoclonium* and *Polysiphonia* | *Punctaria tenuissima* microthallus (*Streblonema effusum*) |
| 109b. | Elongate more or less cylindrical, plurilocular sporangia. Endophytic in *Nemalion* | 110 |
| 110a. | Plurilocular sporangia are uniseriate and relatively long, on upright branched filaments. Brown algal hairs with sheath occur | *Microspongium stilophorae* |
| 110b. | Sporangia uni- or multiseriate, cylindrical or elongate lanceolate, and may be branched. They are sessile on the creeping filaments or terminal on short upright filaments. With true brown algal hairs | *Streblonema fasciculatum* |

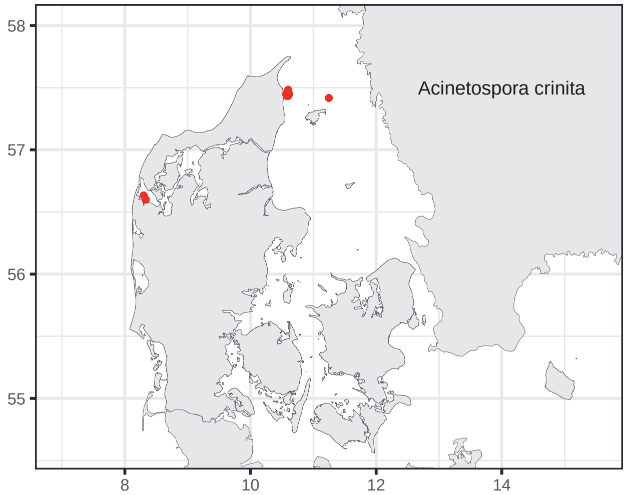
# Collection localities for Phaeophyceae – Brown algae

The distribution maps are based on information from the algal herbarium, Natural History Museum of Denmark, which contains information of c. 60.000 Danish seaweeds. The dots in the maps show collection localities for the different species and include algae growing attached when collected, as well as loose and drift specimens.

There is a single map for each of the respective species. For species that have heteromorphic life histories, both generations are shown in a single map.

*Ectocarpus pennicilatus* and *E. siliculosus* are difficult distinguish in the field, therfore collecting localities for both species occur on one map.

There is no map for *Alaria esculenta* or *Himanthalia elongata*, which only occur drift in Danish waters. Maps are also missing for species which are only found at a single or few localities: *Asperococcus ensiformis, Coelocladia arctica, Endodictyon infestans, Hecatonema terminale, Kuckuckia spinosa, Mesogloia lanosa, Pogotrichum setiforme, Pseudolithoderma rosenvingei, Ralfsia lucida, Sphacelaria plumula, Sphacelaria tribuloides* and *Trachynema mortensenii.* There is no map for *Halopteris scoparia,* as this species probably does not occur in Danish waters, and for *Sphacelaria reticulata*, which is probably extinct. Maps are also missing for *Elachista stellaris*, *Phycocelis foecunda*, *Streblonema fasciculatum* and species of *Myriactula*. Collections of these species are few and mainly of older dates so knowledge about their occurrence is uncertain.


Acinetospora crinita
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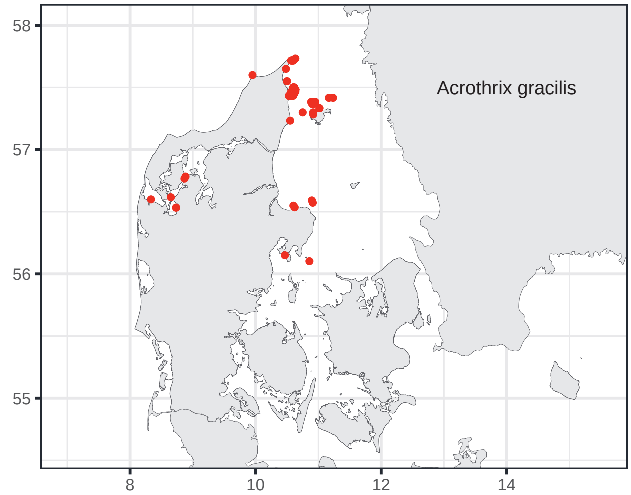
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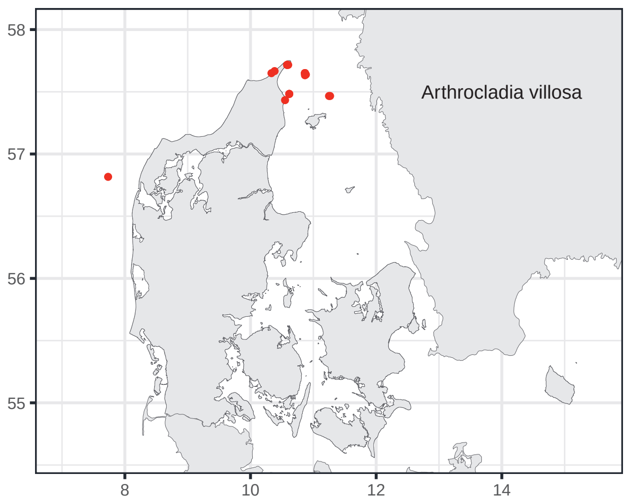
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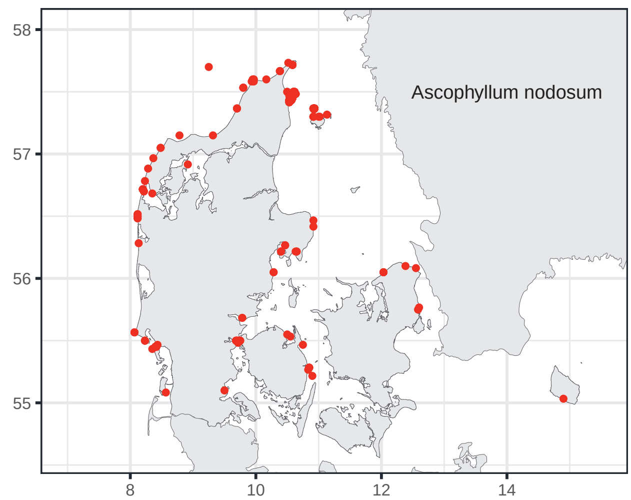
Ascophyllum nodosum
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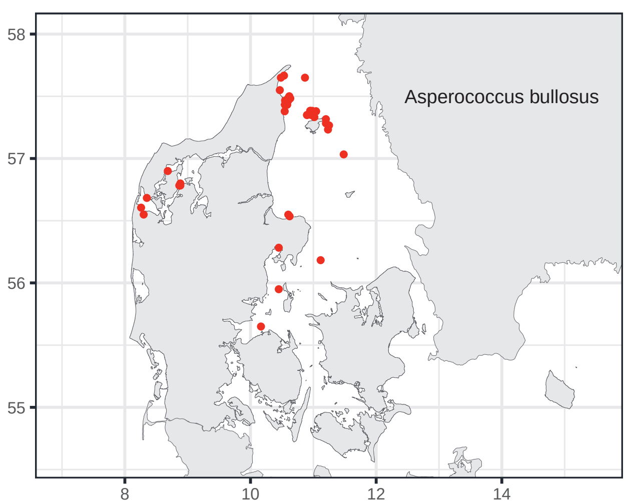
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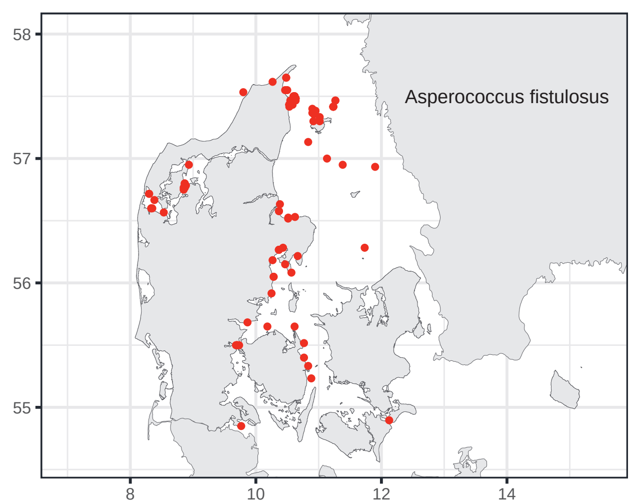
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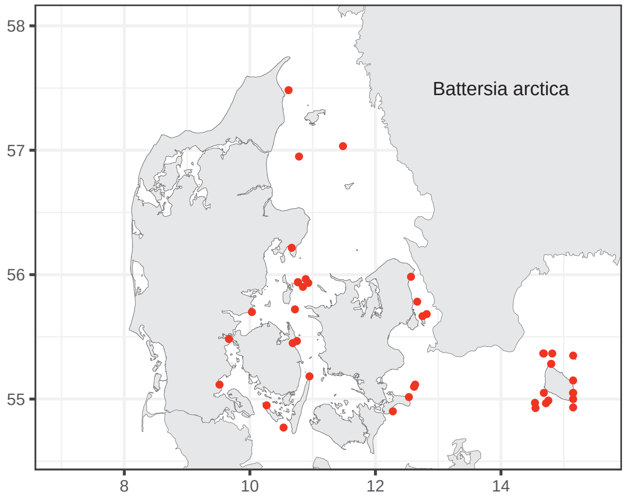
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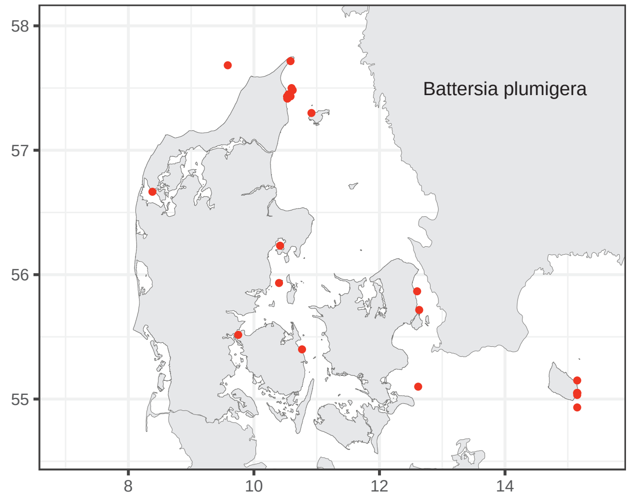
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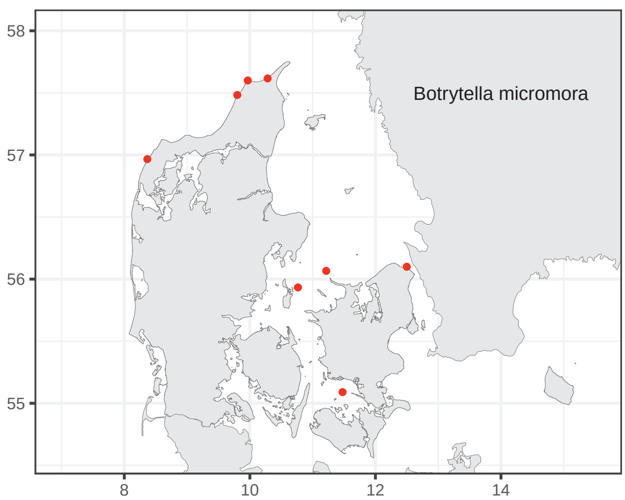
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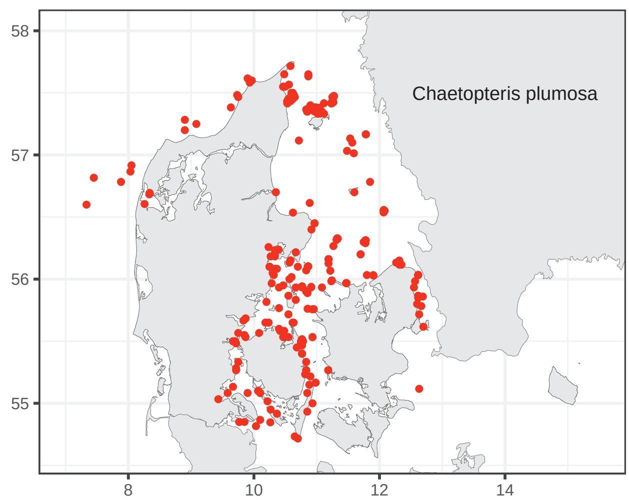
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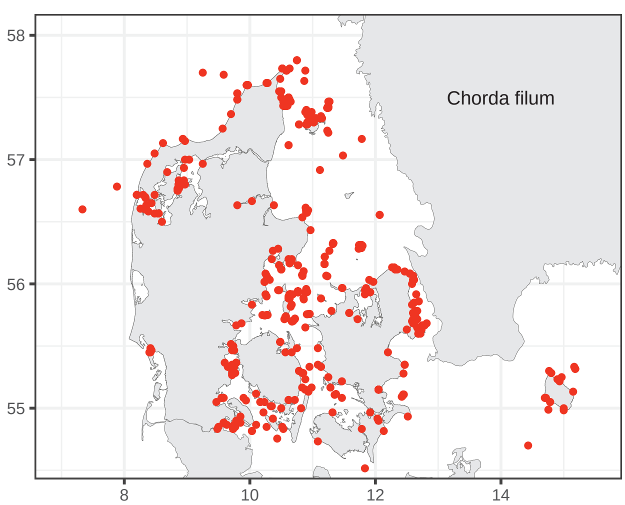
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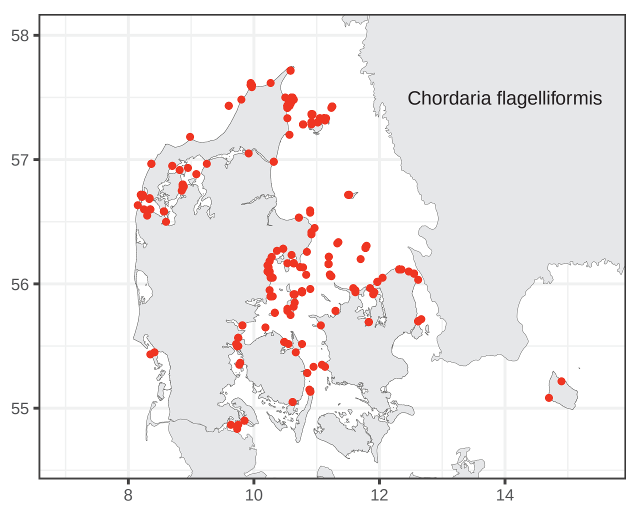
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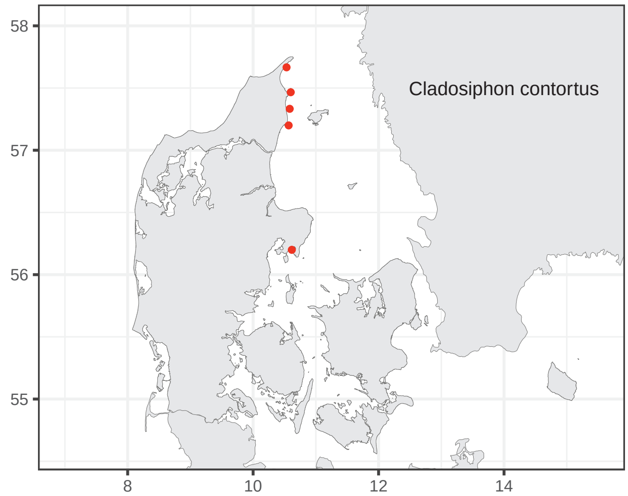
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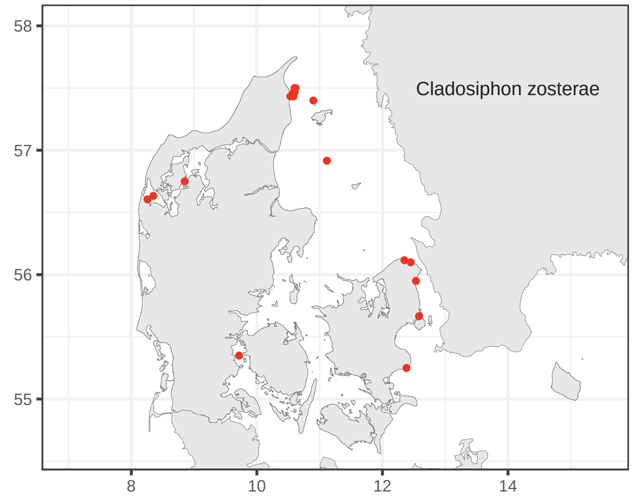
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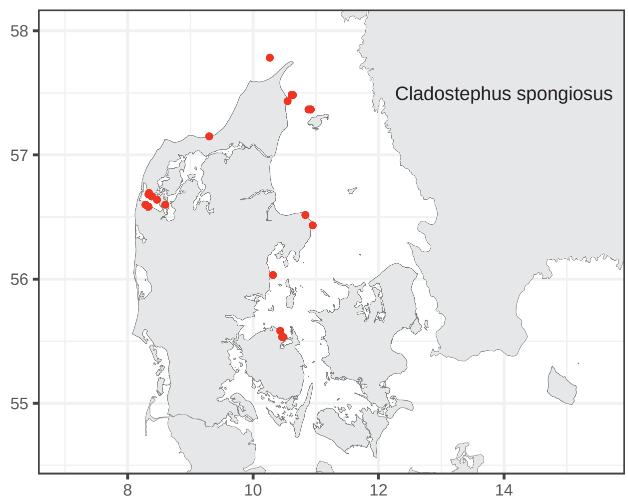
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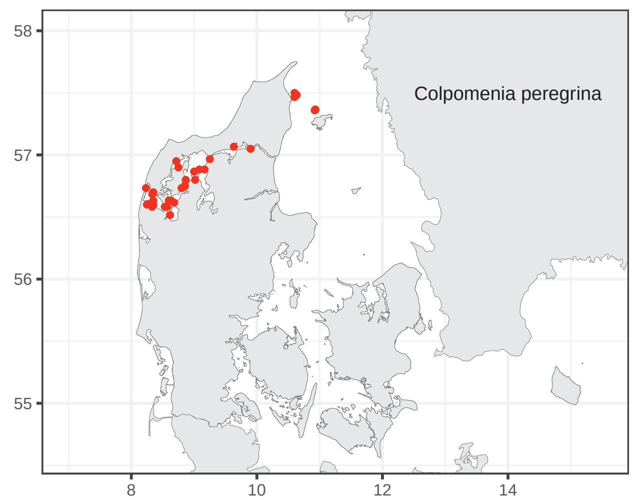
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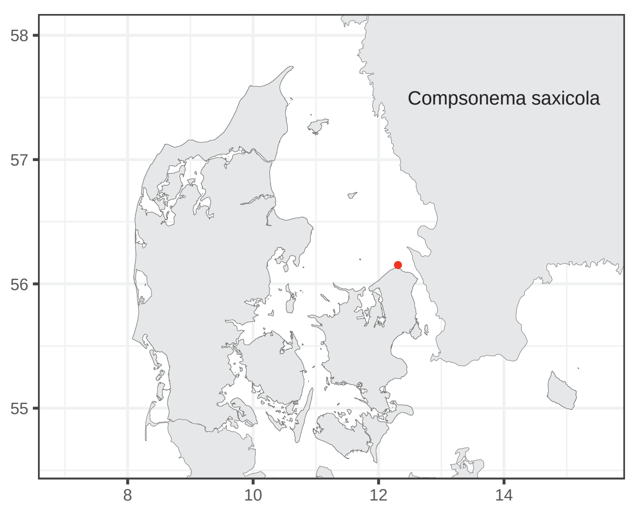
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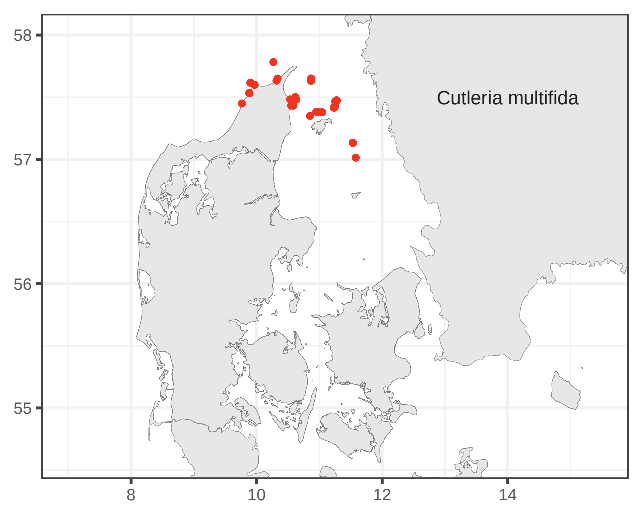
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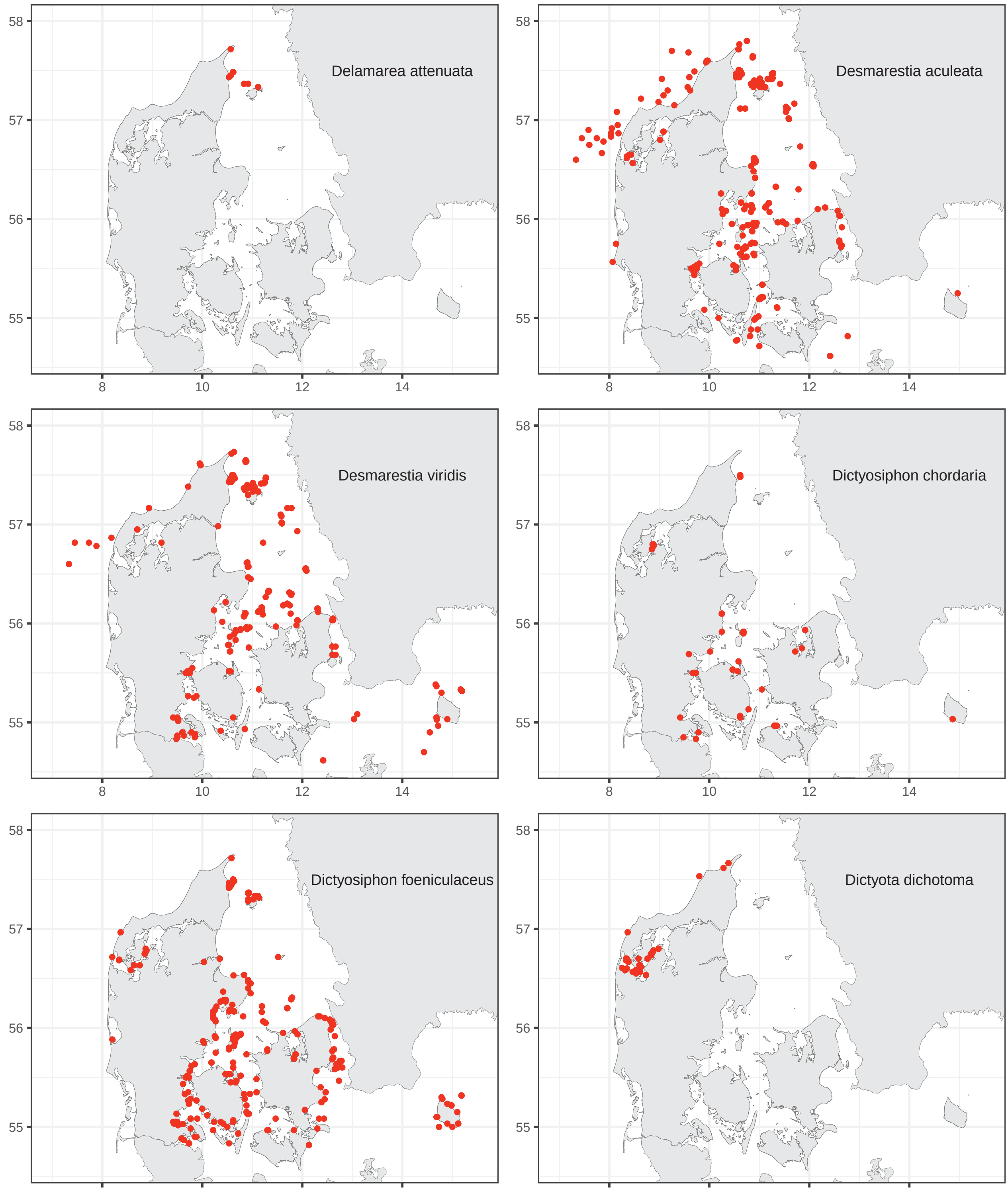
Delamarea attenuata
Desmarestia aculeata
Desmarestia viridis
Dictyosiphon chordaria
Dictyosiphon foeniculaceus
Dictyota dichotoma
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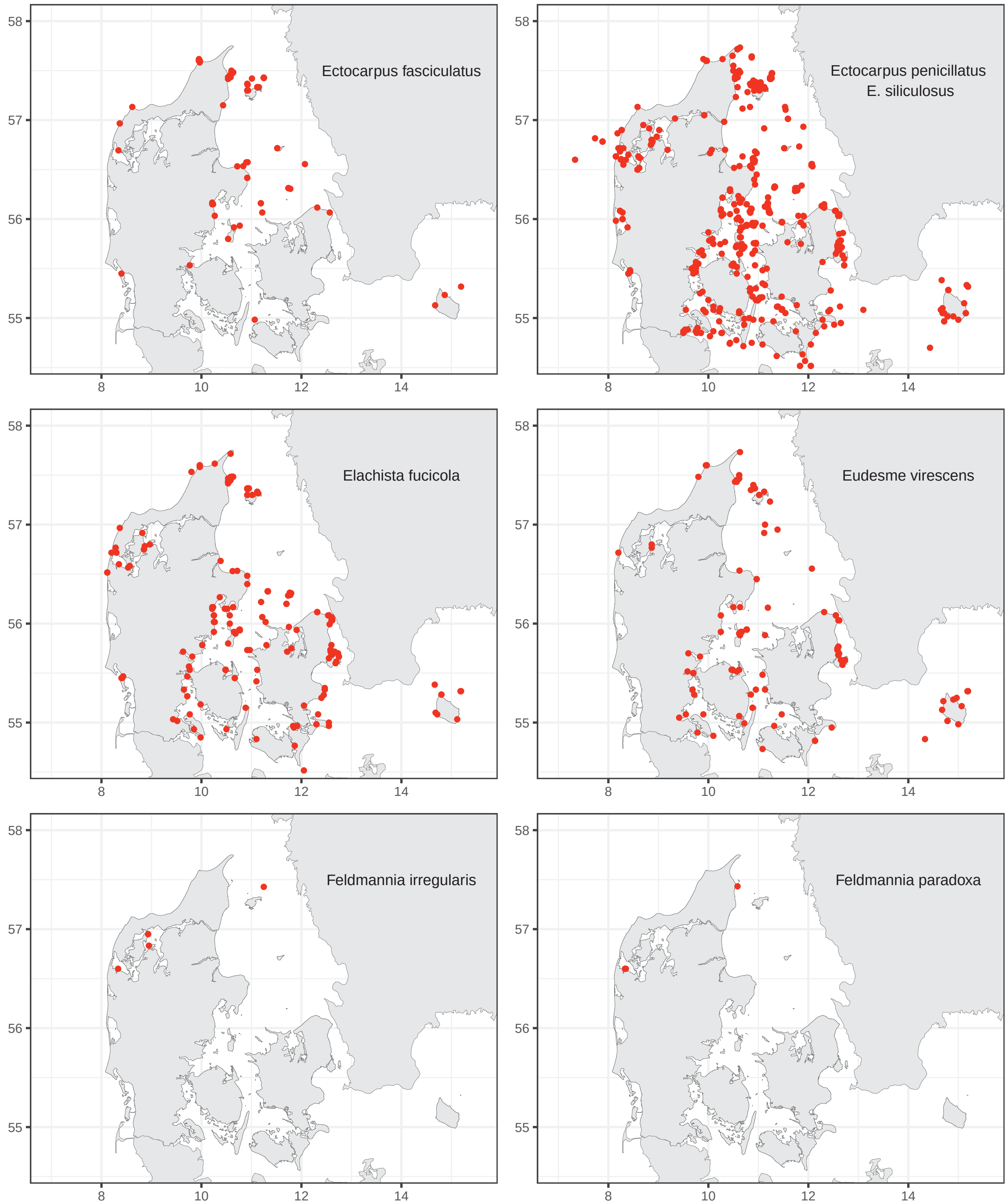
Ectocarpus fasciculatus
Ectocarpus penicillatus
E. siliculosus
Elachista fucicola
Eudesme virescens
Feldmannia irregularis
Feldmannia paradoxa
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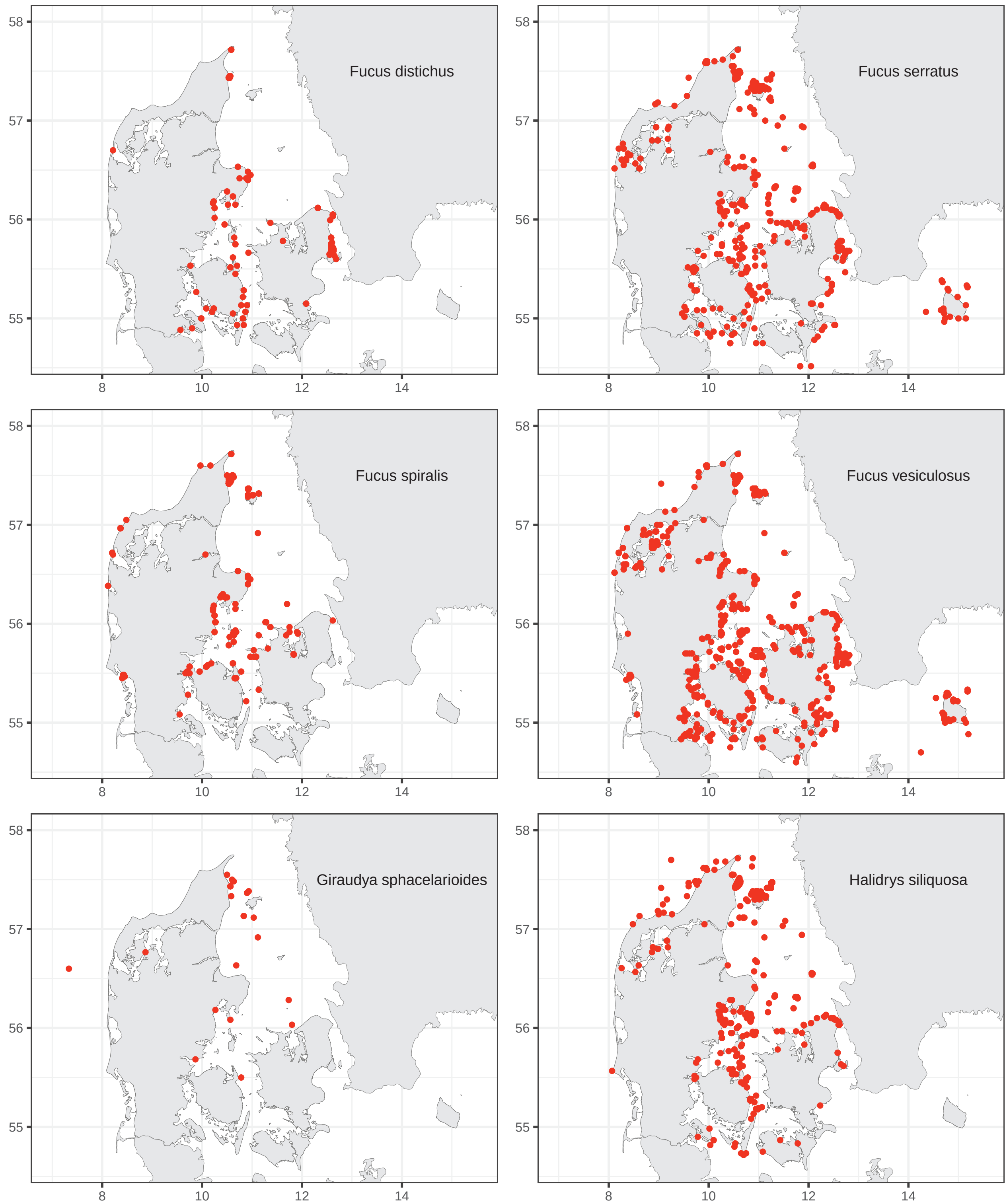
Fucus distichus
Fucus serratus
Fucus spiralis
Fucus vesiculosus
Giraudya sphacelarioides
Halidrys siliquosa
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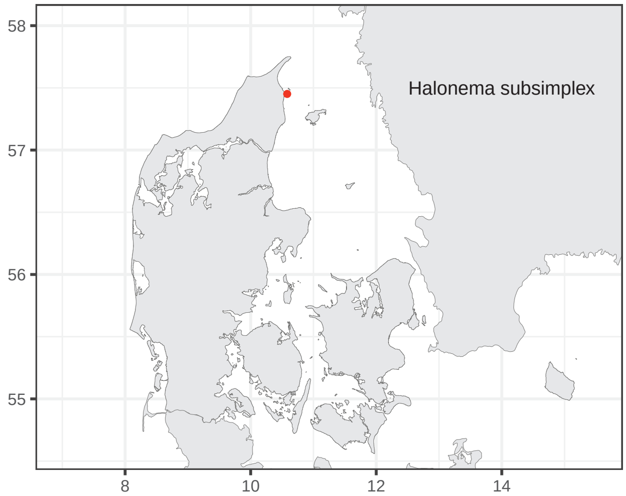
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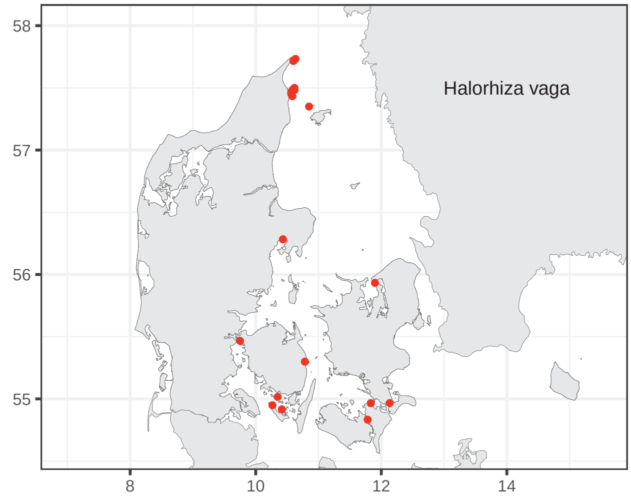
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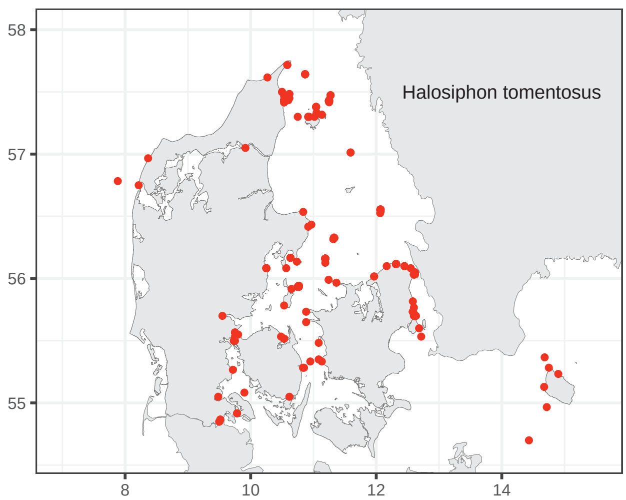
Halosiphon tomentosus
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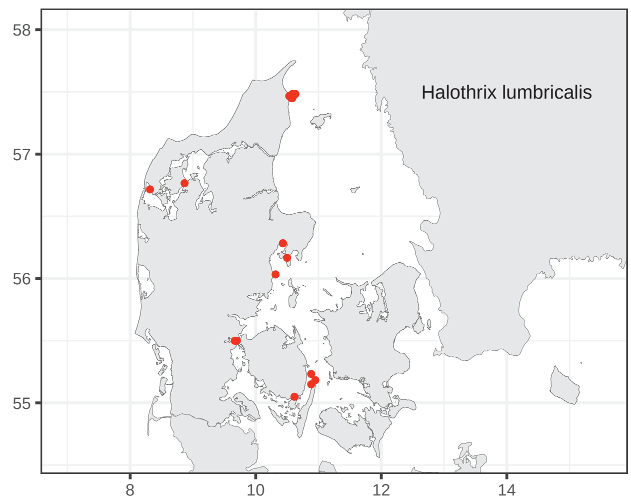
Halothrix lumbricalis
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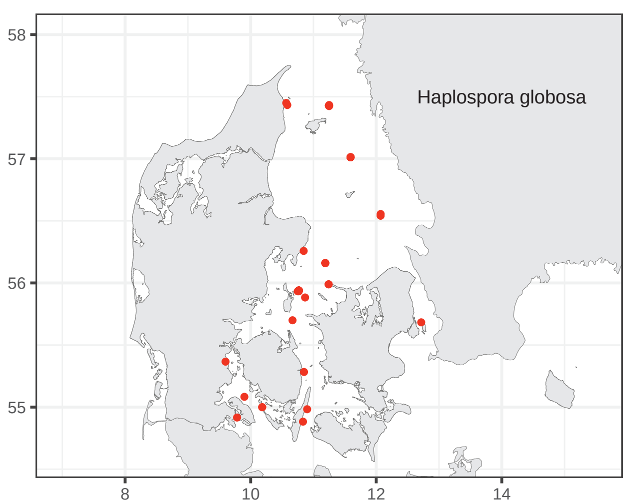
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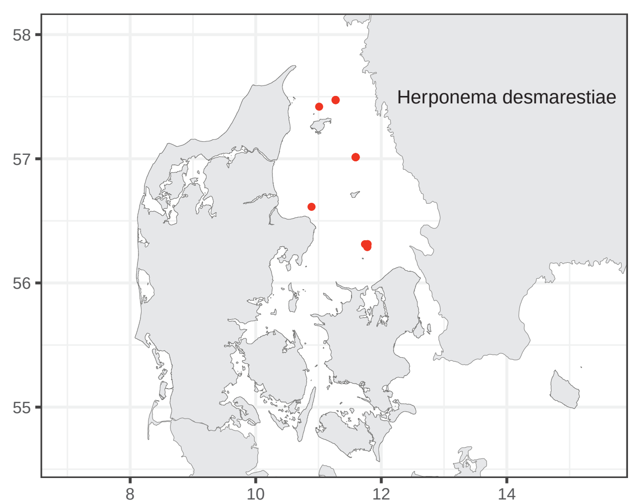
Herponema desmarestiae
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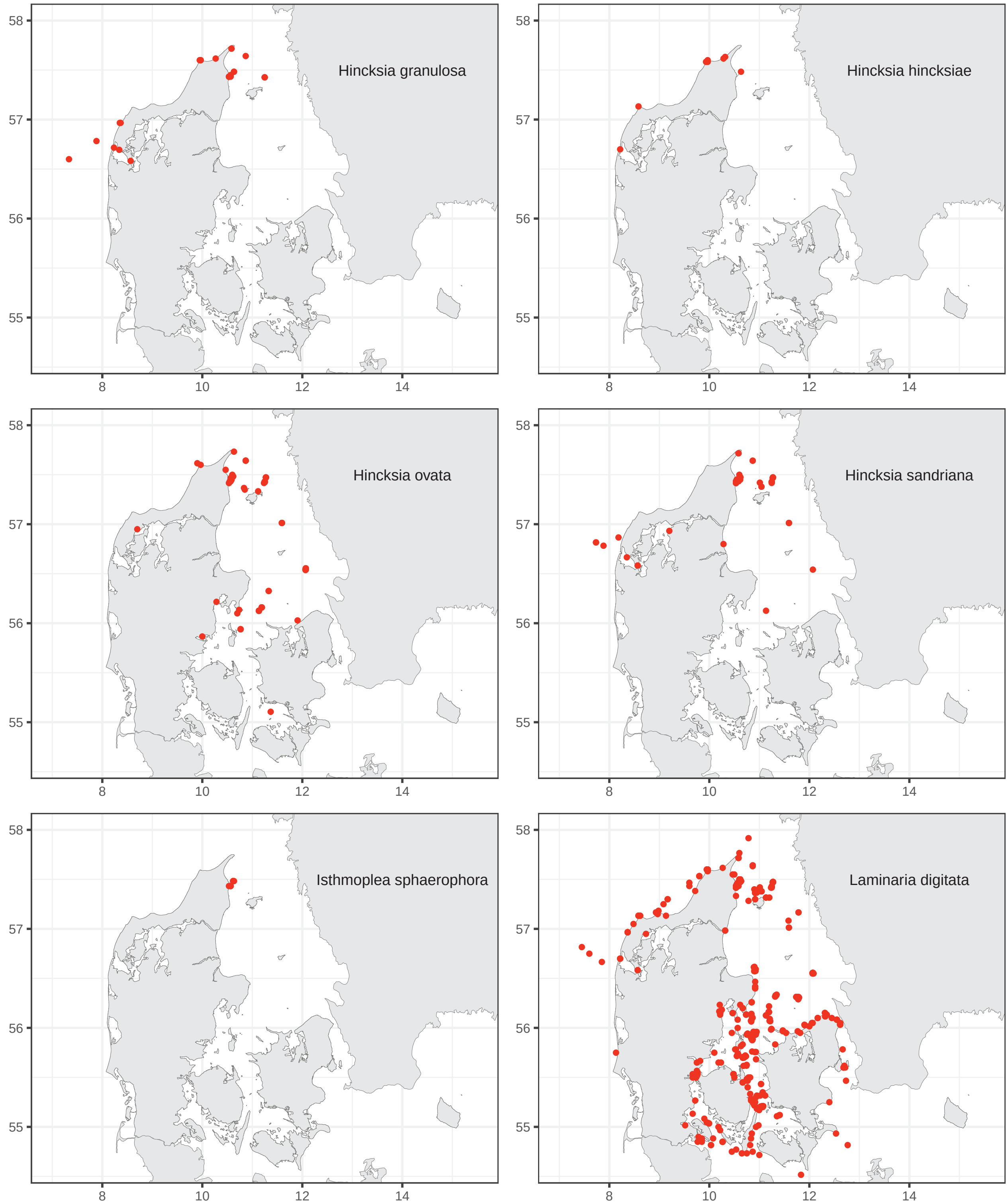
Hincksia granulosa
Hincksia hincksiae
Hincksia ovata
Hincksia sandriana
Isthmoplea sphaerophora
Laminaria digitata
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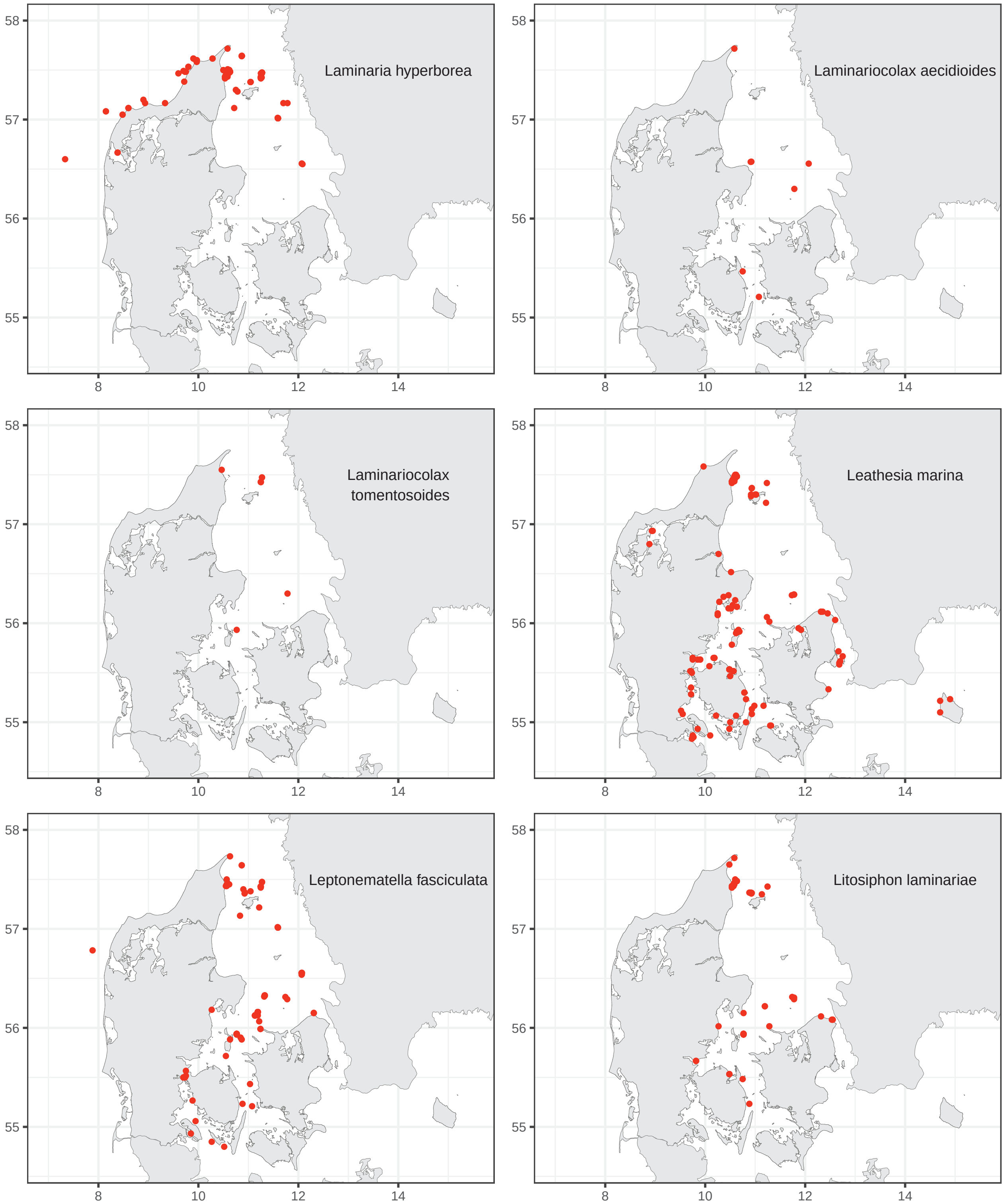
Laminaria hyperborea
Laminariocolax aecidioides
Laminariocolax tomentosoides
Leathesia marina
Leptonematella fasciculata
Litosiphon laminariae
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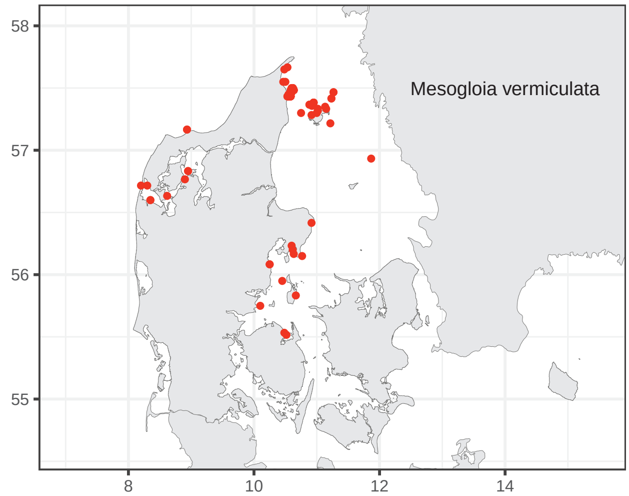
Mesogloia vermiculata
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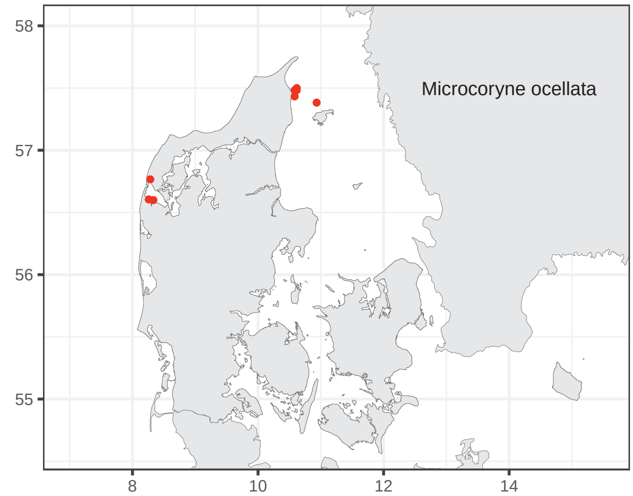
Microcoryne ocellata
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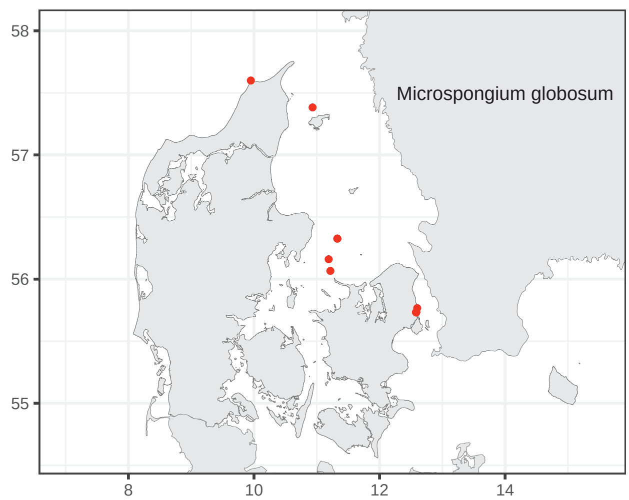
Microspongium globosum
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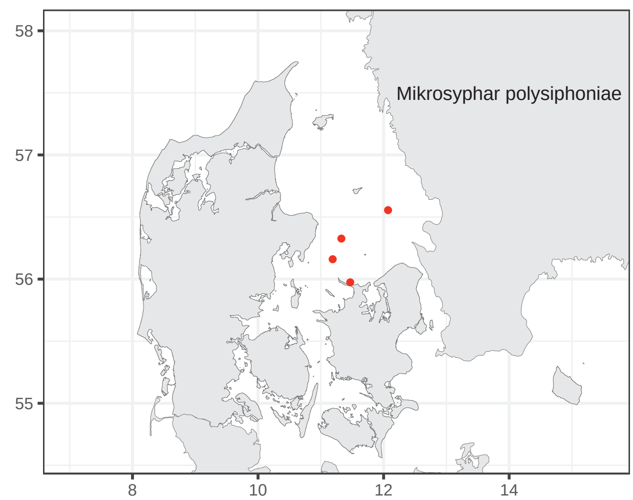
Mikrosyphar polysiphoniae
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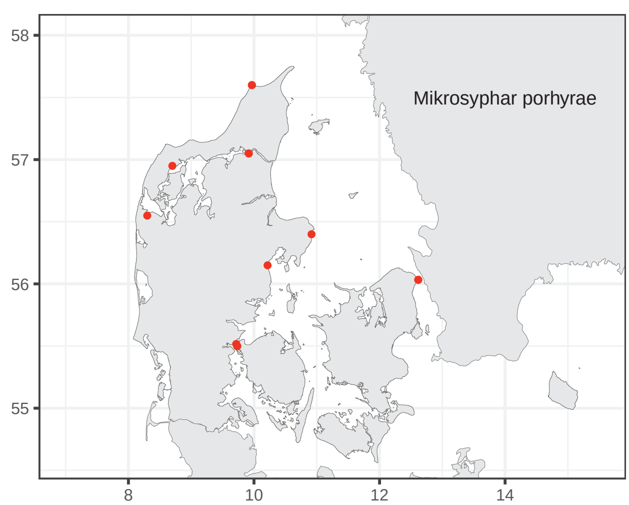
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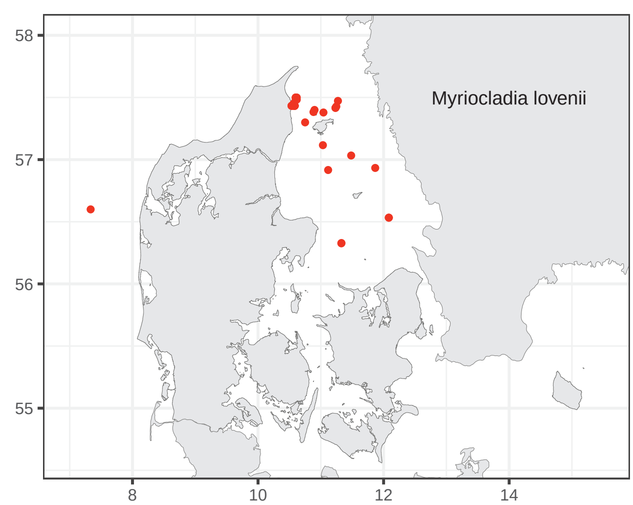
Myriocladia lovenii
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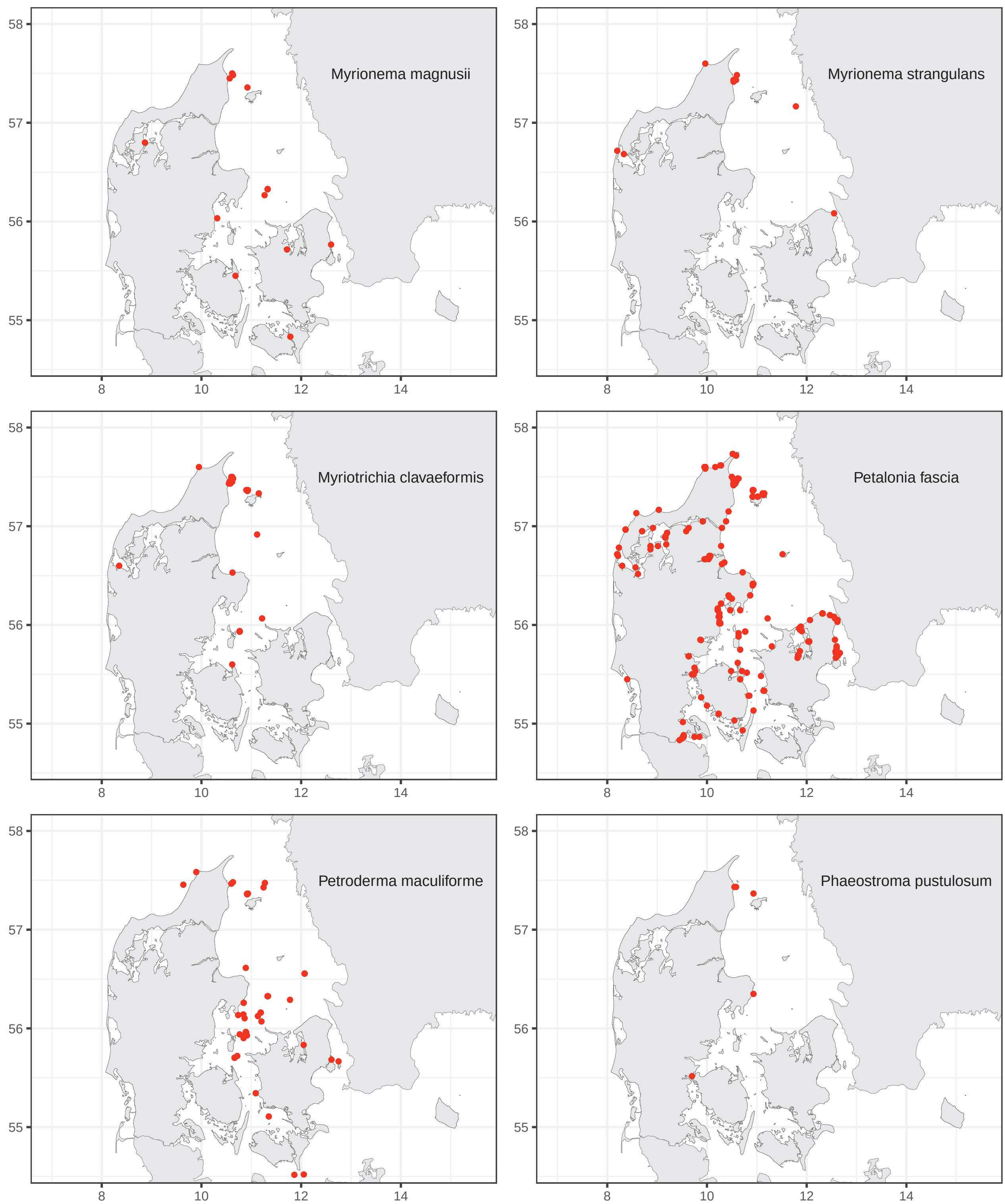
Myrionema magnusii
Myrionema strangulans
Myriotrichia clavaeformis
Petalonia fascia
Petroderma maculiforme
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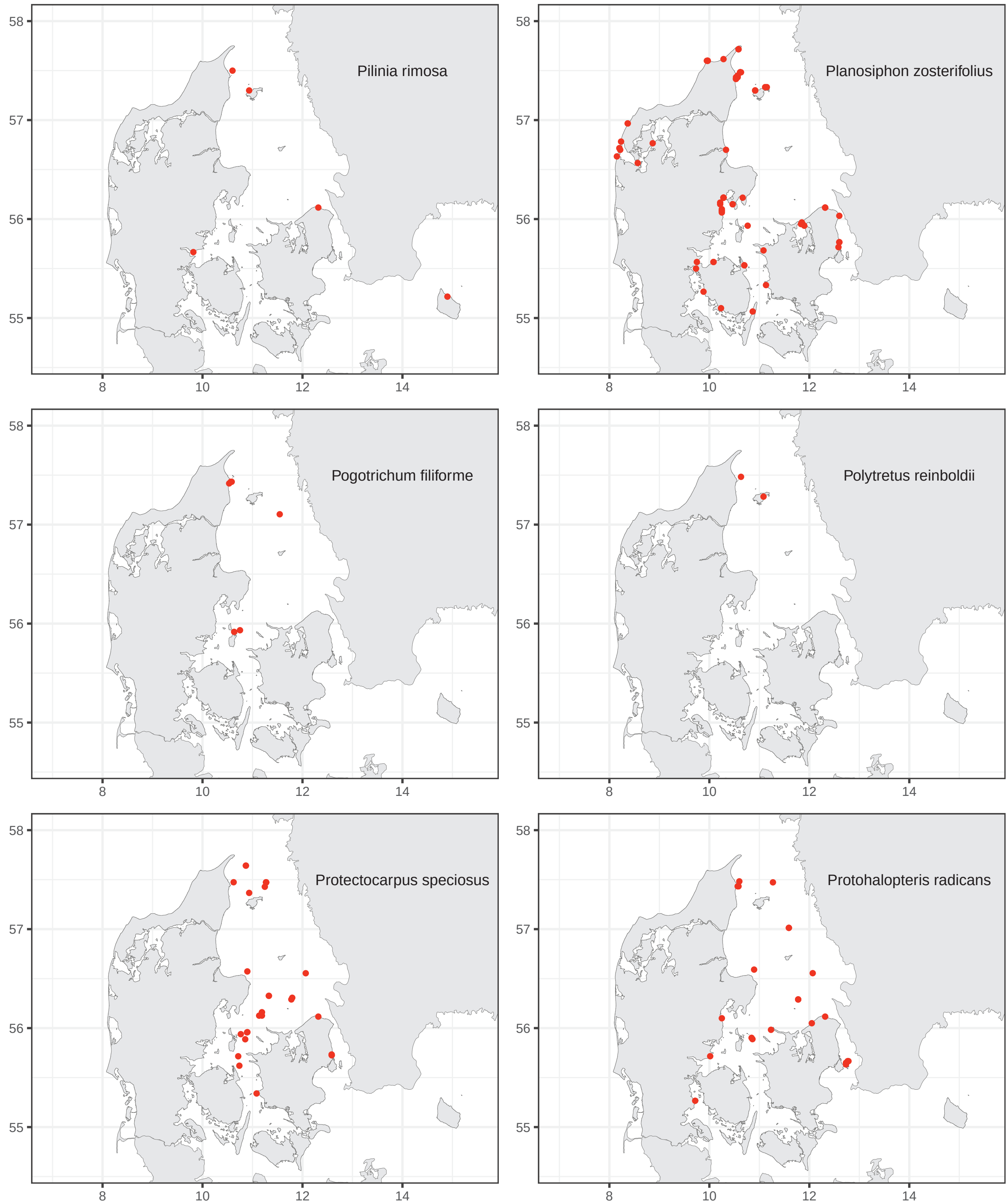
Pilinia rimosa
Planosiphon zosterifolius
Pogotrichum filiforme
Polytretus reinboldii
Protectocarpus speciosus
Protohalopteris radicans
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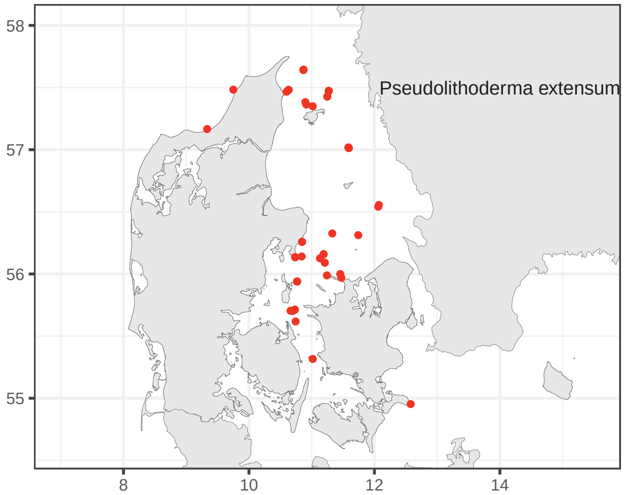
Pseudolithoderma extensum
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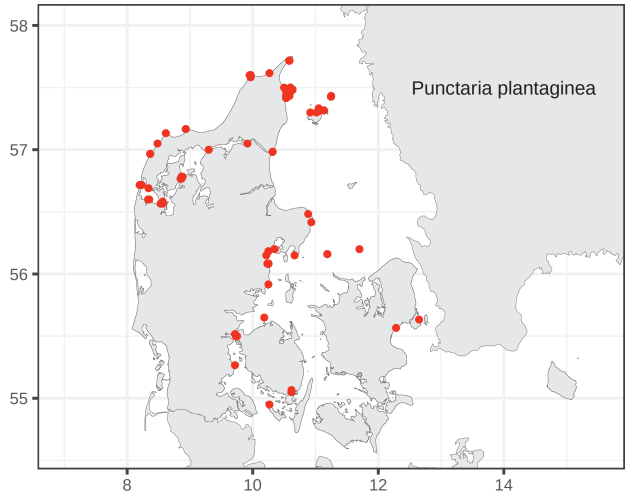
Punctaria plantaginea
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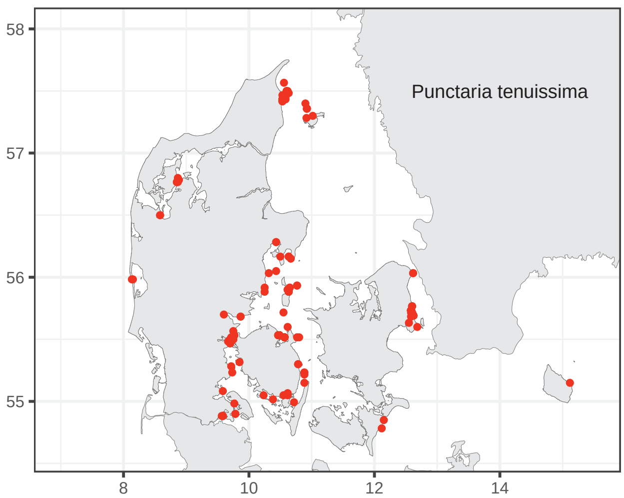
Punctaria tenuissima
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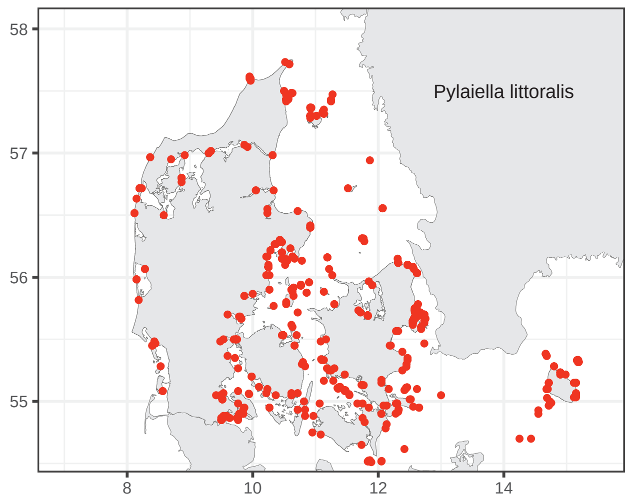
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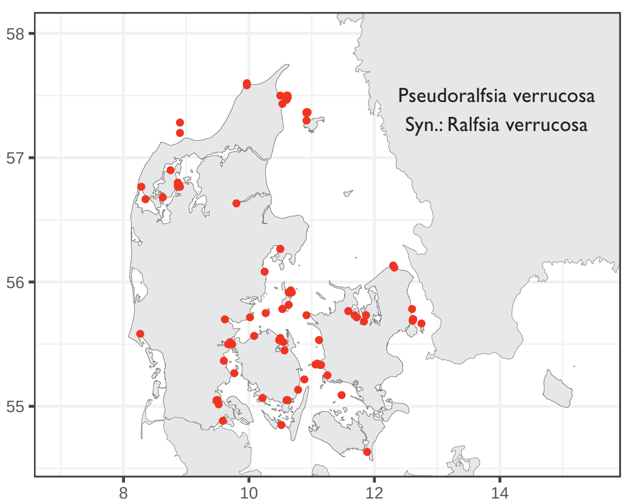
Pseudoralfsia verrucosa
Syn.: Ralfsia verrucosa
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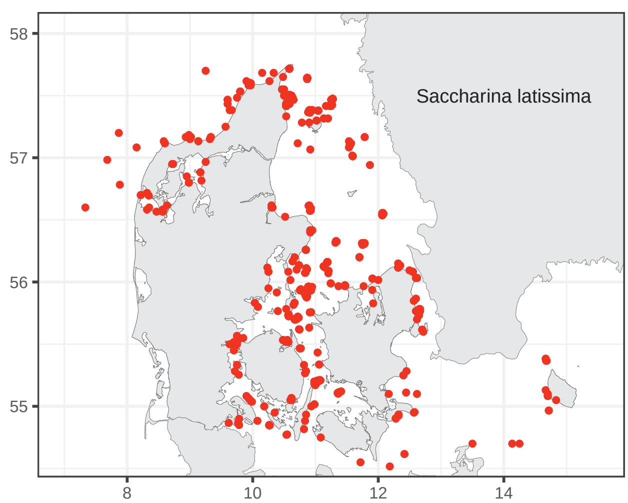
Saccharina latissima
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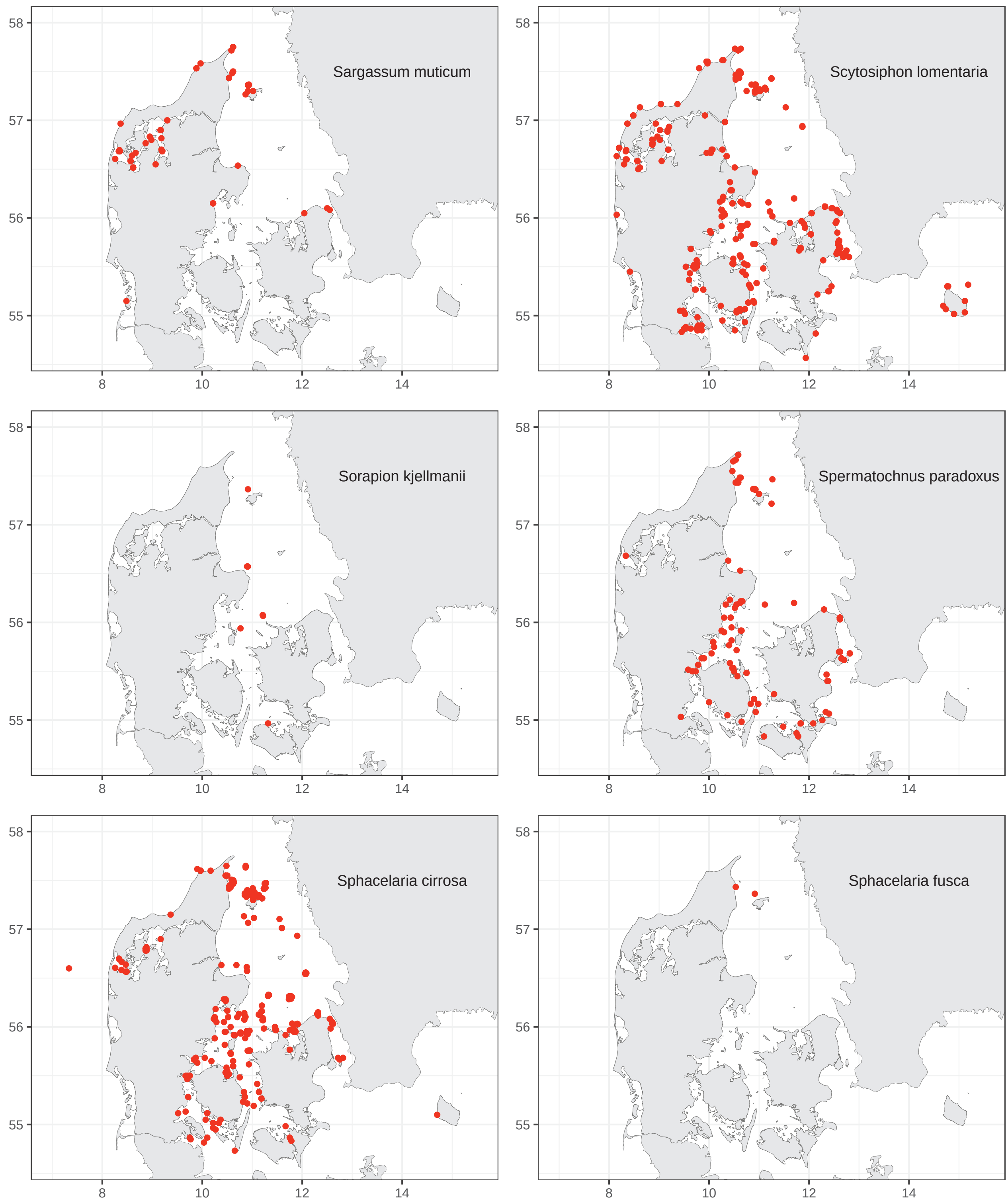
Sargassum muticum
Scytosiphon lomentaria
Sorapion kjellmanii
Spermatochnus paradoxus
Sphacelaria cirrosa
Sphacelaria fusca
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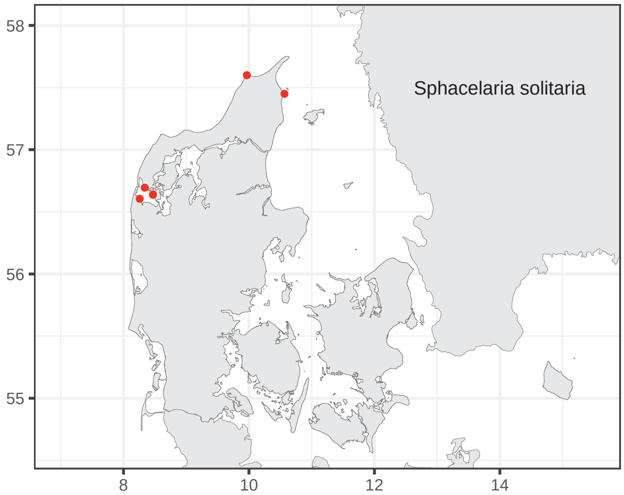
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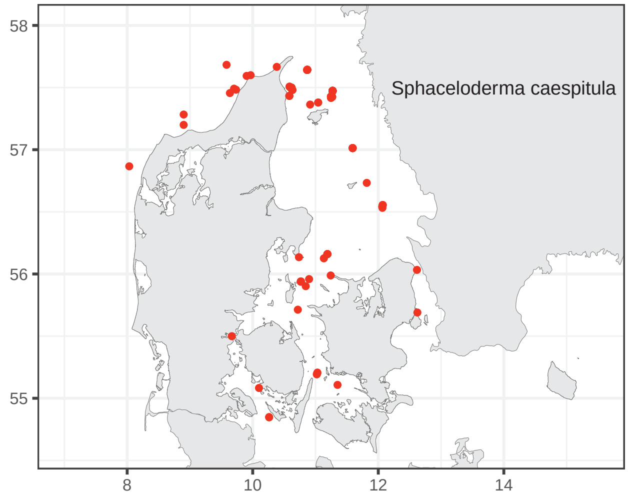
Sphaceloderma caespitula
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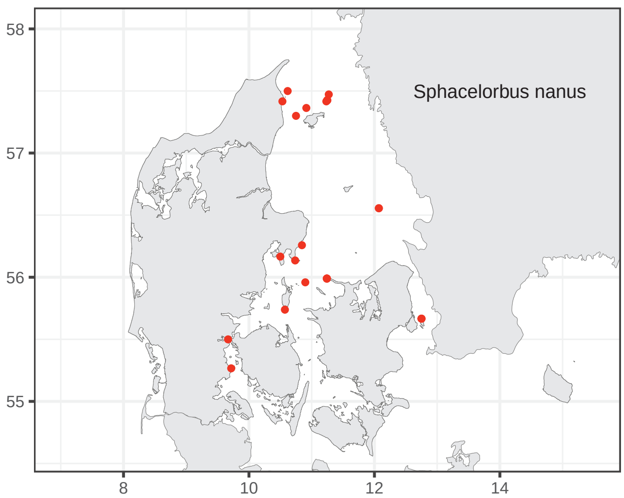
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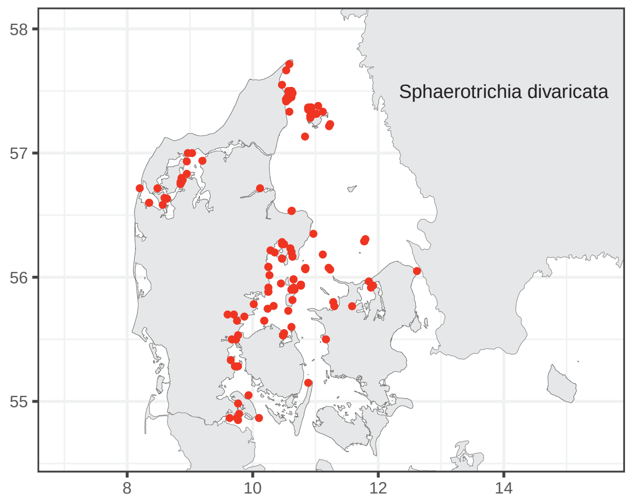
Sphaerotrichia divaricata
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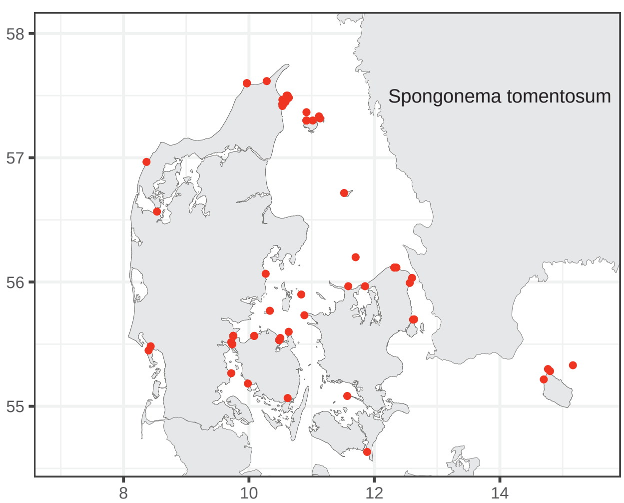
Spongonema tomentosum
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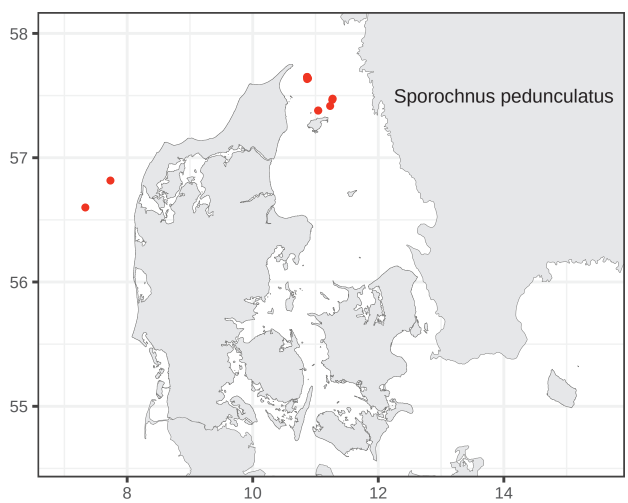
Sporochnus pedunculatus
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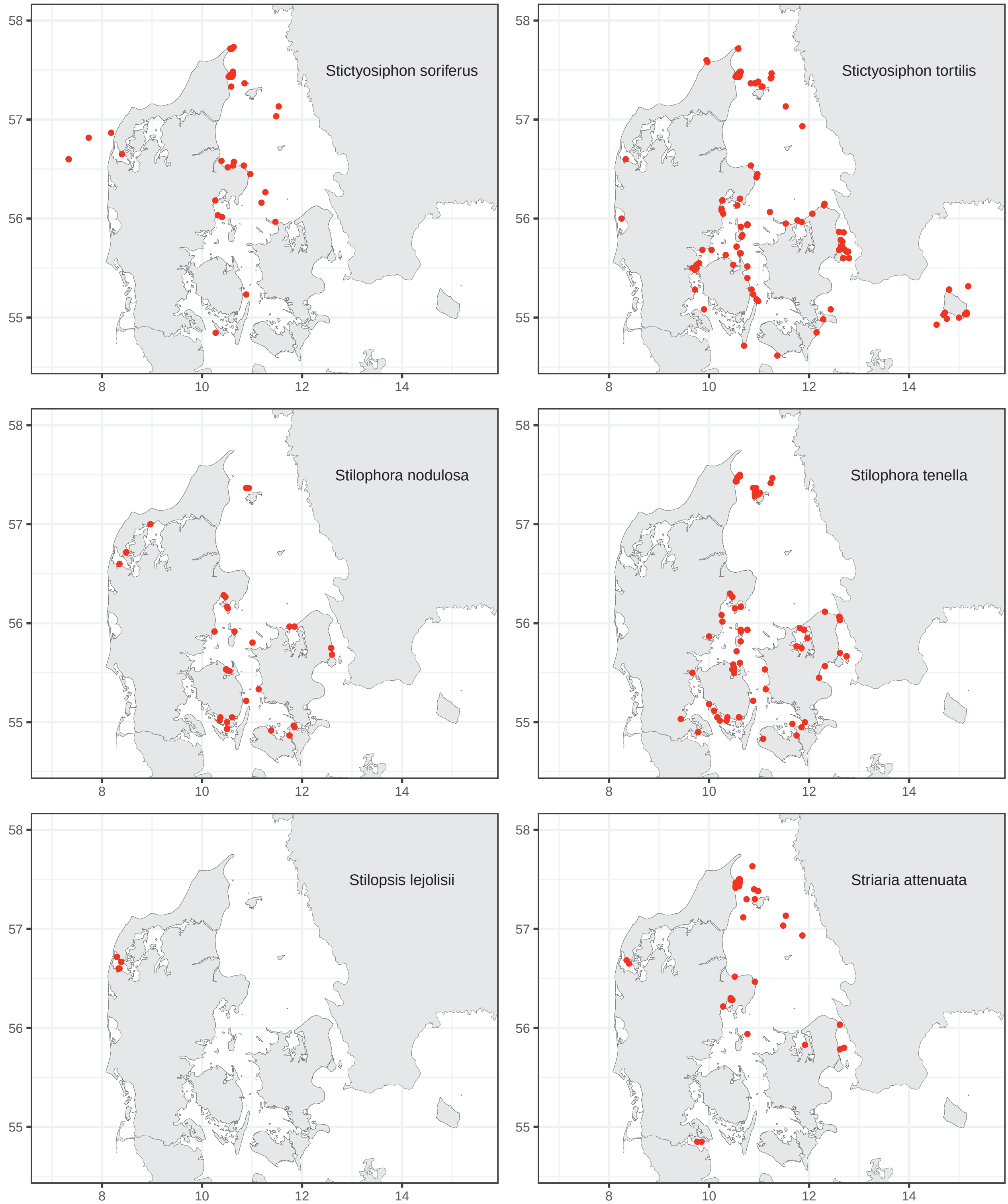
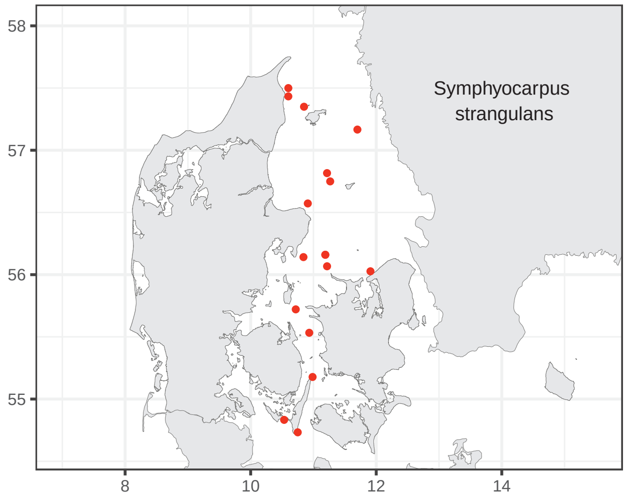

Stictyosiphon soriferus
Stictyosiphon tortilis
Stilophora nodulosa
Stilophora tenella
Stilopsis lejolisii
Striaria attenuata


Symphyocarpus strangulans
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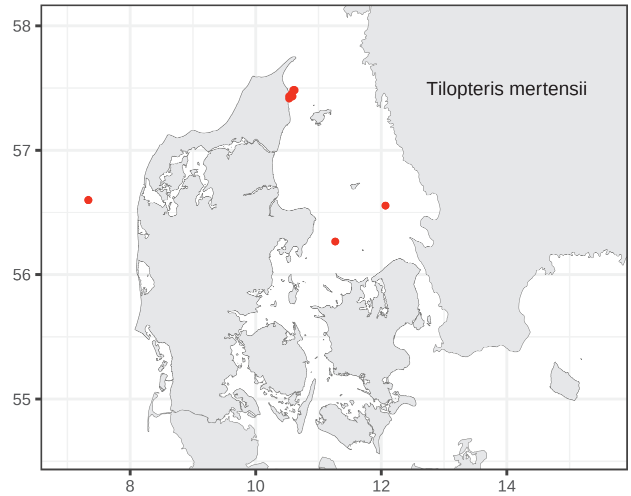
Tilopteris mertensii
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# Phylum: Chlorophyta – Green algae

**Class: Trebouxiophyceae · Order: Prasiolales · Family: Prasiolaceae**

# *Prasiola*

Green Guano Weeds or Parsley Weeds

Thallus consists of uniseriate filaments or monostromatic parenchymatous blades with diffuse growth. Vegetative cells each contains a stellate plastid with one pyrenoid.

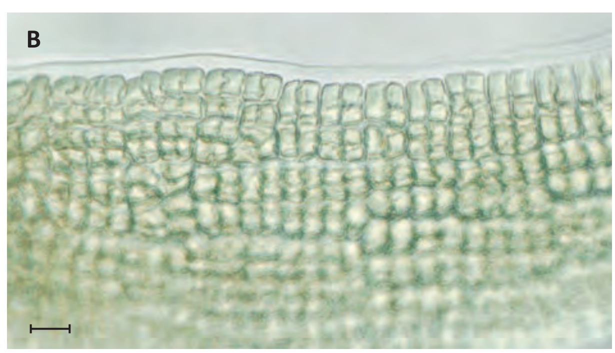
## *Prasiola calophylla*

**(Carmichael ex Greville) Kützing**

Ribbon Guano Weed or Ribbon Parsley Weed

**Appearance:** Narrow ribbon-shaped blades, up to 1 mm in height, appear as small tufts of 3-4 blades.
**Structure:** Parenchymatous monostromatic blades of small quadrangular cells, 4-5 µm in width. Cells form longitudinal and transverse rows. A uniseriate cell row at the base resembles a stipe. Blades are attached to the substratum by a single or a few of the lower cells. Young individuals are uniseriate and consist of short cells. The thallus becomes polystromatic before the production of reproductive cells.
**Reproduction:** Asexual reproduction with aplanospores (vegetative spores without flagella) is the only reproduction known. Aplanosporangia develop from transformed vegetative cells in the upper part of the thallus. They are spherical and surrounded by a thick wall. Released aplanosporangia grow in size and contain various numbers of aplanospores at maturity. These are released by decay of the sporangium wall and germinate into new blades. The life history was revealed by culture studies of Kornmann & Sahling (1974) and Rindi et al. (2004).
**Seasonal variation:** Only a few collections from Danish waters, April and November.
**Habitat:** In the salt-dust zone among Felty Peg Weed (*Rosenvingiella radicans*).
**References:** Kornmann & Sahling (1974), Rindi et al. (1999, 2004, 2007).


A: *Prasiola calophylla*. Ribbon-shaped blades. Scale 50 µm.
A-B: Upper part of the bulwark, northern harbour jetty, Vesterø Havn, Læsø, 11.11.2013.




B: *Prasiola calophylla*. Monostromatic parenchyma of small quadrangular vegetative cells. Scale 10 µm.

## *Prasiola furfuracea*

**(Mertens ex Hornemann) Trevisan**

Scaly Green Guano Weed or Scaly Green Parsley Weed

**Appearance:** Small tufts of rounded blades with slightly inrolled margin. The blades are less than 2 mm in height and have a very short stipe (Rindi in Brodie et al., 2007, Wærn, 1952).

**Comment:** Type locality at Hofmansgave, Fyen, Denmark according to Burrows (1991). Unfortunately, original material, collected by Hofmann Bang, has not been found in the algal herbarium, Natural History Museum of Denmark, and the drawing in *Florae Danicae* (Hornemann 1813, Tavle MCCCCLXXXIX [1489]) was selected as the lectotype by Burrows (1991). The species is not recorded in the database of Danish algae at the Natural History Museum of Denmark and the status in Danish waters is uncertain.

**Habitat:** On stone in the middle of the salt-dust zone.

**References:** Burrows (1991), Hornemann (1813), Kornmann & Sahling (1974), Rindi in Brodie et al. (2007), Wærn (1952).

## *Prasiola stipitata*

**Suhr ex Jessen in Jessen**

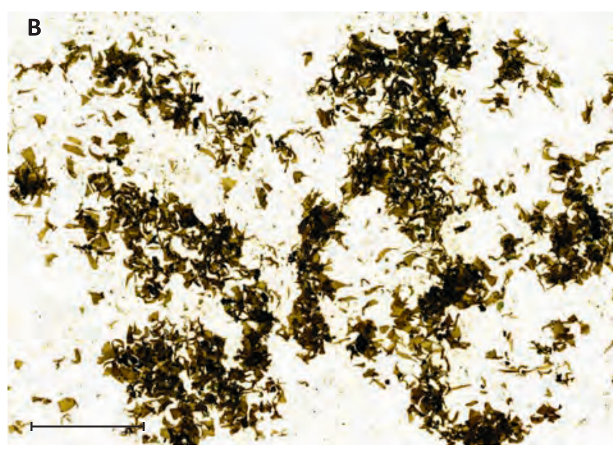
Stalked Green Guano Weed or Stalked Green Parsley Weed

**Appearance:** Spatula- or fan-shaped dark green blades, typically rolled up, few millimetres to 1 cm in height. The lower part of blade is narrow, resembling a stipe with a gradual transition to the blade.

**Structure:** Vegetative cells are quadrangular, 5-8 µm in width, forming longitudinal and transverse rows, particularly in the lower part of the blade. Several cells group together in squares surrounded by thicker walls. The narrow stipe-like part is multiseriate and attaches to the substratum with several cells. The blades become polystromatic before production of reproductive cells.

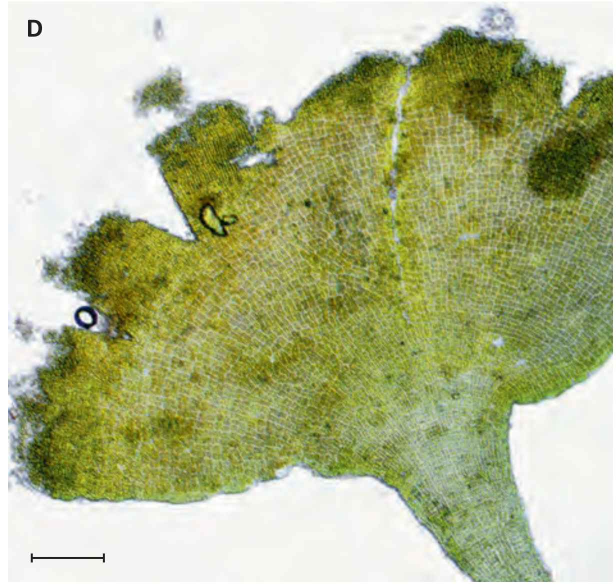
**Reproduction:** The thallus is diploid and has vegetative or sexual reproduction. Vegetative reproduction takes place by thick-walled rounded spores (cysts), 10-12 µm in width (fig. A p. 24 Vol. 1). They develop individually in transformed vegetative cells in the upper part of the blade. Sexual oogamous reproduction takes place in blades resembling a chessboard. The monoecious blade is divided into squares and reproductive structures develop in the polystromatic area. Small male spermatozoids with 2 flagella develop in pale squares and female egg-cells without flagella


A: *Prasiola stipitata*. Top of boulder covered by Stalked Green Guano Weed (*Prasiola stipitata*). Photo by K.L. Krabbe. A, D: Hirsholm, 11.10.2015.

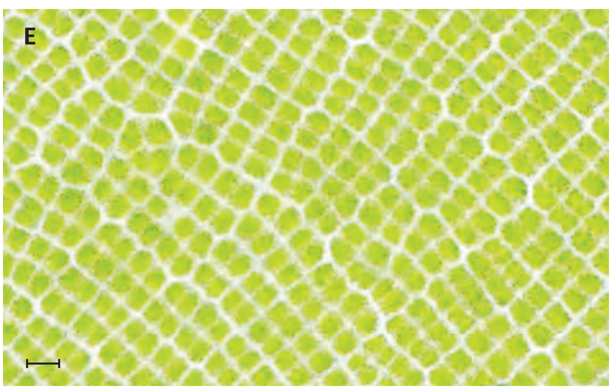



B: *Prasiola stipitata*. Almost triangular blades dried on paper. Gilleleje, 6.11.1989. Scale 2 cm.

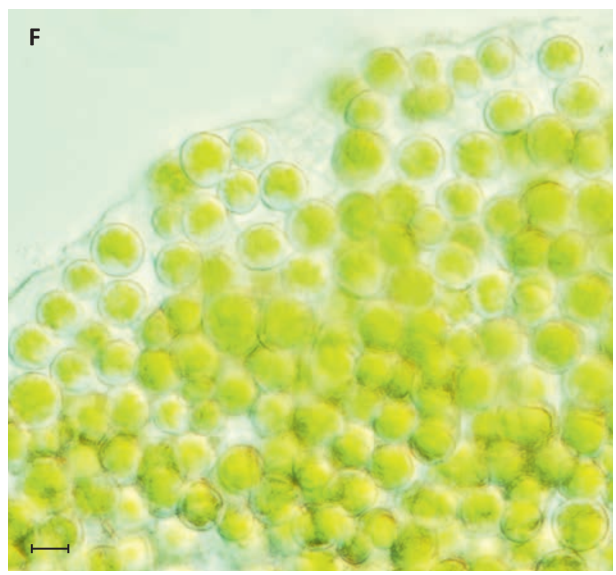

C: *Prasiola stipitata*. Monostromatic blade with gradual transition to the stipe. Northern harbour jetty, Vesterø Havn, Læsø. 11.11.2013. Scale 50 µm.



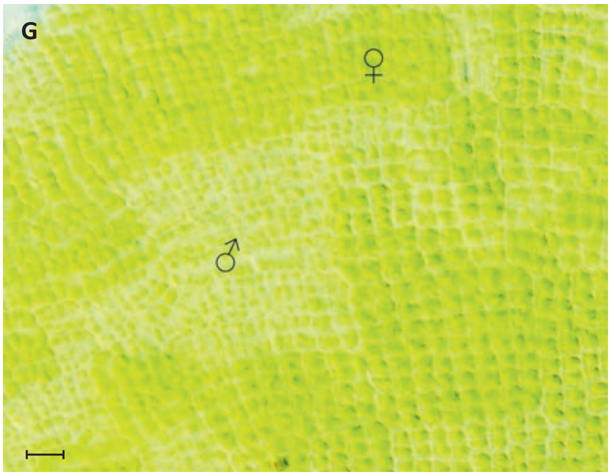

D: *Prasiola stipitata*. Broad fan-shaped blade with cysts in the upper part. Scale 200 µm.




E: *Prasiola stipitata*. Parenchyma of vegetative cells each with a central stellate plastid. Gilleleje, 29.5.2014. Scale 10 µm.




F: *Prasiola stipitata*. Cysts at the margin of blade. Scale 10 µm. F-G: Hirsholm, 14.4.2015.




G: *Prasiola stipitata*. Chessboard pattern in sexual reproductive blade. Male squares with small pale cells, female squares with large green cells. Vegetative squares monostromatic. Scale 10 µm.

in dark green squares. Monostromatic vegetative squares occur in between. Sexual cells are produced after meiosis and released after decay of the cell walls. Immobile female egg-cells are fertilised by male spermatozoids, and zygotes develop into new diploid blades.

**Seasonal variation:** All year but reduced in warm and dry periods. Cysts recorded all year, blades with male and female squares in April and August.

**Habitat:** On boulders in the upper part of the wave-splash zone, typically in nitrate rich area fertilised by birds.

**Resembles:** *Prasiola furfuracea* is reminiscent but smaller, up to 2 mm in height, and has a distinct stipe as opposed to Stalked Green Guano Weed (*P. stipitata*), which has a gradual transition between the blade and the stipe.

**References:** Friedmann (1959, 1969), Kristiansen (1972), Moniz et al. (2014).

## *Rosenvingiella radicans*

**(Kützing) Rindi, L.McIvor & Guiry**

Felty Peg Weed

**Appearance**: Narrow filaments, typically entangled into a felty cover, yellow-green when dry.

**Structure:** Uniseriate, unbranched filaments of cylindrical cells, (7.6-) 9-13 (-19) µm in width and 0.2-1 times as long as wide. Attached to the substratum by short rhizoids from vegetative cells. Rhizoids occur scattered but often in pairs from two adjacent cells. Vegetative cells each contains a central, stellate plastid with a central pyrenoid.

**Reproduction:** Vegetative reproduction by spherical cysts, which occur individually or in series of 2-6 cells. Sexual reproduction not reported in the alga from Danish waters, but multiseriate pseudoparenchymatous areas occasionally observed and considered to be young sexual stages, similar to those reported by Rindi in Brodie et al. (2007).

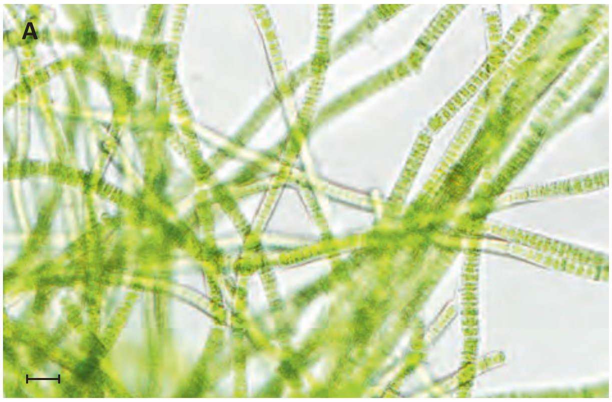
**Seasonal variation:** All year, well-developed in winter.

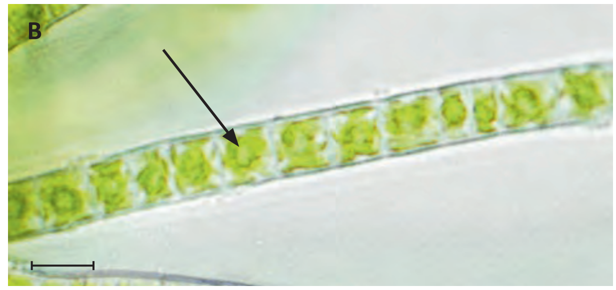
**Habitat:** On stone-walls and bulwarks in the salt-dust zone. Also occurs inland at moist, nitrate rich places.

**Resembles:** *Rosenvingiella polyrhiza* (Rosenvinge) P.S.Silva is similar but distinguished by the rhizoids, which occur in series of up to 6, on a similar number of adjacent cells, according to Rindi in Brodie et al. (2007).

**Comment:** *Rosenvingiella radicans* is accepted as a separate species by Rindi et al. (2004). Most collections from Danish waters were previously identified as *R. polyrhiza*, but it is uncertain if *R. polyrhiza* occurs in Denmark as only a single individual with 4 rhizoids from the same number of adjacent cells, was noticed in a recent search through all the individuals in the algal herbarium, Natural History Museum of Denmark. This specimen was collected from the Fishing Harbour, Esbjerg, 22.4.1984.

**References:** Kornmann & Sahling (1974, *R. polyrhiza*), Kristiansen (1972, *R. polyrhiza*), Rindi in Brodie et al. (2007), Rindi et al. (1999, *R. polyrhiza*, 2004, 2007).






A: *Rosenvingiella radicans*. Vegetative, uniseriate, unbranched filaments of short cells. Scale 20 µm. A-B, D: Vesterø Havn, Læsø, 13.3.2013.

B: *Rosenvingiella radicans*. Vegetative cells, each with a stellate plastid (arrow). Scale 10 µm.

C: *Rosenvingiella radicans*. Short rhizoids from 2 adjacent cells. Vesterø Havn, Læsø, 14.3.2014. Scale 10 µm.

D: *Rosenvingiella radicans*. Filament with a single rhizoid. Scale 10 µm.

**Class: Ulvophyceae · Order: Cladophorales · Family: Chaetosiphonaceae**

## *Blastophysa rhizopus*

**Reinke**

Polygon Green Weed

**Appearance:** Small to microscopic cells, might appear as dark green dots with the naked eye.

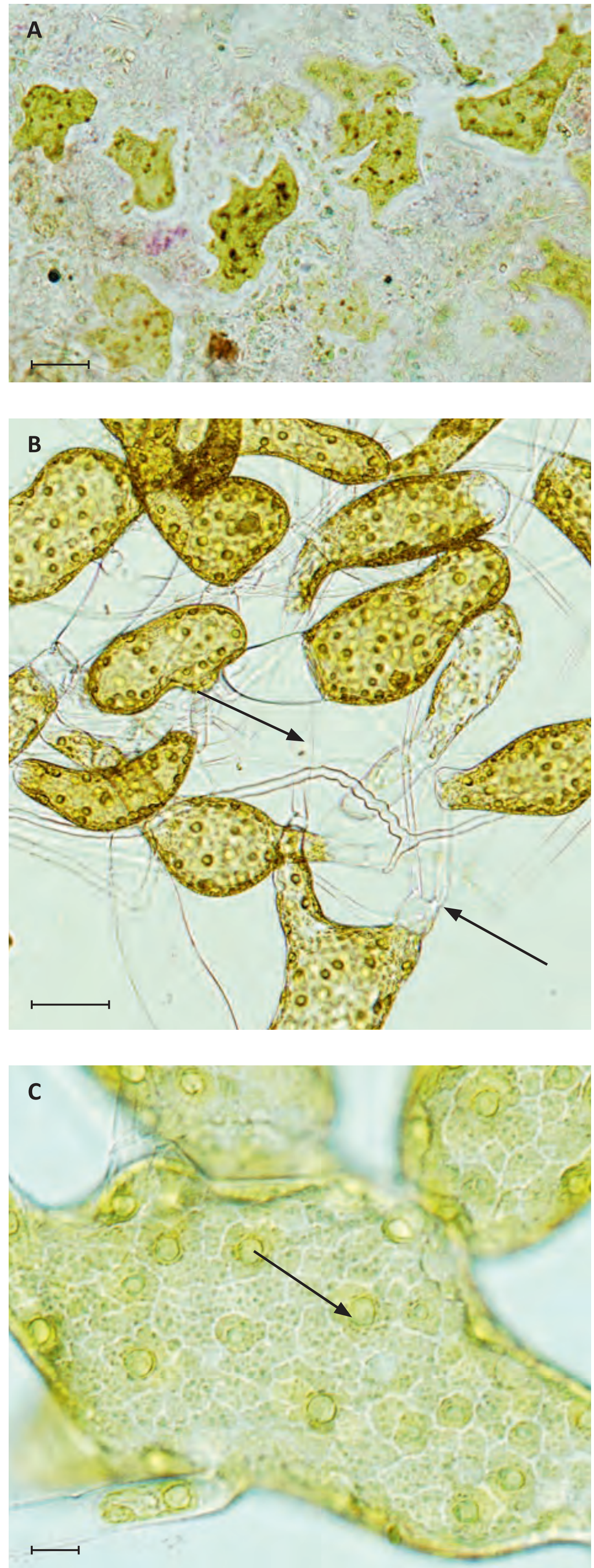
**Structure:** Rounded or irregular angular cells, 26-120 µm in width. The cells may be close to each other or at some distance, connected by narrow colourless filaments. Vegetative cells each contains several nuclei and a parietal plastid, which is split in many small angular plates, of which only some contain a large pyrenoid. One or a few colourless, unicellular hairs with a slightly swollen base might occur on some cells.

**Reproduction:** Asexual reproduction with zoospores is known from culture studies. Sporangia develop from vegetative cells, which remain the same size and shape as in the vegetative condition. A relatively long exit-tube develops, and a large number of zoospores are released at maturity. During the germination process, a narrow colourless germination tube is formed, which together with the evacuated spore wall is cut off from the developing alga, but visible in germlings.

**Seasonal variation:** Present all year, collected in January, March-October.

**Habitat:** Epiphytic, and in part or completely endophytic in the surface of soft red and brown algae such as old Purple Claw Weed (*Cystoclonium purpureum*) and old parts of Sugar Kelp (*Saccharina latissima*), on Eelgrass (*Zostera marina*) and on stone among crustose red- and brown algae, 1-18 m depth.

**References:** Chappell et al. (1991), Iima & Tatewaki (1987), Nielsen in Brodie et al. (2007).




A: *Blastophysa rhizopus*. Irregularly angular cells on stone with other small algae. Søndre Stenrøn, Little Belt, 6.5 m, 6.9.1993. Scale 20 µm.

B: *Blastophysa rhizopus.* Large irregularly rounded cells in culture. Two hairs in one cell (right arrow) and connecting filament (left arrow). Scale 50 µm. B-C: Culture of alga from Bergen, Norway.

C: *Blastophysa rhizopus.* Irregular cell in culture. Plastid of angular plates, some of them with pyrenoids (arrow). Scale 10 µm.

## Family: Cladophoraceae

### *Chaetomorpha*

Brick Weeds

**Appearance:** Uniseriate, unbranched, relatively stiff filaments attached by the basal cell or unattached. Attached individuals are typically straight, increasing in width from the base towards the apex. Unattached individuals have curled filaments and are uniform in width.
**Structure:** Filaments consist of cylindrical to barrel-shaped or approximately spherical cells. Cell divisions occur in scattered cells (diffuse growth) but might be localized to cells just above the base. Cell walls are regularly striate due to oblique cellulose fibrils. Vegetative cells each contains a parietal plastid with many pyrenoids and typically, > 50 nuclei. The plastid consists of angular plates connected by slender filaments, apparently filling the cell like a sponge (spongy plastid), but the shape is often hidden by deposits of storage products.
**Reproduction** isomorphic, haploid or diploid thalli with both sexual and asexual reproduction by swarmers. Sporangia develop from vegetative cells in the upper part of attached algae and are the same shape and size as in the vegetative condition. They contain large numbers of swarmers at maturity, either sexual gametes or vegetative zoospores. The swarmers are released through one or more pores in the sporangium wall. Unattached algae typically reproduce by fragments which continue the growth.
**Comment:** Species of Brick Weed (*Chaetomorpha*) might be difficult to discriminate from Green Thread Weeds (*Rhizoclonium*) when rhizoids are absent. The cells in Green Thread Weeds (*Rhizoclonium*) have a few, centrally placed nuclei, whereas there are many scattered nuclei in cells of Brick Weed (*Chaetomorpha*).
**References:** Cormaci et al. (2014), Kim et al. (2010), Leliaert & Boedeker in Brodie et al. (2007).

**Identification key to species of *Chaetomorpha***

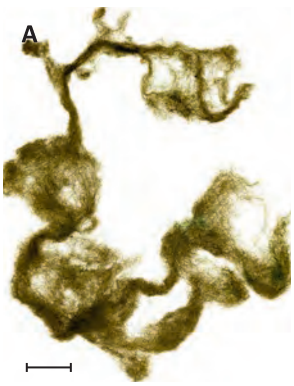
| | | |
|---|---|---|
| 1a. | Attached, very stiff, dark blue-green threads, approximately 600 µm in width | *C. melagonium* |
| 1b. | Attached or unattached thinner green threads | 2 |
| 2a. | Attached on other algae, or unattached, entangled, curled masses, filaments 15-60 µm in width | *C. ligustica* |
| 2b. | Attached on stone, or unattached entangled masses, filaments 150-450 µm in width | *C. linum* |

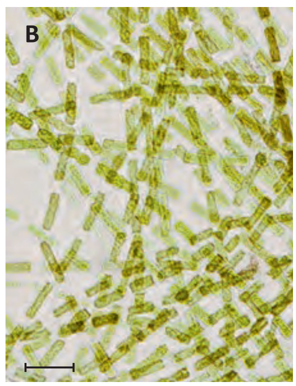
# *Chaetomorpha ligustica*

**(Kützing) Kützing**

Ligurian Sea Brick Weed

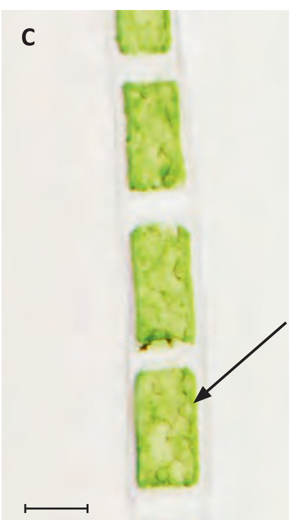
**Appearance:** Entangled masses of thin, curled filaments, a few cm in width and 10-20 cm in height.
**Structure:** Uniseriate, unbranched filaments of cylindrical cells, 15-60 µm in width and 1.5-4 times as long as wide. Basal cell approximately 3 times as long as wide.
**Reproduction:** Sporangia in attached alga with 1-2 exit pores per sporangium.
**Seasonal variation:** Collected in March, May-August. Sporangia recorded in May-June.
**Habitat:** Typically entangled between other algae or drift at shallow water, 0.5-3.5 m depth. Individuals at greater depth epiphytic on other algae at stone reefs, 8-18 m depth.
**Comment:** Few Danish collections, the first from the western part of the Limfjord, 1964.
**References:** Christensen 1975 (*C. capillaris*).




A: *Chaetomorpha ligustica.* Entangled mass of unattached threads. Bay in the harbour, Hirsholm, 6.8.1979. Scale 2 cm.

B: *Chaetomorpha ligustica.* Uniseriate, unbranched vegetative filaments of cylindrical cells. Helligsø, 3.5 m, 22.8.2000. Scale 50 µm.





C: *Chaetomorpha ligustica.* Cylindrical cells with many pyrenoids (arrow). Læsø Trindel, 18 m, 3.6.1993. Scale 50 µm.

D: *Chaetomorpha ligustica.* Basal cell with attachment disc. Scale 25 µm. D, F: Tønneberg Banke, 11 m, 3.6.1993.



E: *Chaetomorpha ligustica.* Almost mature sporangium with rounded swarmers. Tønneberg Banke, 18 m, 3.6.1993. Scale 25 µm.

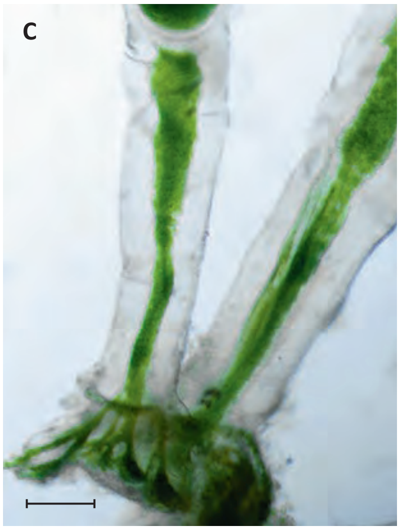
F: *Chaetomorpha ligustica.* Empty sporangia, 1 or 2 exit pores (P) in each. Scale 50 µm.

## *Chaetomorpha linum*
**(O.F.Müller) Kützing**
Flax Brick Weed

**Appearance:** Stiff, unbranched, light green threads. Attached at exposed localities as small tufts of a few threads from the same point, a few centimetres in height. Also occurs at sheltered localities, as unattached mats of entangled curly threads, up to 3 m in length. Firmly entangled threads, with an outline resembling an elongate ball the size of walnuts or tennis balls, occur as drift in autumn. They are named "falske gedeboller" in Danish [false goat rolls].
**Structure:** Uniseriate, unbranched filaments of cylindrical to barrel-shaped cells, slightly constricted at cross walls, 100-450 µm in width and 0.5-2 times as long as wide. Attach to the substratum by short downward-growing rhizoids from the lower part of the basal cell. Diffuse growth, the daughter cells after cell division of unequal length. Immediately above the elongate basal cell, there is a series of short dividing cells.
**Reproduction:** Upper cells in attached specimens at wave exposed localities are continuously transformed into sporangia which contain a large number of swarmers at maturity. These individuals only become 2-5 cm in height due to the constant sporangia formation from the upper cells. Unattached individuals continue the diffuse growth and reproduce by fragments. Culture studies of the alga from the type locality in Denmark (Kornmann, 1972a) revealed both gametophytes and sporophytes.
**Seasonal variation:** Present all year, well-developed in summer. Collected in January-November, with sporangia in summer.
**Habitat:** On wave exposed harbour jetties of boulders, 0.5-1 m depth and unattached at shallow water in sheltered localities. Collected by divers to 11 m depth.
**Resembles:** *Chaetomorpha aerea* (Dillwyn) Kützing appears similar, and some authors consider it to be a form of Flax Brick Weed (*C. linum*), by others a separate species. After cell divisions, daughter cells are unequal in height in Flax Brick Weed (*C. linum*), whereas they are equal in height in *C. aerea* according to Kornmann (1972a).
**Comment:** Type locality, Nakskov Fjord, Lolland, Denmark.
**References:** Christensen (1957), Kornmann (1972a), Kristiansen (1978).


A: *Chaetomorpha linum*. Tufts of short, attached threads, with empty sporangia in upper part. Exposed side, southern harbour jetty, Hirsholm, 0.5 m, 13.8.1965. Scale 2 cm.

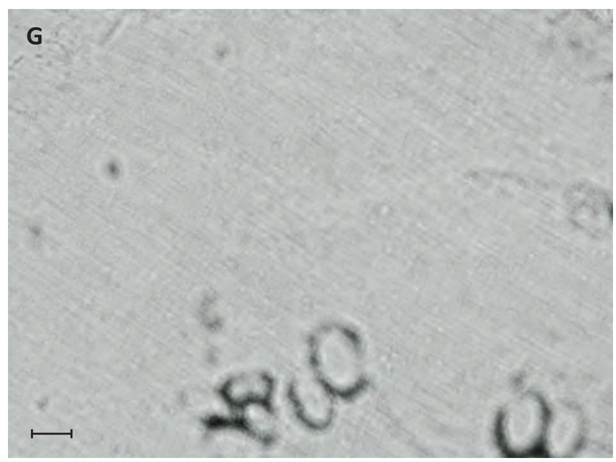

B: *Chaetomorpha linum*. Unattached mass of curly threads. Frederiksholms Kanal, Copenhagen, 3 m, 23.9.2007. Scale 2 cm.




C: *Chaetomorpha linum*. Basal cells of attached threads, with attachment rhizoids. Scale 100 µm. C, F-G: Outside Vinderup, Venø Bugt, 0.5 m, 6.10.2015. Leg.: M.B. Rasmussen.


D: *Chaetomorpha linum*. Daughter cells after cell division of unequal height. Scale 100 µm. D-E: Northeastern part of Refshaleøen, Copenhagen, 0.5 m, 21.9.2007.


E: *Chaetomorpha linum*. Plastid of small plates, connected by slender filaments, many pyrenoids. Scale 50 µm.


F: *Chaetomorpha linum*. Sporangium being emptied (arrow). Sporangia with 1 or 2 exit pores (P). Scale 100 µm.

G: *Chaetomorpha linum*. Empty cell wall with striae of oblique cellulose fibrils. Oval shapes of epiphytic diatoms. Scale 25 µm.

## *Chaetomorpha melagonium*

**(F.Weber & D.Mohr) Kützing**

Glaucous Brick Weed

**Appearance:** Dark blue-green, stiff, unbranched threads, typically 5-10 cm in height, but occasionally up to 33 cm in height. Typically as individual threads but may occur in groups of several individuals.

**Structure:** Filaments of barrel-shaped cells, constricted at cross walls and becoming more rounded towards the apex. Cells c. 600 µm in width and 1-2 times as long as wide. Basal cell is long and consists of several fused cells, followed by relatively short cells.

**Seasonal variation:** Collected all year (January-December).

**Habitat:** On stone and other solid substrata in shade between boulders of harbour jetties, c. 1 m depth and collected by divers at stone reefs to 27 m depth.

**Resembles:** Grows as individual threads as opposed to Flax Brick Weed (*C. linum*) which occurs in tufts of several threads.

**References:** Novaczek et al. (1990).



A: *Chaetomorpha melagonium*. Short, stiff, thick threads. In shade between boulders, Vesterø Havn, Læsø, 0.75 m, 26.5.1988. Scale 2 cm.

B: *Chaetomorpha melagonium*. Attached individuals of long dark threads. Kulhuse Havn, Isefjord, 0.5 m, 3.10.1987. Scale 2 cm.

C: *Chaetomorpha melagonium*. Long basal cell. Southern harbour jetty, Hirsholm, 0.75 m, 15.4.2015. Scale 200 µm.

# *Cladophora*

Green Branched Weeds

**Appearance:** Bush-like alga of much branched, narrow filaments, light to dark green, up to 50 cm in height. Branches are stiff and seem rough, so filaments do not easily slide from each other if gently pulled apart. It appears that branches are bristly when the thallus is lifted out of the water.

**Structure:** Branches are mainly found uniseriate with main branches and scattered lateral branches. Pseudodichotomous branches often occur, developing by displacement of lateral branches. Branches are mutually free and consist of cylindrical cells. Growth is apical and diffuse. Lateral branches typically develop immediately after a cell division and arise from the upper part of the daughter cell below the new cross wall. In some species branches are mainly found in the upper part of the thallus, where a lateral branch develops immediately after transverse division of the apical cell. This process continues in the apical part of the new lateral branches with the youngest lateral branches developing closest to the original apical cell. Thus, older branches appear with several new lateral branches in the upper end (acropetal growth). In such thalli, intercalary cell divisions without formation of lateral branches, or with secondary lateral branches occur further down and the frond appearing as long branches with a tuft of lateral branches in the upper end. Other species do not form lateral branches immediately after division of the apical cell and develop lateral branches after some intercalary cell divisions. One or several lateral branches occur at a single branching point. Thalli attach by rhizoids from the lower cells of main branches or with a basal attachment disc. Cells contain many nuclei and a single plastid of angular plates connected by tiny filaments, so the plastid appears similar to a spongy net and fills the cell (figs F, G page 28 Vol. 1). Many pyrenoids, are embedded in the plastid, but not all of the plates contain a pyrenoid. Starch around the pyrenoids resemble two semi-circular shells. Cell walls consist of cellulose fibrils, visible as tiny longitudinal and transverse striae in the microscope.

**Reproduction:** Isomorphic gametophytes and sporophyte. Sporangia develop from vegetative cells and keep the same shape and size as in the vegetative condition or become barrel-shaped. Swarmers are released through a round pore, or sometimes through a small exit-tube. Sporangia formation begins in the upper end of the thallus and continues downwards. Sporangia are typically in series and a large part of thallus is lost after release of swarmers. Sexual reproduction takes place by copulation of similar swarmers (isogametes) with two flagella (biflagellate). Haploid gametophytes (n) and diploid sporophytes (2n) may alternate regularly. Haploid zoospores (n) with 4 flagella develop after meiosis and develop into new gametophytes. Swarmers with 2 flagella may act as sexual gametes or as vegetative zoospores. Swarmers with 4 flagella are always vegetative regardless the development with or without meiosis (Hoek et al., 1995).

Many species are easily torn off the substratum and are able to continue growing. Unattached fragments of thalli may also continue to grow.

**Resembles:** Tarantula Weed (*Acrosiphonia*) and Spongy Weed (*Spongomorpha*), might appear similar, but have hyphae-like filaments which entangle the branches, and pseudodichotomous branches are absent.

**Comment:** *Cladophora* contains many species, but species identification is difficult, particularly for grass-green and light-green species. The distinctive characters, such as the general appearance, size, cell dimensions, attachment system and branching patterns vary according to habitat and level of nutrients. In addition, unattached individuals are often morphologically different from the same species when growing attached. Mass-production of swarmers also results in morphological variation as major parts of the thalli are transformed into sporangia and lost after release of swarmers.

A revision has not been undertaken of all specimens in the algal herbarium, Natural History Museum of Denmark, and recent collections from Danish waters are not very detailed or comprehensive but there is a need to obtain a better understanding of *Cladophora* species and distribution in Danish waters, particularly for the grass-green and light-green species.

**References:** Boedeker et al. (2016), Christensen (1988), Christensen et al. (1985), Hoek (1963), Hoek & Chihara (2000), Hoek et al. (1995), Jónsson et al. (1989), Leliaert & Boedeker in Brodie et al. (2007), Leliaert et al. (2009a), Noailles (1995), Söderström (1963).

### Identification key to species of *Cladophora*

| | | |
|---|---|---|
| 1a. | Cross walls in upper part of thallus are almost exclusively formed after divisions of apical cells, and soon after a new branch develops just below the new cross wall (acropetal branching). Therefore, only a few cross walls occur without a branch just below | 2 |
| 1b. | Cross walls form in all cells of the thallus, therefore there are many cross walls without a branch just below and many cells between branches | 5 |
| 2a. | Often 2, rarely 3 branches at each branching point. Branching dense. Apical cells cylindrical with rounded apex, mainly $> 45$ µm wide | *C. laetevirens* |
| 2b. | Often 3 or several branches at each branching point. Apical cells mainly $< 50$ µm wide | 3 |
| 3a. | Branching dense. Main branches much wider than lateral branches, which are of a regular thickness | *C. dalmatica* |
| 3b. | Upper part of thallus with dense branching, lower part with much intercalary growth, and thallus appears as a bunch of tufts on stipes. Branches in coarse algae are distinctly tapering towards the apex | 4 |
| 4a. | Occurs in fresh- and brackish water with salinity up to 15. Only vegetative reproduction | *C. glomerata* |
| 4b. | Occurs in saltwater with salinity down to 6 | *C. vagabunda* |
| 5a. | Dark green, branches arise in acute angles with 1-6 branches at each branching point | *C. rupestris* |
| 5b. | Grass-green, branches more or less protruding, rarely more than 3 branches at each branching point | 6 |
| 6a. | Apical cells 90-220 µm in width. Branches of regular width | *C. hutchinsiae* |
| 6b. | Apical cells $< 50$ µm in width | 7 |
| 7a. | Many cells with 2, sometimes 3 branches. Most cells c. 20 µm in width, very few $> 50$ µm. Thallus dense parsley-like in exposed localities, whereas branches are straight and distant in sheltered localities | *C. albida* |
| 7b. | Most cells with a single branch. Branches of last order, typically in unilateral series | 8 |
| 8a. | Branches of last order with cylindrical cells. Apical cells rounded | *C. flexuosa* |
| 8b. | Branches of last order taper towards the pointed apical cell. Short branches may appear thorn-like | *C. sericea* |

# *Cladophora albida*

**(Nees) Kützing**

Pale Green Branched Weed

**Appearance:** Bush-like thallus. In exposed localities, very spongy, tufted, grass-green, parsley-like branches. In sheltered localities branches are straight and thallus light green.

**Structure:** Pseudodichotomous main axis. The apical cell divides several times before the first branch develops, so 3-5 cells occur above the first branch. A branch occurs at each cross wall further down in the thallus. Branches grow fast and it is typical that the apical cells in the upper 3-4 branches reach the same height. Branches are in unilateral series near the apex. Apical cells are approximately cylindrical and rounded, 31-39 µm in width. Further down in the branches growth is intercalary with 2-3 branches at each branching point. The main axis has cells with thick walls. There are many intercalary cell divisions throughout. Branches curve backwards and branches of different age and length occur between each other. The thallus is attached by several rhizoidal filaments from the lower cells.

**Reproduction:** Sporangia are cylindrical to barrel-shaped.

**Seasonal variation:** Collected in March, May-September.

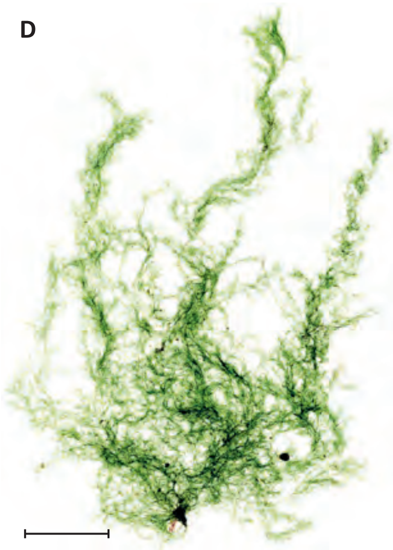
**Habitat:** On stone and epiphytic on coarse algae, 0.5-6 m depth.

**References:** Hoek and Chihara (2000), Kim et al. (2010), Söderström (1963, *C. albida*, *C. hamosa*).


A: *Cladophora albida*. Bush-like thallus with spongy growth. Scale 2 cm. A-C: Søndre Stenrøn, 3 m, 7.9.1993.

B: *Cladophora albida*. Apex with first branch on the 6th cell, followed by unilateral branches and a branching point with 2 branches. Scale 50 µm.

C: *Cladophora albida*. Branches in the upper part with cylindrical to barrel-shaped sporangia, many empty. Branching point with 3 branches (arrow) of unequal length. Scale 50 µm.

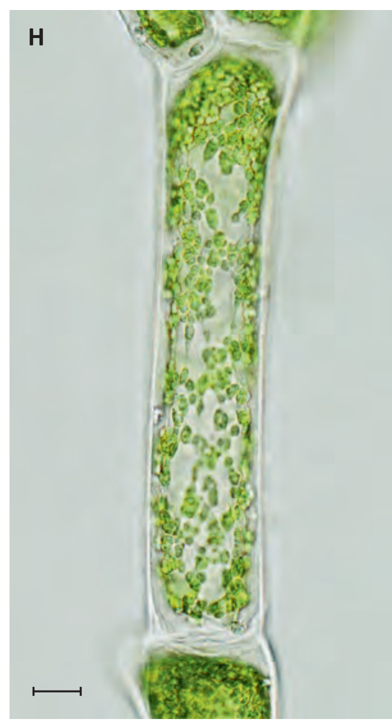

D: *Cladophora albida*. Bush-like thallus with straight branches and elongate shape. Scale 2 cm. D-H: Pole of pier in harbour basin, Vesterø Havn, Læsø, 0.5 m, 23.8.2016.


E: *Cladophora albida*. Apical part, first branch at 5$^{th}$ cell below apex. Branching point with 2 branches (arrow). Scale 100 µm.


F: *Cladophora albida*. Rounded apical cells of branches. Scale 20 µm.

G: *Cladophora albida*. Branching point with 3 branches. Scale 50 µm.

H: *Cladophora albida*. Plastid of angular plates, connected by slender filaments. Scale 20 µm.

# *Cladophora dalmatica*

**Kützing**

Dalmatian Green Branched Weed

**Appearance:** Much branched, light-green bush-like thallus, up to 28 cm in height. Upper branches curved backwards.

**Structure:** Thallus with acropetal growth. Branches are straight and regular in width. Typically, 2-4 (-5) protruding branches arise from a single branching point, which repeats at intervals of 2-3 cells. The main axis is in the upper part of the thallus, therefore it has several consecutive branching points with many branches. Branches terminate in clusters of short branches that are slightly curved backwards. Apical cells are rounded, 26-29 µm in width and 2-3 times as long as wide.

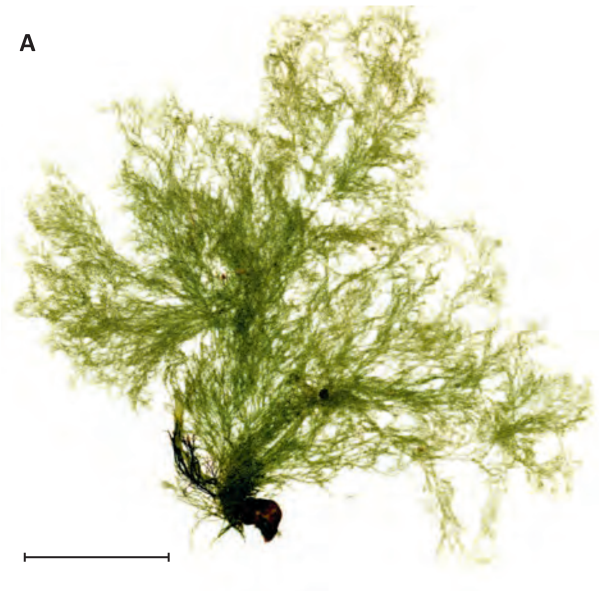
**Reproduction:** Seriate, barrel-shaped sporangia in upper part of thalli, 35-42 µm in width, slightly longer or up to 2 times as long as wide.

**Seasonal variation:** Collected in May-October.

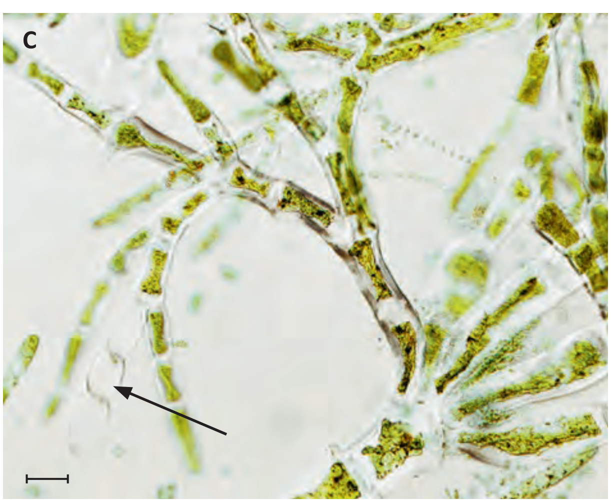
**Habitat:** On stone and epiphytic on Bladder Wrack (*Fucus vesiculosus*) and other coarse algae, 0.1-1 m depth. Also collected in shallow water in a beach-pond, Fynshoved.

**Resembles:** Reminiscent of Clustered Green Branched Weed (*C. glomerata*), see notes for this species.

**References:** Söderström (1963, *C. oblitterata*).








A: *Cladophora dalmatica*. Bush-like densely branched thallus with branches curved backwards. Southern part of Lille Stenholm, Nordre Rønner, Læsø, 0.5 m, 15.8.2005. Scale 2 cm.

B: *Cladophora dalmatica*. Apex with dense branching. Branches regular in width. Scale 200 µm. B-C: Southern part of Spirholm, Nordre Rønner, Læsø, 0.5 m, 19.8.2005.

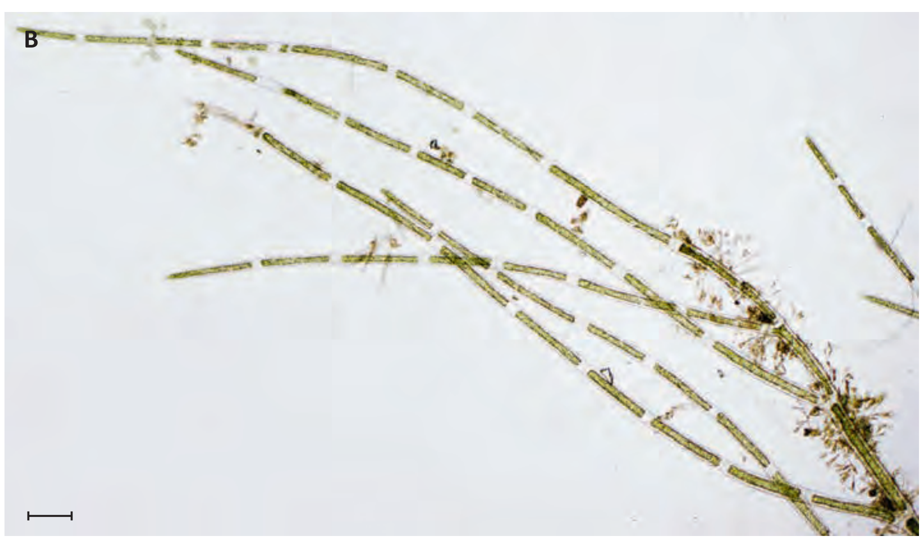
C: *Cladophora dalmatica*. Branching point with 4 branches. Empty sporangia (arrow). Scale 50 µm.

# *Cladophora flexuosa*

**(O.F.Müller) Kützing**

Green Branched Weed


**Appearance:** Bush-like thallus with narrow light-green branches on all sides. Typically, an elongate shape in outline and may form large hanging masses.
**Structure:** Main axis pseudodichotomously branched, rarely more than a single branch at each branching point. Branches typically adpressed or coherent with main axis at a short distance from the origin. Branches are unilateral and relatively long with many cells. Branches are regular in width or become slightly narrower towards the rounded apical cell, 19-30 µm in width. Young and older branches occur in a mixed sequence. Young branches are straight and originate in a lateral position, later the wall is displaced, and the branching becomes pseudodichotomous. Loosely attached, and often drift while still growing.
**Reproduction:** Sexual reproduction with biflagellate gametes, and vegetative reproduction with quadriflagellate zoospores, reported for the alga in Britain, with barrel-shaped sporangia in series in the upper part of branches (Leliaert & Boedeker in Brodie et al., 2007).
**Seasonal variation:** Present all year, recorded in January-December.
**Habitat:** In shallow water at protected localities and epiphytic on other algae to 15 m depth.




A: *Cladophora flexuosa*. Elongate bush-like alga, without tufts of branches at the apex. Scale 2 cm. A-D: Horneks Odde, Læsø. 24.8.2016.

B: *Cladophora flexuosa*. Apex with long unilateral branches. Scale 100 µm.

**Resembles:** Difficult and not always possible to distinguish from Silky Green Branched Weed (*C. sericea*) without molecular studies. The map of distribution in Danish waters therefore includes both species.

**References:** Hoek (1963, *C. sericea*), Hoek & Chihara (2000), Leliaert & Boedeker in Brodie et al. (2007), Söderström (1963).


C: *Cladophora flexuosa*. Cylindrical apical cell, rounded apex. Scale 20 µm.


D: *Cladophora flexuosa*. Typically confluent lower part of pseudodichotomous branches. Scale 50 µm.

# *Cladophora glomerata*

**(Linnaeus) Kützing**

Clustered Green Branched Weed

**Appearance:** Openly branched light to dark yellow-green bush-like thallus, 5-30 cm in height. Branches terminate in tufts of short branches. The size and branching is very variable, dependent on habitat and season.

**Structure:** Apical growth with many branches in apical part (acropetal growth). Further down the thallus cell divisions are intercalary, without development of branches. Branches on all sides, with up to 4-5 branches from each branching point in the upper part of the alga. Apical cells, 25-70 µm in width, at least 20 µm in width.

**Reproduction:** Sporangia are barrel-shaped and form series in the upper part of branches. They contain swarmers with 2 flagella at maturity.

**Seasonal variation:** Occurs all year, collected in January-December. The largest thalli collected in September, and the smallest in November-December.

**Habitat:** On stone and other solid substrata and may occur unattached, 0.5-8 m depth.

**Resembles:** Confusion is possible with Dalmatian Green Branched Weed (*C. dalmatica*), Bright Green Branched Weed, (*C. laetevirens*) and Wandering Green Branched Weed (*C. vagabunda*), which all have acropetal growth. Cell size is best way to discriminate between them although there is some overlap in the dimensions. Apical cells are smallest in Dalmatian

A

A: *Cladophora glomerata*. Small alga recommencing growth. Wave exposed side, Margretheholms Havn, Copenhagen, 0.5 m, 19.2.2008. Scale 1 cm.

B

B: *Cladophora glomerata*. Well-developed bush-like alga, branches terminate in tufts of small branches. Sheltered side, Margretheholms Havn, Copenhagen, 0.5 m, 15.4.2004. Scale 2 cm.

Green Branched Weed (*C. dalmatica*), 26-29 µm in width and largest in Bright Green Branched Weed (*C. laetevirens*), > 45 µm in width.

**Comment:** Freshwater species which tolerates brackish water at a salinity up to 15 (-17). A dominant element in the summer vegetation (July-September) in Copenhagen harbour.

**References:** Kristiansen (1972).


C: *Cladophora glomerata*. Branching point with 4 branches. Scale 50 µm. C-F: Exposed side, eastern harbour jetty, Gilleleje, 0.5 m, 16.7.2006.


D: *Cladophora glomerata*. Branch with series of empty sporangia, exit-tube in upper part of the sporangia. Scale 50 µm.


E: *Cladophora glomerata*. Wall of empty sporangium with striae of cellulose fibrils. Scale 10 µm.


F: *Cladophora glomerata*. Drop-shaped swarmer with two flagella in the pointed front, plastid and a red eye-spot (arrow). Scale 10 µm.

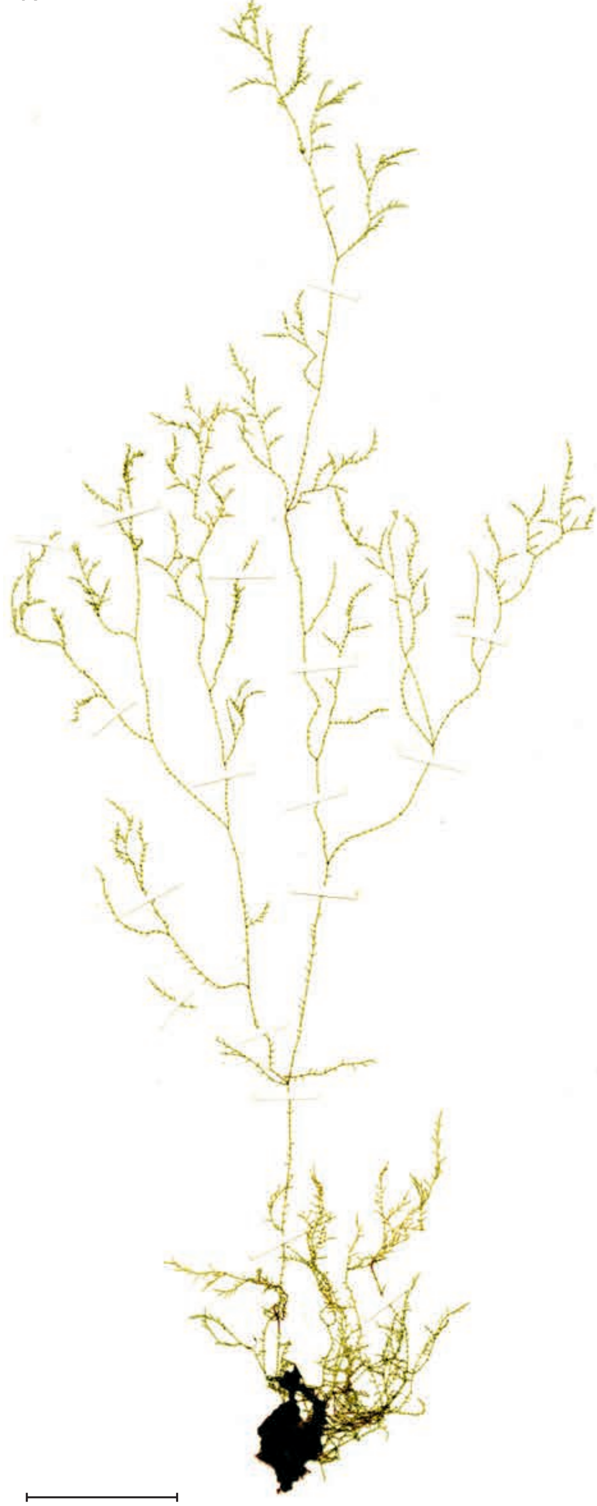
# *Cladophora hutchinsiae*

**(Dillwyn) Kützing**

Ellen Hutchin's Green Branched Weed

**Appearance:** Grass-green coarse bush-like thallus.
**Structure:** Protruding branches are regular in width with apical cells, 90-220 µm in width. Rarely more than 3 branches at a single branching point. Intercalary cell divisions, often without development of branches. Therefore many cross walls without branches at some distance below the apex.
**Comment:** Only a few older collections of this species in the algal herbarium, Natural History Museum of Denmark. The most recent collection is a drift specimen dated 1943. The status of the species in Danish waters is uncertain and needs confirmation by new collections.

A



A: *Cladophora hutchinsiae*. Grass-green bush-like alga with short protruding branches. Maleklit, Mors, drift, 7.8.1943. Leg. & det.: T. Christensen.

## *Cladophora laetevirens*

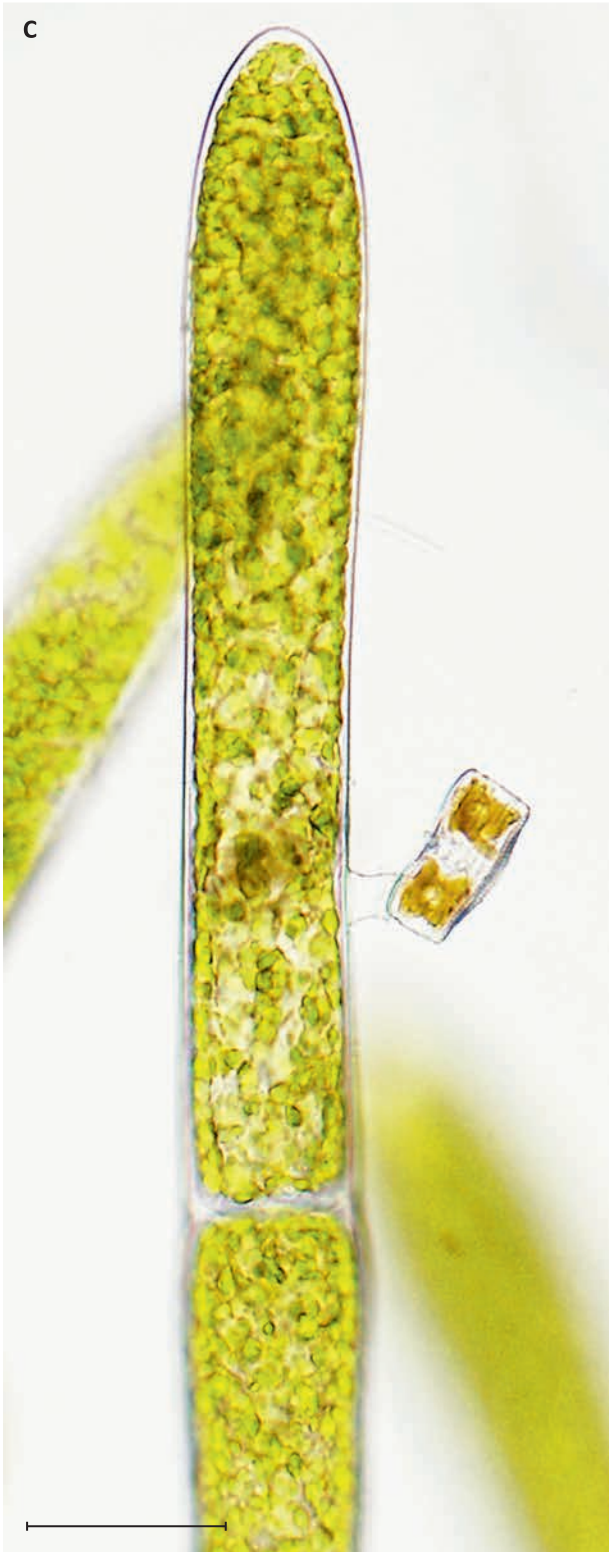
**(Dillwyn) Kützing**

Bright Green Branched Weed

**Appearance:** Much branched, grass-green to light-green bush-like thallus with clusters of small branches in upper part and many branches along the main branches. Relatively coarse, up to 17 cm in height.
**Structure:** Apical growth, and immediately after cell division, a new branch develops just below the new cross wall. There are many branches in the apical part (acropetal growth). Diffuse growth occurs further down in the thallus. Pseudodichotomous main branches, dense branching often with 2 (3) branches at each branching point. Apical cells, cylindrical with rounded apex, (35-) 45-75 (-110) µm in width and 2-10 times as long as wide. Cells in main axes, 100-260 µm in width.
**Reproduction:** Sporangia form series of barrel-shaped cells in the upper part of branches.
**Seasonal variation:** Collected in April-October.
**Habitat:** On small stones and bivalve shells in sheltered localities with sandy bottom, 0.2-3 m depth.
**Resembles:** See comment for Clustered Green Branched Weed (*C. glomerata*).
**References:** Leliaert & Boedeker in Brodie et al. (2007).


A: *Cladophora laetevirens.* Bush-like much branched alga. Sheltered locality to northeast, Deget, Frederikshavn, 13.7.1966. Leg. & det.: T. Christensen. Scale 2 cm.


B: *Cladophora laetevirens.* Bush-like alga with dense branches. Scale 2 cm. B-E: Rønnerne, Frederikshavn, 0.1 m, 22.9.2017.




C: *Cladophora laetevirens*. Cylindrical, apical cell. Scale 50 µm.


D: *Cladophora laetevirens*. Branching point with 2 branches. Scale 50 µm.

E: *Cladophora laetevirens*. Part of alga with dense branches, several typical branching points with 2 branches. Scale 200 µm.

# *Cladophora rupestris*

**(Linnaeus) Kützing**

Common Green Branched Weed

**Appearance:** Dark green bush-like thallus with dense, straight, stiff branches on all sides. Typically up to 15-20 cm in height, but occasionally 30 cm in height.
**Structure:** Branches consist of cylindrical cells with thick walls, growth is diffuse. Many branches arise in acute angles to the main axes. They develop in the upper part of the supporting cell with an oblique wall, and in time they become displaced and branching is pseudodichotomous. Two to several branches may occur from the same branching point, particularly in the older part of the frond. Vegetative cells contain cubic crystals, which consists of protein (Leliaert & Coppejans, 2004).
**Reproduction:** Life history of the alga from Roscoff comprised isomorphic haploid and diploid individuals. Haploid individuals reproduced by gametes with 2 flagella and the diploids by zoospores with 4 flagella (Jónsson & Perrot, 1967).
**Seasonal variation:** Occurs all year, collected in January-December.
**Habitat:** On gravel and boulders, collected by divers, 0-17.5 m depth, and in older collections obtained by dredge to 28 m depth.
**References:** Jónsson & Perrot (1967), Leliaert & Coppejans (2004), Lund (1934).



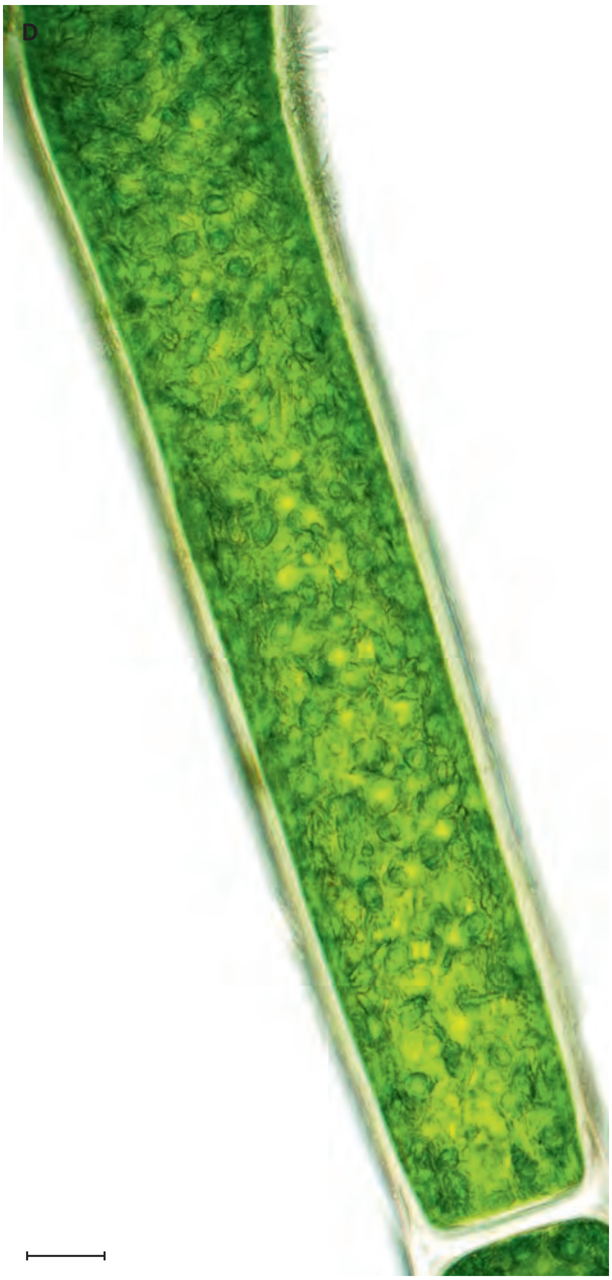
A: *Cladophora rupestris.* Dark green alga with dense, straight branches. Lysegrund, 5 m, 5.8.1990. Scale 2 cm.

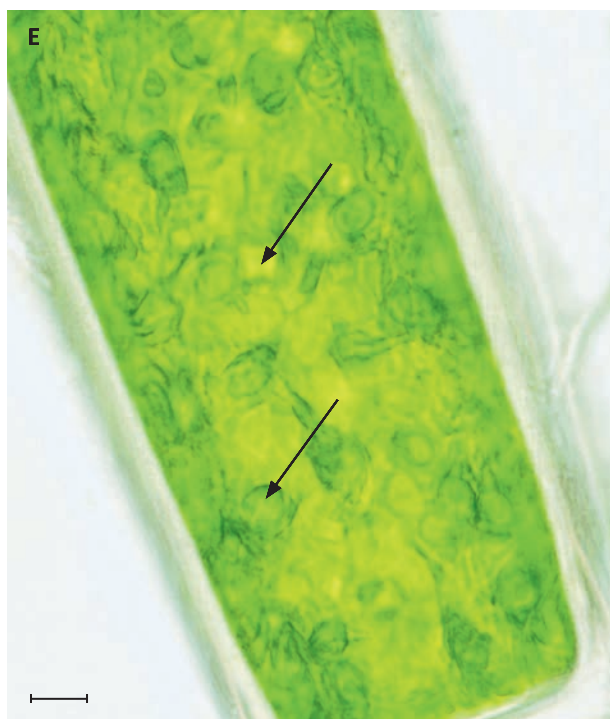
B: *Cladophora rupestris.* Pseudodichotomous branches. Hirsholm, 0.5 m, 1.10.2015. Leg.: K.L. Krabbe. Scale 100 μm.

C: *Cladophora rupestris*. Branching point with acute branch angles and 3 branches. Scale 100 µm. C-E: Hirsholm, 0.5 m, 14.4. 2015.

D: *Cladophora rupestris*. Vegetative cell with spongy plastid, many pyrenoids and cubic crystals. Scale 50 µm.

E: *Cladophora rupestris*. Cubic crystal (upper arrow) and pyrenoid (lower arrow), the same cell as in fig. D. Scale 10 µm.

# *Cladophora sericea*

**(Hudson) Kützing**

Silky Green Branched Weed

**Appearance:** Light-green bush-like thallus of narrow branches, with an elongate morphology.

**Structure:** Main axes have many unilateral branches which taper towards a slightly pointed apical cell, 11-26 µm in width. The base consists of a multicellular attachment disc, which develop from the basal cell of the main axis.

**Reproduction:** Cylindrical to barrel-shaped sporangia develop in the upper cells. Biflagellate gametes and zoospores with 2 or 4 flagella are reported by Leliaert & Boedeker in Brodie et al. (2007).

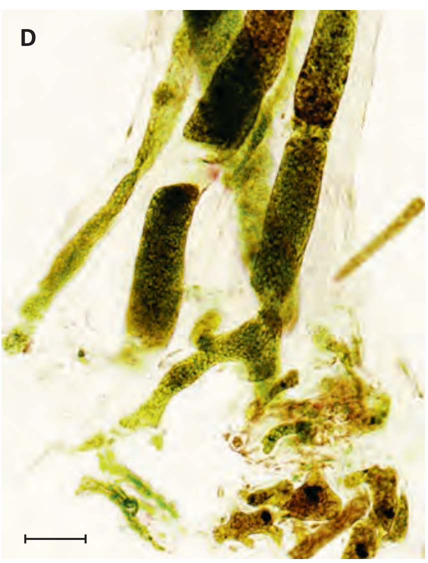
**Seasonal variation:** Collected in February, April-October. Sporangia recorded in July.

**Habitat:** On stone and drifting, 0.5-11.5 m depth.

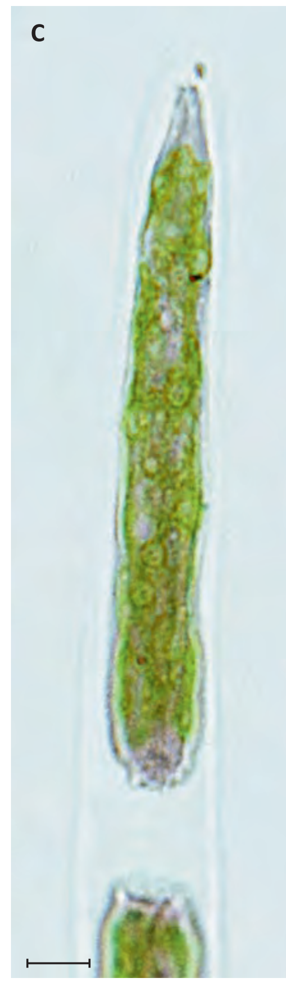
**Resembles:** Very similar to *C. flexuosa*, and often impossible to discriminate from it by morphology. The map of distribution in Danish waters therefore includes both species.

**References:** Leliaert & Boedeker in Brodie et al. (2007), Söderström (1963, *C. glaucescens*).


A: *Cladophora sericea*. Bush-like elongate alga. Klatterne, Nordre Rønner, Læsø, 0.75 m, 15.8.2005. Scale 2 cm.




D: *Cladophora sericea*. Basal system, multicellular attachment disc. Scale 50 µm.


B: *Cladophora sericea*. Apex with unilateral, pointed branches. Scale 100 µm. B-D: Ebbeløkke, 7 m, 26.7.1994.

C: *Cladophora sericea*. Pointed apical cell. Scale 10 µm.

# *Cladophora vagabunda*

**(Linnaeus) Hoek**

Wandering Green Branched Weed

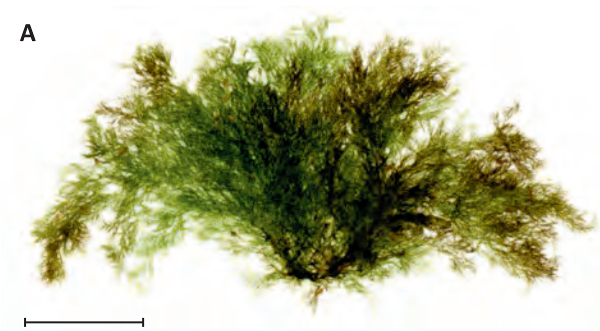
**Appearance:** Grass-green bush-like thallus, with clusters of small branches at the apex and along main branches.

**Structure:** Acropetal growth, branches develop just below the apical cell. Diffuse growth further down in the branches. Pseudodichotomous main axes, with up to 2-3 branches at each branching point. Apical cells, (17-) 25-60 (-80) µm wide and 1.5-10 (-15) times as long as wide according to Leliaert & Boedeker in Brodie et al. (2007).

**Reproduction:** Sporangia have the same shape and size as in the vegetative condition. Isogametes with 2 flagella and zoospores with 4 flagella are reported.

**Resembles:** Reminiscent of Clustered Green Branched Weed (*C. glomerata*), a freshwater species which tolerates brackish water and only reproduces by biflagellate swarmers. Bright Green Branched Weed (*C. laetevirens*) has a similar growth form, but apical cells > 45 µm in width and much coarser than Wandering Green Branched Weed (*C. vagabunda*).

**References:** Leliaert & Boedeker in Brodie et al. (2007).




A: *Cladophora vagabunda*. Bush-like alga with dense branches from the apex and along main branches. Scale 2 cm. A-D: Vejrø, 0.5 m, 2.9.1993.


B: *Cladophora vagabunda*. Branches develop immediately below the apical cell and are present at each of the following cross walls. A branch with apical sporangium (arrow). Scale 10 µm.


C: *Cladophora vagabunda*. Branching point with 2 branches. Scale 20 µm.


D: *Cladophora vagabunda*. Empty sporangium. Scale 20 µm.

## *Lychaete pygmaea*

**(Reinke) M.J.Wynne**

Mini Green Branched Weed

**Appearance:** Up to 3 mm in height, relatively stiff, dark green bush-like alga.
**Structure:** Branches scattered on all sides. A single relatively large basal cell with attachment disc. The cells are cylindrical to barrel-shaped, 17-57 µm in width and 1-4 times as long as wide with thick walls. Diffuse growth and branches cut off by oblique walls.
**Reproduction:** Upper cells of branches develop into seriate sporangia. Swarmers escape through a round pore in the middle of the sporangium. Zoospores with 4 flagella are recorded in the species in Britain.
**Seasonal variation:** Collected in January-September. Sporangia recorded in May-September.
**Habitat:** On sheltered side of small stones and in crevices in boulders, often in dense patches. Collected in 3-27 m depth.
**Resembles:** Differs from Danish species of Green Branched Weeds (*Cladophora*) by the small size and the relatively large basal cell.
**Comment:** Jónsson & Chesnoy (1991) studied Danish material and found 9-32 small nuclei in each cell.
**References:** Boedeker et al. (2016, *Acrocladus pygmaeus*), Jónsson & Chesnoy (1991, *Cladophora pygmaea*), Leliaert et al. (2009a, *C. pygmaea*), Wynne (2017), Wærn (1940, *C. pygmaea*).


A: *Lychaete pygmaea.* Much branched bush-like alga with scattered branches on all sides. Søndre Stenrøn, 9.5 m, 7.9.1993. Scale 50 µm.

B: *Lychaete pygmaea.* Small alga, large basal cell with attachment disc. Broen, 9.5 m, 9.9.1991. Scale 20 µm.

C: *Lychaete pygmaea.* Series of empty and mature (arrow) sporangia. Tønneberg Banke, 10.5 m, 12.8.1990. Scale 20 µm.


# *Rhizoclonium riparium*

**(Roth) Harvey**

Rooting Green Thread Weed

**Appearance**: Matted green cover of narrow threads. Thalli appear curled when occurring on soil in salt marshes.

**Structure:** Uniseriate filaments of cylindrical cells. They are unbranched apart from tiny protruding rhizoids on scattered cells. Rhizoids occur at irregular intervals or absent. Growth is diffuse. Cells, 10-20 µm in width and 2-4 times as long as wide with several (2-4) nuclei in the middle. The parietal plastid is net-like, perforated and contains several pyrenoids, but often difficult to see because of accumulations of storage products.

**Reproduction:** Vegetative reproduction from fragments, which continue growth. Nienhuis (1975) studied Rooting Green Thread Weed (*R. riparium*) in the Netherlands and found vegetative reproduction by zoospores with 2 or 4 flagella, and sexual reproduction with biflagellate gametes. Sporangia developed from series of cells and had the same shape and size as in the vegetative condition.

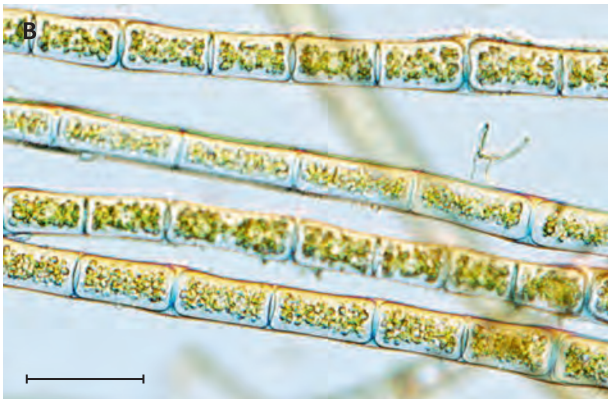
**Seasonal variation:** Occurs all year, collected in April-November.

**Habitat:** Common as matted threads on soil in salt marshes. Also recorded woven together with other algae, 1.5 m depth (Christensen, 1975).

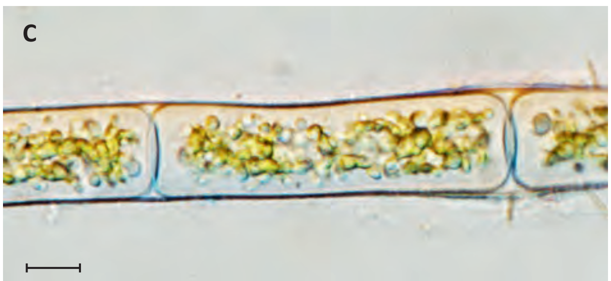
**Comment:** *Rhizoclonium implexum* (Dillwyn) Kützing was previously considered a separate species with cells (10-) 14-18 (-21) µm in width and 1-8.5 times as long as wide, and *R. riparium* with cells 18-48 µm in width and (0.5-) 1-2 (-4.5) times as long as wide (Koster, 1955). Nienhuis (1975) found large variation in the dimensions of filaments and considered *R. implexum* a synonym of *R. riparium*. The name *R. riparium* is used here in agreement with Leliaert & Boedeker in Brodie et al. (2007), who mention that *R. riparium* comprises "… a complex of several genetically divergent, truly cryptic species. In the field it can only be identified to the genus levell…"

**References:** Christensen (1975), Ichihara et al. (2013), Kornmann & Sahling (1977), Koster (1955), Leliaert & Boedeker in Brodie et al. (2007), Nienhuis (1975).


A: *Rhizoclonium riparium*. Green cover of narrow threads, on soil in salt marsh. Photo by Fl. Thorning Lund. A-D: Sønder Nyland, Læsø, 28.4.2016.




B: *Rhizoclonium riparium.* Vegetative filaments of cylindrical cells, unequal in length. Scale 50 µm.




C: *Rhizoclonium riparium.* Vegetative cells. Scale 10 µm.


D: *Rhizoclonium riparium.* Rhizoid from vegetative cell. Scale 10 µm.

## Family: Okellyaceae

# *Okellya curvata*

**(Printz) Leliaert & Rueness**

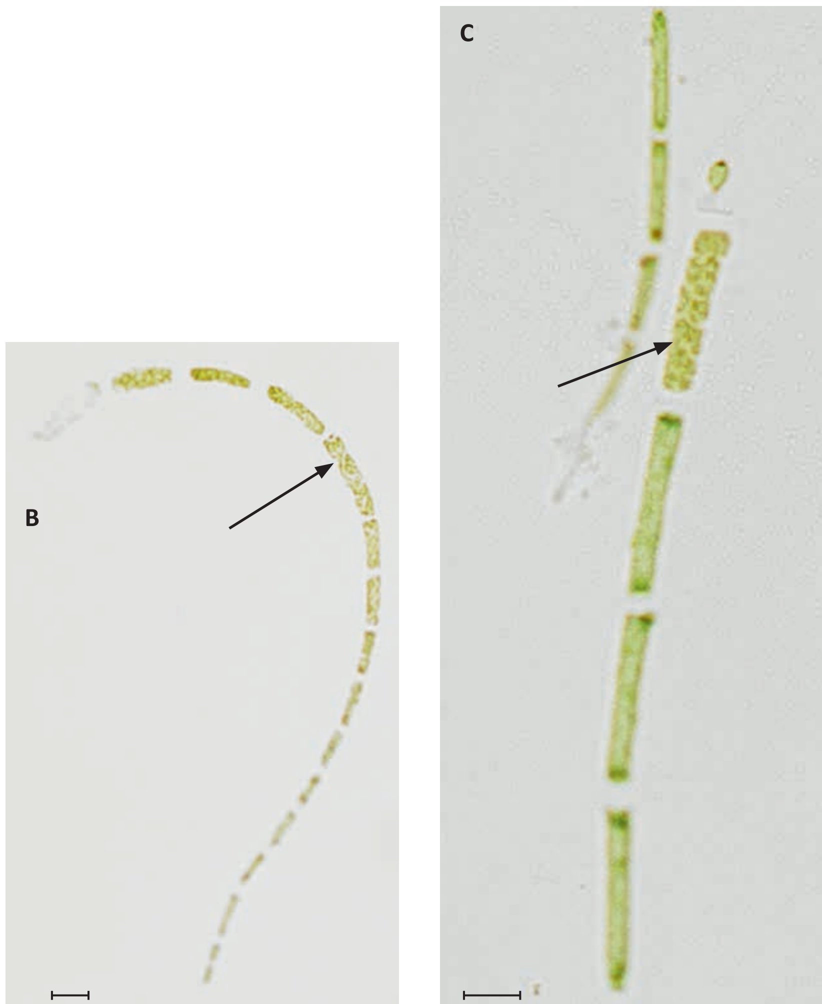
O'Kelly's Curved Thread Weed

**Appearance:** Slightly curved, yellow-green microscopic filaments. Often in dense stocks of many individuals.

**Structure:** Uniseriate, unbranched filaments, 100-180 µm in length and slightly curved. They attach by a small disc on the basal cell, and the apical cell has a rounded apex. The filaments consist of up to 12 cells and increase in width from 4-6 µm at the base to 7-14 µm in the upper part with cells, 1.5-6 times as long as wide. Vegetative cells contain a parietal plastid without pyrenoid.

**Reproduction:** Vegetative reproduction by zoospores. Sporangia formation begins at the apex. The apical cell transforms into a sporangium followed by the cell below. Sporangia contain many zoospores, which at maturity are released through a small exit-tube in the upper part of the sporangia. After the evacuation and decay of the sporangium walls the new apical cell has a straight upper wall.
**Seasonal variation:** Probably occurs all year, collected in January-June and August-September.

**Habitat:** On stone and pebbles, frequent epiphyte on Peysonnel's Brick-red Crust (*Peyssonnelia dubyi*) and on unicellular blue green alga (*Cyanocystis* sp.), 4-27 m depth.
**References:** Leliaert et al.(2009b), Maggs & Kelly in Brodie et al. (2007, *Uronema curvatum*), Rueness (1992, *U. curvatum*).




A: *Okellya curvata*. Dense patch of curved filaments on Peysonnel's Brick-red Crust (*Peyssonnelia dubyi*). Tønneberg Banke, 12 m, 11.6.1990. Scale 20 µm.

B: *Okellya curvata*. Sporangia formation in upper cells (arrow). Store Middelgrund, 24 m, 9.6.1993. Scale 10 µm.

C: *Okellya curvata*. Evacuated sporangium, with a single zoospore left and an almost mature sporangium (arrow). Læsø Trindel, 11 m, 3.6.1993. Scale 10 µm.

**Order: Bryopsidales · Family: Bryopsidaceae**

## *Bryopsis hypnoides*

**J.V.Lamouroux**

Mossy Feather Weed

**Appearance:** Bush-like alga with a bright yellow-green colour and slightly shiny surface. Typically 10-15 cm in height, and occasionally up to 28 cm in height in the Northern Kattegat. Branching appears feather-like with a distinct main axis and several generations of branches, although these are on all sides. Branches scattered and decrease in length from bottom to top so the alga has a pyramidal outline.

**Structure:** Branches without internal transverse walls (siphonous). They contain many nuclei, many plastids and other cellular organelles just below the outer wall, and have a large central vacuole. Plastids are elongate oval to spindle-shaped, each with 1 (-3) pyrenoids. Branches are regular in width, with a basal constriction. Upright axis arises from creeping, irregularly branched filaments, sometimes with several short uprights.

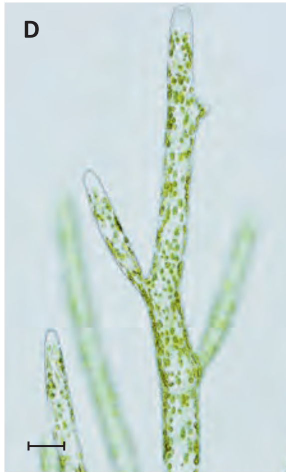
**Reproduction:** The life history comprises an upright thallus and a phase of creeping filaments. Vegetative and sexual reproduction by swarmers. Sporangia develop from transformed branches. This process begins with the formation of a wall which separates the branch from the main axis, and all contents of the branch become swarmers. These are released through a pore, leaving an empty sporangium wall, which decays. The lower branches first transform into sporangia and the process continue upwards. The lower part of the alga is therefore often without branches. Upright thalli are gametophytes. Swarmers are drop-shaped with two flagella at the pointed front end. Sexual swarmers are anisogametes, with small pale male and larger green female gametes. Zoospores resemble female gametes. Male gametes can already be recognized from the others within the sporangia as they look orange coloured whereas female gametes and zoospores are green. Different kinds of swarmers may form in separate sporangia and occasionally in the two opposite ends of the same sporangium. Zoospores grow up into new individuals, similar to the former generation. Gametes copulate and the zygote grows into creeping irregularly branched filaments, reminiscent of the basal filaments of upright thalli.

A

A: *Bryopsis hypnoides.* Young algae. Exposed side of jetty, Margretheholms Havn, Copenhagen, 1 m, 19.2.2008. Scale 2 cm.

B

B: *Bryopsis hypnoides.* Well-developed alga, distinct main axis. Vesterø Havn, Læsø, 0.5 m, 5.6.2017. Scale 2 cm.

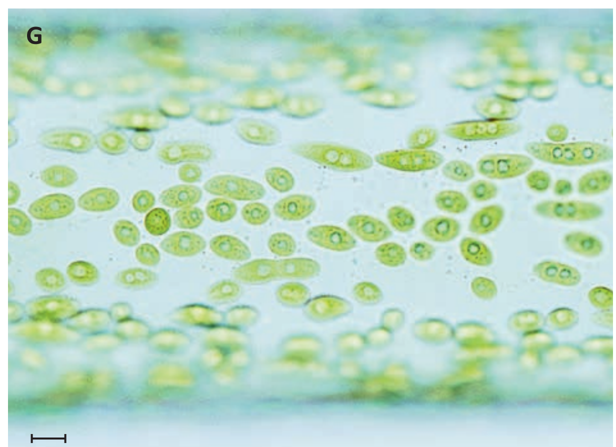


C: *Bryopsis hypnoides*. Feather-like alga, which developed branches on all sides in culture. Southern harbour jetty, Hirtshals, 1 m, 5.8.1979. Scale 1 cm.

D: *Bryopsis hypnoides*. Apex with siphonous branches on all sides. Scale 50 µm. D-G: Flakfortet, Copenhagen, 6 m, 22.6.2016.

E: *Bryopsis hypnoides*. Branches with constricted base. Scale 50 µm.

F: *Bryopsis hypnoides*. Base of branch, optical longitudinal section. Scale 20 µm.



G: *Bryopsis hypnoides*. Spindle-shaped plastids with 1 (-3) pyrenoids. Scale 10 µm.

New upright thalli may arise from the creeping filaments, or all of the content in the creeping filaments transforms into swarmers. These swarmers are spherical with many flagella in a whorl around the middle of the cell (stephanocont swarmers). They act as zoospores, germinate and develop into new upright thalli. The life history was studied in culture by Rietema (1969, 1970, 1971).

**Seasonal variation:** Occurs all year, well-developed in early summer.

**Habitat:** On solid substrata such as concrete wall in harbours, poles and boulders or epiphytic on coarse algae, 1-20.5 m depth.

**Resembles:** Creeping filaments are reminiscent of Silky Thread Weed (*Derbesia marina*) and young tufts of Green Spongy Fingers (*Codium fragile*), see comment to Silky Thread Weed (*D. marina*).

**Comment:** Named *B. plumosa* (Hudson) C.Agardh or *B. hypnoides* in previous Danish checklists, because the two species temporarily were considered identical, with *B. hypnoides* as synonym of *B. plumosa*. Molecular studies showed them to be separate species (Krellwitz et al., 2001, Lam & Zechman, 2006). *Bryopsis plumosa* has flat, feather-like branches, whereas branches are on all sides in *B. hypnoides*. Young thalli with flat feather-like branches occasionally occur in *B. hypnoides*. Such individuals were collected at Hirtshals and in culture developed into thalli with branches on all sides (personal observation, RN).

**References:** Kelly et al. in Brodie et al. (2007), Krellwitz et al. (2001), Lam & Zechman (2006), Rietema (1969, 1970, 1971).

## Family: Codiaceae

### *Codium fragile* subsp. *fragile*

**(Suringar) Hariot**

Green Spongy Fingers

**Appearance:** Coarse dark green thallus of terete branches, up to 20-40 cm in height and branches 2-6 (-10) mm in width. Branching is dichotomous and repeated one or several times, secondary, often unilateral branches may occur. One or several upright branches arise from a sponge-like, cushion-shaped base. The branches tapper slightly from the base towards the apex. Branches in large thalli may be 10 mm in width at the base and 2-3 mm at the apex. Surface somewhat rough due to the special construction of thallus (see below).

**Structure:** Multiaxial syntagma of siphonous filaments. Medulla consists of slender intertwined filaments and the surface of closely adpressed bladders (utricles). These are apical on medullary filaments, which curve towards the surface. Medullary filaments continue the upwards growth from the base of the utricles by a narrow filament which has an internal wall thickening at the base. It is a type of sympodial growth. Utricles are elongate, irregularly cylindrical or club-shaped, 800-1005 (-1600) µm long, 225-465 (-600) µm in width, and 2.5-5.5 times as long as wide. They are rounded at the top, often with a small point in the centre, which in some cases is elongated into a short spike. Utricles contain many small plastids in a layer just below the outer wall. Plastids are spindle-shaped and without pyrenoids. One or two narrow hairs with a few plastids may arise from the upper part of the utricles. Hairs occur mainly in the upper part of thallus, as they are worn away further down, leaving a scar.

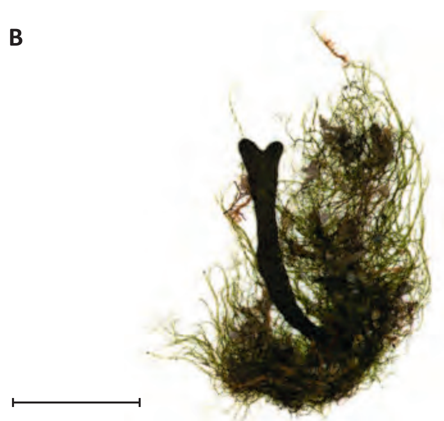
**Reproduction:** Sexual reproduction with swarmers from monoecious gametophytes. Sporangia (gametangia) are elongate ovoid protrusions from the middle to upper part of the utricles and cut off from the rest of the thallus by a wall. They are 200-365 µm long and 80-115 µm in width, they contain many biflagellate swarmers at maturity. Female gametangia are dark green and contain relatively large green gametes, male gametangia are yellowish and contain smaller gametes. In some thalli only dark green gametangia occur, and it is possible that swarmers from these may germinate without copulation and function as zoospores. Young thalli are tufts of slender mutually free filaments. From these arise new coarse upright syntagmatic thalli. Vegetative reproduction may occur from released branches or fragments which continue the growth.

**Seasonal variation:** Present all year, gametangia recorded in January, March, May-October.

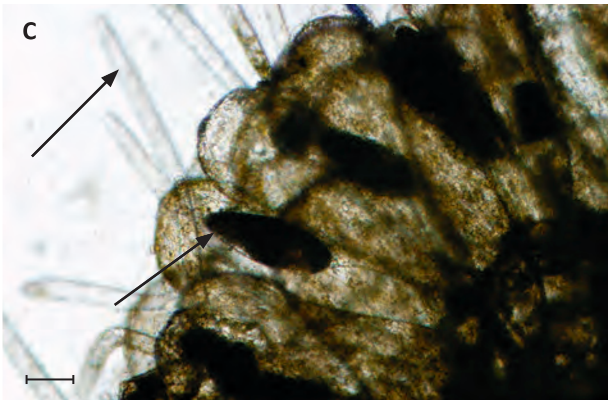
A

A: *Codium fragile*. Several terete repeated dichotomous branches from same basis. Hirsholm, 12.5 m, 16.11.1989. Scale 2 cm.

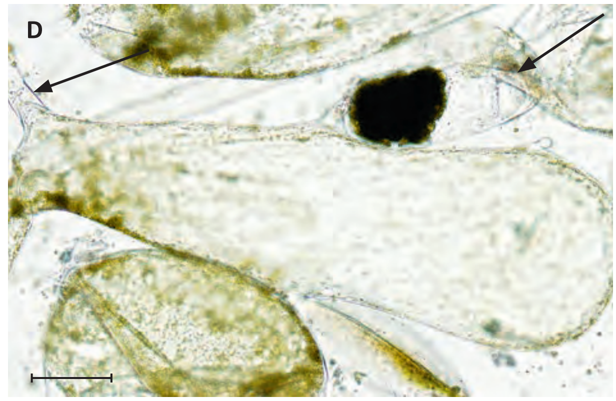
B



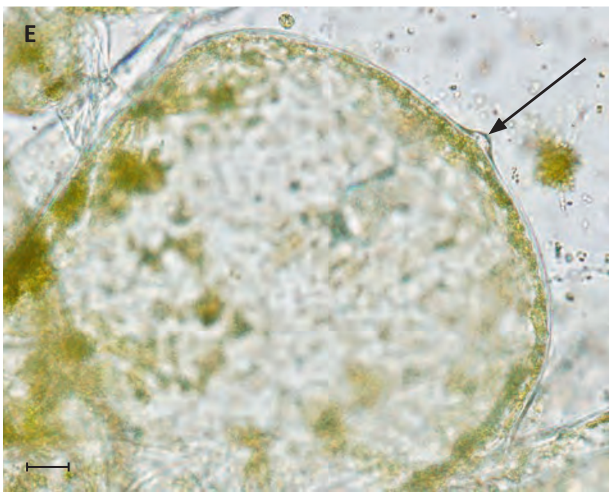
B: *Codium fragile*. Young alga, a tuft of filaments and a single upright branch. Herthas Flak, 13 m, 21.8.1991. Scale 1 cm.



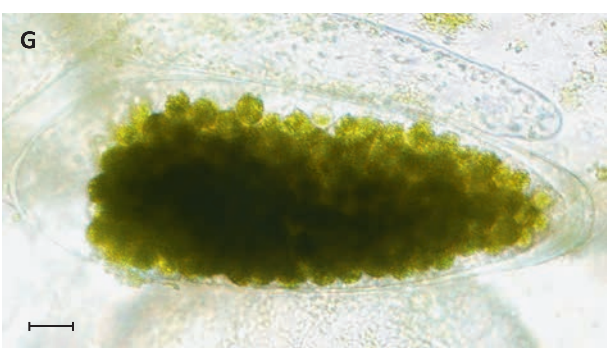

C: *Codium fragile*. Surface of closely adpressed utricles with pale hairs (upper arrow) and dark gametangia (lower arrow). Transverse section. Scale 100 µm. C-G: Storedal, Læsø, drift, 29.8.2014.



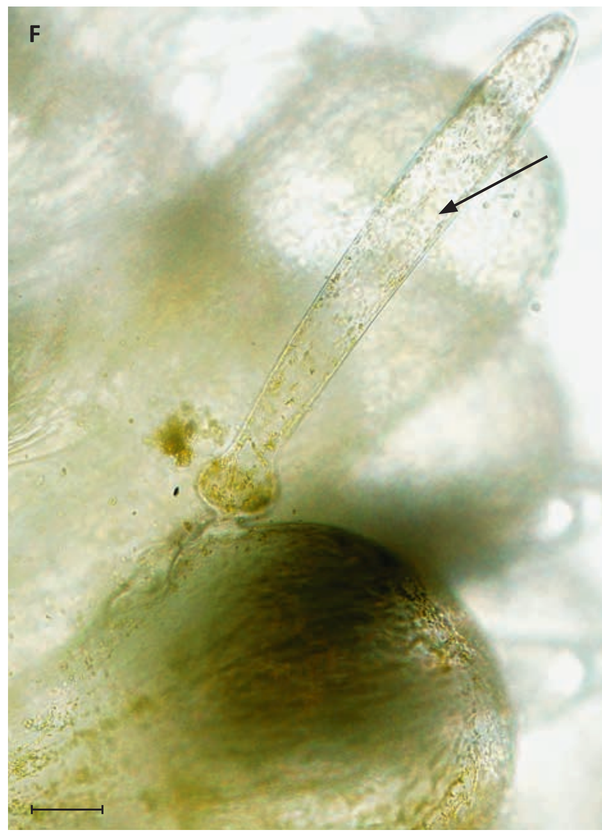

D: *Codium fragile*. Utricle with gametangium (right arrow) and upward-growing medullary filament, with internal wall thickening (left arrow). Scale 100 µm.




E: *Codium fragile*. Upper part of utricle with a small point (arrow). Scale 20 µm.




G: *Codium fragile*. Gametangium with large green swarmers. Scale 20 µm.




F: *Codium fragile*. Part of utricle with a young hair (arrow). Scale 50 µm.

**Habitat:** On stone, wooden poles, shells of Acorn Barnacles (*Semibalanus balanoides*), bivalve shells and worm tubes, 1-16 m depth.
**Resembles:** Tufts of young thalli are difficult to distinguish from creeping filaments of Mossy Feather Weed (*Bryopsis hypnoides*) and Silky Thread Weed (*Derbesia marina*), see comment for Silky Thread Weed (*D. marina*).
**Comment:** Considered an invasive species in Europe, probably originating in Japan. Arrived in Danish waters in 1913-19 according to Lund (1940).

Several subspecies are referred to *C. fragile*; in Norwegian waters subsp. *fragile* and subsp. *atlanticum* (A.D.Cotton) P.C.Silva occur documented by molecular studies by Armitage & Sjøtun (2016). These researchers mention much overlap in morphological characters, previously used to distinguish between the two taxa, and recommend that the identity be confirmed by genetic data. The name *C. fragile* subsp. *fragile* as used here is based on older morphological observations and considered temporary until the Danish *C. fragile* has been examined using molecular studies.
**References:** Armitage & Sjøtun (2016), Fralick & Mathieson (1972), Lund (1940, *C. dichotomum*, *C. fragile* var. *typicum*), Maggs & Kelly in Brodie et al. (2007), Provan et al. (2005), Silva (1955, 1957).

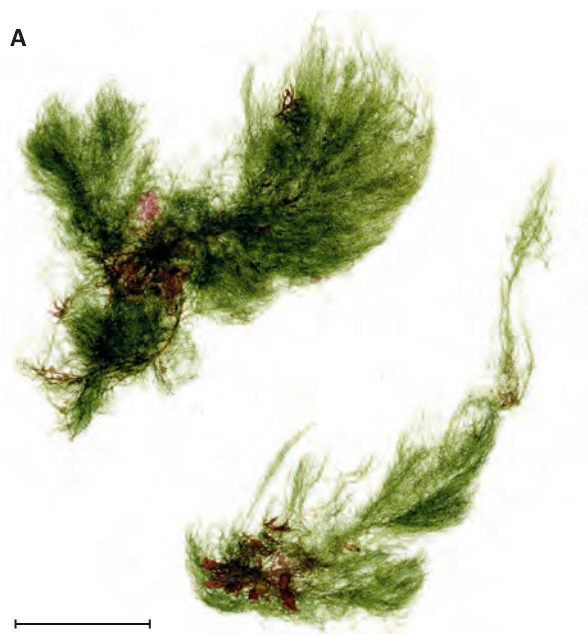
## Family: Derbesiaceae

### *Derbesia marina*

**(Lyngbye) Solier**
Silky Thread Weed

**Appearance:** Soft tufts of narrow, dark yellow-green filaments with scattered branches, up to 3 cm in height. The tuft is the sporophyte generation which alternates with a spherical or ellipsoid bladder-shaped gametophyte the the size of a pea (*Halicystis*-phase).
**Structure:** The filamentous thallus is siphonous tubes, regular in width, 15-40 (-60) µm wide. The few branches are scattered and occur at irregular intervals. Older branches, mainly in the lower part of the thallus, may be separated from the rest of the thallus by a thick wall at the base. The wall appears as if it is double and consists of two cross walls curving towards each other, giving the wall an hourglass appearance, or a small cell between the two cross walls. Upward filaments arise from creeping filaments, which may penetrate the substratum, and be endozoic in bryozoans. Plastids are small and disc-shaped without pyrenoids.
***Halicystis*-phase**, previously known as *Halicystis ovalis* (Lyngbye) Areschoug is approximately spherical 500-712 µm in width and 550-860 µm in height with creeping filaments at the base. It is siphonous and has small disc-shaped plastids resembling those of the filamentous phase.
**Reproduction:** The life history is known from culture studies. The *Halicystis*-phase represents isomorphic male and female gametophytes. During reproduction, all the contents are transformed into drop-shaped biflagellate swarmers, female gametes slightly larger

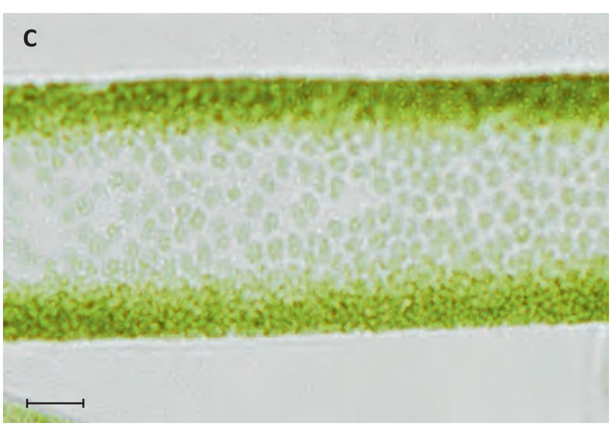
A



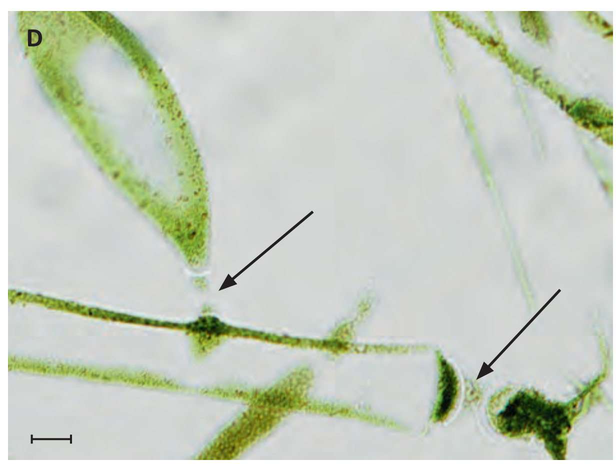
A: *Derbesia marina.* Yellow-green, soft tufts of narrow upright filaments. Scale 2 cm. A, C-D: Munkegrunde, 13 m, 4.8.1994.

than male gametes (anisogametes). The gametes amalgamate during fertilization, but the two nuclei remain separate, and the developing filamentous offspring contain many haploid nuclei, both male and female. Sporangia develop as short branches in the filaments and become separated from the rest of the thallus by a thick double wall. Sporangia are ellipsoid to obovate, 185-232 µm in height. Male and female nuclei copulate to produce diploid nuclei within the sporangium, but the diploid phase only persists for a short time as the swarmers develop after a meiotic division and become haploid male and female zoospores. These are approximately spherical or broadly pyriform with a whorl of flagella close to the front end (stephanocont swarmers). Zoospores develop into male- or female *Halicystis*-phase. Kornmann detected the connection between the two phases in 1938 for the species from Helgoland (Kornmann, 1938). The alga from Danish waters has not been studied in culture.
**Seasonal variation:** Occurs probably all year, filamentous thalli collected in February, April-September and November, young sporangia recorded in July-August. *Halicystis*-phase collected in August, but only observed a few times in Danish waters.
**Habitat:** On solid substrata such as concrete walls at shaded places in harbours, 1-1.5 m depth. Also on perennial red algae, bryozoans and sponges on stone reefs, 8-20 m depth. Older collections by dredge, to 31 m depth. *Halicystis*-phase observed as green spheres on crustose calcified red algae at 14.5 m depth, Kims Top, 17.8.1994, probably with basal filaments penetrating the host.
**Resembles:** Difficult to distinguish from juvenile filaments of Mossy Feather Weed (*Bryopsis hypnoides*) and Green Spongy Fingers (*Codium fragile*) but recognized by the thick cross walls. In addition, plastids are spindle-shaped with a pyrenoid in Mossy Feather Weed (*B. hypnoides*), spindle-shaped without pyrenoid in Green Spongy Fingers (*C. fragile*) and disc-shaped without pyrenoid in Silky Thread Weed (*D. marina*).
**References:** Brodie & Bunker in Brodie et al. (2007), Eckhardt et al. (1986), Hoek et al. (1995), Kornmann (1938, 1981).


B: *Derbesia marina*. Tiny filaments on the bryozoan Hornwrack (*Flustra foliacea*). Herthas Flak, 15 m, 5.6.1989. Scale 2 cm.




C: *Derbesia marina*. Filament with many disc-shaped plastids without pyrenoids. Scale 10 µm.




D: *Derbesia marina*. Branch and young sporangium, both with a double wall at base (arrows). Scale 20 µm.

**Family: Ostreobiaceae**

## *Ostreobium quekettii*

**Bornet & Flahault**

Chalk-boring Net Weed

**Appearance:** Microscopic filaments, growing within calcified material and giving the substratum a yellow green colour.

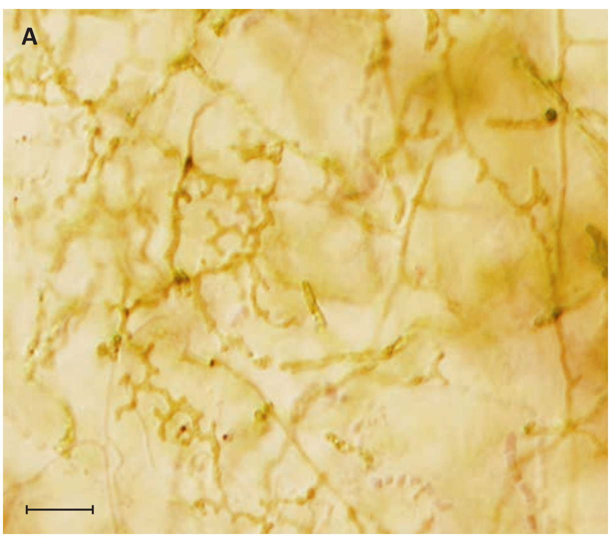
**Structure:** Siphonous, branched filaments. Branching occurs at relatively short intervals, but long straight filaments without branches occasionally occur. Branches typically arise at 90° branch angle and branches often curved backwards so the alga appears like a net. Filaments are 3-5 µm in width tapering to 2 µm at the apex, occasionally with irregular swellings. Plastids are spindle-shaped without pyrenoids.

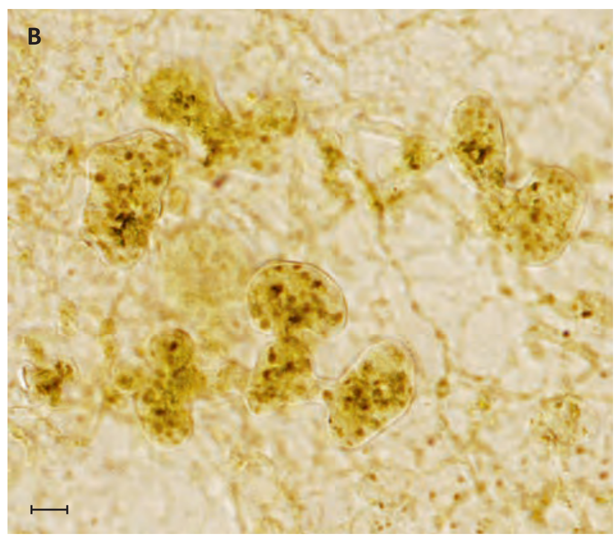
**Reproduction:** Vegetative reproduction by zoospores known from culture studies. Sporangia are irregularly swollen and may have long extensions of which one or more function as exit-tubes for the zoospores. Sporangia only observed a few times in the alga in nature.

**Seasonal variation:** Present all year, collected in January-November. Sporangia observed in September.

**Habitat:** Grows into calcified material. Frequent in oyster shells, calcified tubes of the Sinistral Spiral Tubeworm (*Spirorbis spirorbis*) and *Spirobranchus* (*Pomatoceros*) *triqueter*. Occurs in shallow water and collected by divers to 27 m depth and by dredge to 31 m depth.

**References:** Gunnarsson & Nielsen (2016), Kornmann & Sahling (1980), Nielsen in Brodie et al. (2007), Woolcott et al. (2000b).




A: *Ostreobium quekettii*. Densely branched filaments, short branches arise at 90° branch angle, so branching appear net-like. Munkegrunde, 12 m, 18.9.1991. Scale 20 µm.
A-B: Calcified shell, decalcified in 2 % acetic acid.

B: *Ostreobium quekettii*. Filaments with irregularly rounded sporangia. Middelflak, 8.5 m, 15.9.1991. Scale 10 µm.

**Order: Acrosiphoniales · Family: Acrosiphoniaceae**

## *Acrosiphonia*

Tarantula Weeds

**Appearance:** Densely branched bush-like alga with straight branches, typically looking like a paint brush, 5-10 cm in height. Young individuals are typically hemispherical with a bright green colour. Branches are tangled and may form rope-like bundles in older thalli and fade to yellow green.

**Structure:** Uniseriate branches consist of cylindrical cells with scattered, occasionally opposite branches. Growth is apical with long cylindrical cells in the upper part of thallus. Further down the thallus growth is diffuse and in the older part of the alga the cells are relatively short. Downward-growing, slender, curving rhizoids entangle the branches in the basal part. Vegetative cells contain many nuclei and a parietal cylindrical reticulate plastid with many pyrenoids. The upright phase of the alga has considerable capacity to regenerate, so a new thallus develops from worn down fragments. The alga overwinters as basal filaments.

**Reproduction:** Heteromorphic life history with upright bush-like gametophytes. Sporophytes are unicellular endophytes (*Codiolum*-phase) in crustose red algae, previously known as *Codiolum petrocelidis* Kuckuck. Upright bush-like thalli reproduce by swarmers, which form in intercalary sporangia, transformed from vegetative cells in the upper part of thallus. Sporangia are only slightly different from vegetative cell in size and shape, they become dark olive-green. Swarmers are released through a circular pore which opens by a small lid. Swarmers have 2 or 4 flagella and act as gametes or zoospores. Life history is known from culture studies by Jónsson (1958, 1959a, b, 1962, 1966, 1967, 1969) and Kornmann (1964c) for European algae. The relationship between the unicellular sporophyte and upright bush-like phase is also supported by molecular studies in British Columbia, Canada (Sussmann et al., 1999).

**Resembles:** Spongy Weed (*Spongomorpha*) may appear similar but only has a single nucleus per cell and is smaller than Tarantula Weeds (*Acrosiphonia*). Green Branched Weeds (*Cladophora*) may also look similar, but have mutually free branches without rhizoids, many pseudodichotomous branches, and a spongy plastid.

**Comment:** Species discrimination is questionable. In the British flora *A. centralis* is recorded as a synonym of Green Tarantula Weed (*A. arcta*) (Brodie & Bunker in Brodie et al., 2007). Molecular studies by Sussmann et al. (1999), showed that individuals of Green Tarantula Weed (*A. arcta*), which were identified on morphological characters, were polyphyletic. Further molecular studies are still needed to support species discrimination.

**References:** Brodie & Bunker in Brodie et al. (2007), Jónsson (1958, 1959a, b, 1962, 1966, 1967, 1969), Kornmann (1962b, 1964c, 1965, 1972b), Sussmann & DeWreede (2007), Sussmann & Scrosati (2011), Sussmann et al. (1999).

### Identification key to species of *Acrosiphonia*

| | | |
|---|---|---|
| 1a. | With short pointed or curved to hook-shaped branches | *A. arcta* |
| 1b. | Without short pointed or hook-shaped branches | 2 |
| 2a. | Many unilateral branches. Sporangia occur individually. Branches 80-160 µm in width | *A. sonderi* |
| 2b. | Most branches are scattered. Sporangia in series. Branches 40-90 (-116) µm in width | *A. centralis* |

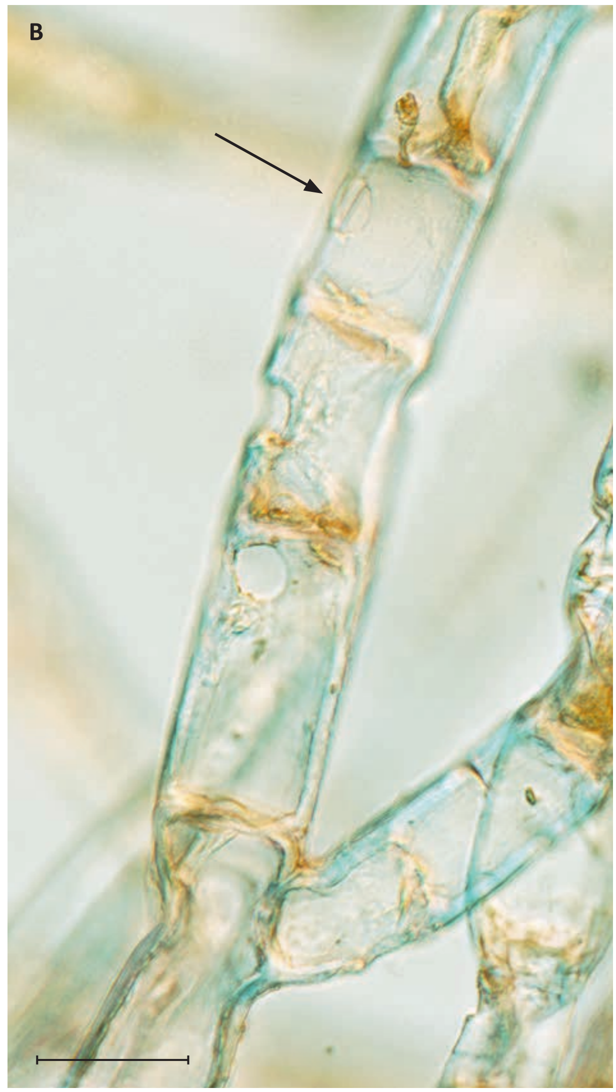
## *Acrosiphonia arcta*

**(Dillwyn) Gain**

Green Tarantula Weed

**Appearance:** Coarse, branched bush-like alga.
**Structure:** Short pointed branches are typical, they may be curved or hook-shaped, particularly in the lower part of thallus. Branches, 40-120 µm in width. Sporangia occur individually or in series of 3-9 cells.
**Seasonal variation:** Collected in July.
**Habitat:** Only recorded drift at the shores of Skagerrak in Danish waters.
**Comment:** Common it the North Atlantic as the British Islands, the Faroe Islands, Iceland and Norway.
**References:** Jónsson (1958, 1959a, *A. spinescens*, 1962, 1991).


A: *Acrosiphonia arcta.* Pointed apical cell in short branch. Scale 50 µm. A-B: Rehydrated herbarium material. Skallerup, drift, 4.7.1953. Leg.: T. Christensen.




B: *Acrosiphonia arcta.* Empty sporangia with circular exit-pores, one with a small lid (arrow). Scale 50 µm.

## *Acrosiphonia centralis*

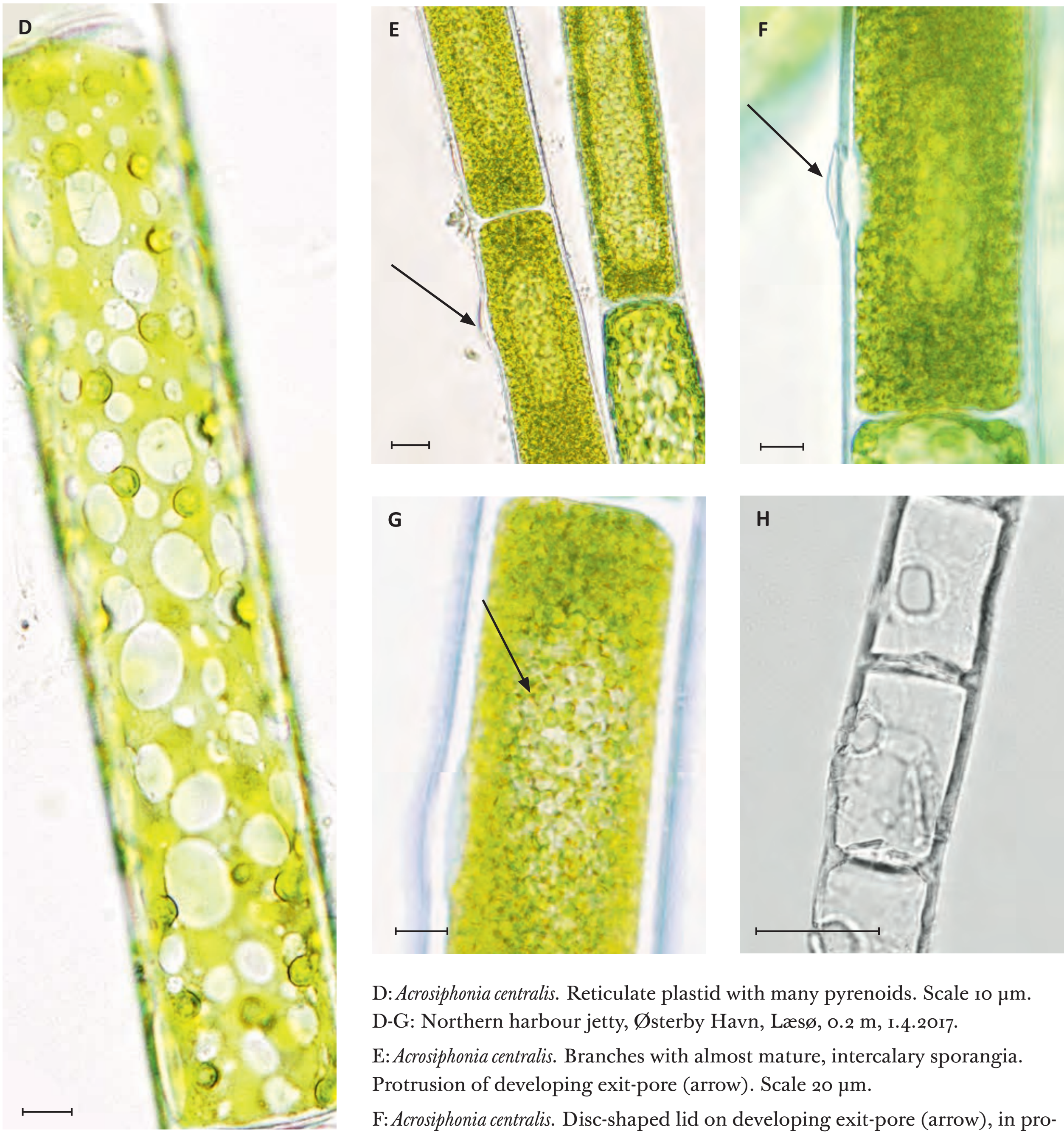
### (Lyngbye) Kjellman

**Appearance:** Densely branched, coarse bush-like bright green alga, up to 9 cm in height.
**Structure:** Filaments of cylindrical cells with scattered branches on all sides, 40-90 μm in width, occasionally up to 116 μm in width in the Northern Kattegat. Without short pointed, hook-shaped or curved branches.
**Reproduction:** Sporangia occur in the upper part of branches, individually or in intercalary series of 2-6 cells.
**Seasonal variation:** Upright thalli are a dominant element on harbour jetties in spring. Collected in February-July.
**Habitat:** On boulders in the lower part of the littoral to 4 m depth.
**References:** Kristiansen (1972).

A: *Acrosiphonia centralis.* Hemispherical alga. Scale 2 cm. A, C: Lynetteløbet, Copenhagen, 0.5 m, 15.4.2004.

B: *Acrosiphonia centralis.* Branches entangled to rope-like bundles in old alga. Lynetteløbet, Copenhagen, 0.5 m, 24.4.1998. Scale 2 cm.

C: *Acrosiphonia centralis.* Vegetative branch with downward-growing rhizoid (arrow) and from neighbouring cell an upward-growing branch. Scale 50 μm.




D: *Acrosiphonia centralis*. Reticulate plastid with many pyrenoids. Scale 10 µm. D-G: Northern harbour jetty, Østerby Havn, Læsø, 0.2 m, 1.4.2017.

E: *Acrosiphonia centralis*. Branches with almost mature, intercalary sporangia. Protrusion of developing exit-pore (arrow). Scale 20 µm.

F: *Acrosiphonia centralis*. Disc-shaped lid on developing exit-pore (arrow), in profile. Scale 10 µm.

G: *Acrosiphonia centralis*. Almost mature sporangium, swarmers with red eyespots (arrow). Scale 10 µm.

H: *Acrosiphonia centralis*. Series of empty sporangia with exit-pores. Rehydrated herbarium material. Tuborg Havn, Copenhagen, 30.5.1959. Leg.: Aa. Kristiansen. Scale 50 µm.

# *Acrosiphonia sonderi*

## (Kützing) Kornmann

**Appearance:** Bush-like thallus of stiff, coarse branched filaments, up to 9 cm in height. The upper surface of the alga may appear flat when the upper part is worn away after evacuation of the sporangia.

**Structure:** Branches, 80-160 µm in width with many unilateral branches.

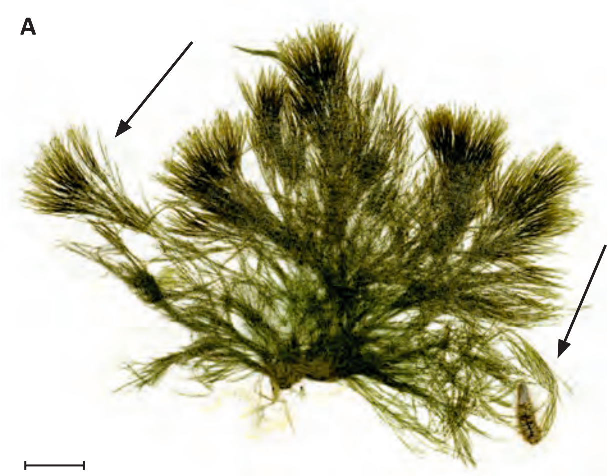
**Reproduction:** Sporangia occur individually as scattered intercalary cells in the upper part of thallus. After the evacuation of sporangia, the thallus is worn away just below the sporangia.

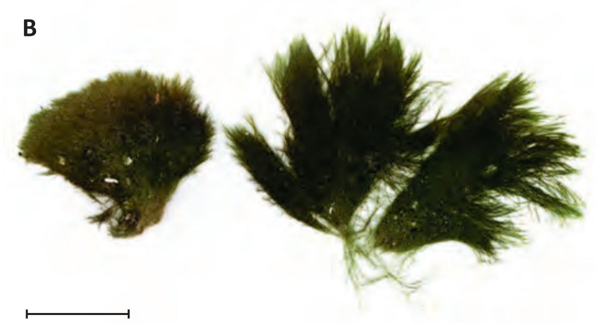
**Seasonal variation:** Upright thallus occurs in spring, collected in March-June.

**Habitat:** On wave exposed harbour jetties, 0-1 m depth.

**Comment:** The species from Helgoland may have branches, up to 300 µm in width.

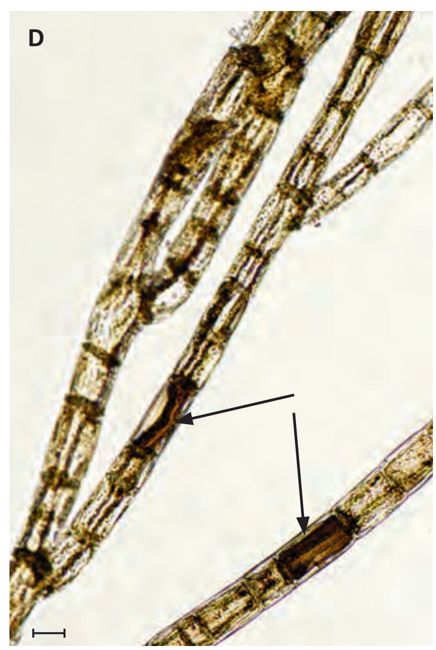
**References:** Jónsson (1967, 1969), Kornmann (1962b).




B: *Acrosiphonia sonderi*. An individual with paintbrush-looking branches and another of densely matted branches with a flat surface. Scale 2 cm. B-D: Vesterø Havn, Læsø, 0.5 m, 21.5.2005.

A: *Acrosiphonia sonderi*. Coarse bush-like alga with unilateral branches (arrows). Exposed side of northern harbour jetty, Frederikshavn, 19.5.1971. Scale 2 cm.


C: *Acrosiphonia sonderi*. Three unilateral branches (arrows). Scale 100 µm. C-D: Rehydrated herbarium material.

D: *Acrosiphonia sonderi*. Individually intercalary sporangia (arrows). Scale 100 µm.

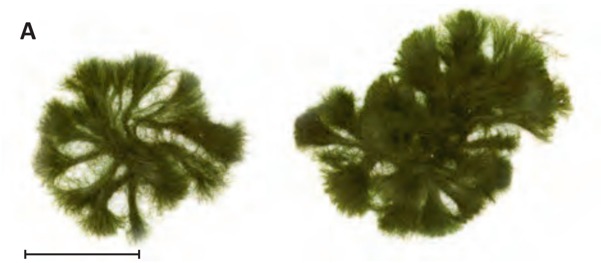
## *Spongomorpha aeruginosa*

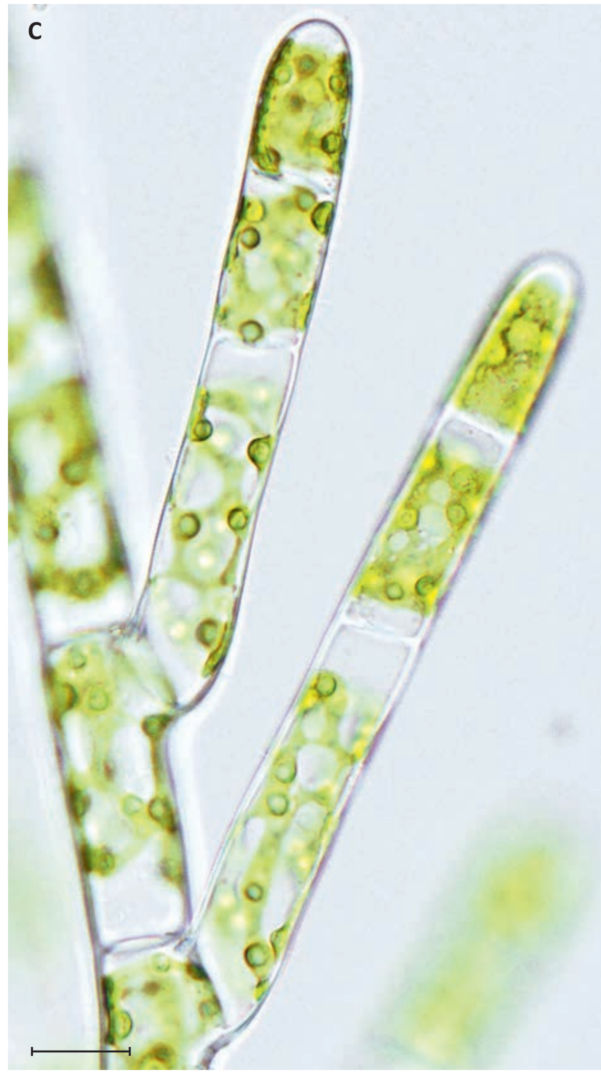
### (Linnaeus) Hoek

Green Fluffy Spongy Weed

**Appearance:** Soft, light-green tufts, up to 2 cm in height, more or less spherical in shape. Branches often intermingled and cotton-like. Life history comprises upright gametophytes and unicellular sporophytes (*Codiolum*-phase), previously known as *Chlorochytrium inclusum* Kjellman.

**Structure:** Main branches with uniseriate, scattered





A: *Spongomorpha aeruginosa.* Small tufts of entangled branches. Scale 1 cm. A, D-F: Eastern harbour jetty, Gilleleje, 0.5 m, 29.5.2014.

B: *Spongomorpha aeruginosa.* Scattered branches and two rhizoids (arrow). Brown epiphytic diatoms. Scale 100 µm. B-C: Flakfortet, Copenhagen, 6 m, 22.6.2016.

C: *Spongomorpha aeruginosa.* Slightly protruding branches, each cell has a parietal reticulate plastid and many pyrenoids. Scale 20 µm.

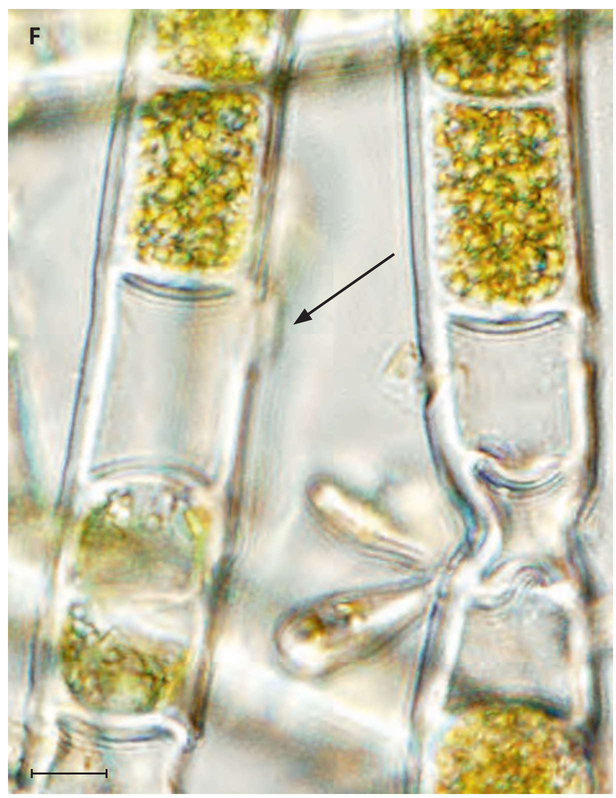
D: *Spongomorpha aeruginosa.* Curled rhizoid. Scale 20 µm.

branches on all sides. Branches consist of cylindrical cells and terminate in a rounded apical cell. Downward-growing narrow pale rhizoids, weave the branches together. Apical growth, and diffuse growth occur further down in thallus. Vegetative cells cylindrical, 11.5-24 µm in width and 1-5 times as long as wide, each contains a single nucleus. The plastid is a parietal reticulate cylinder with many pyrenoids.

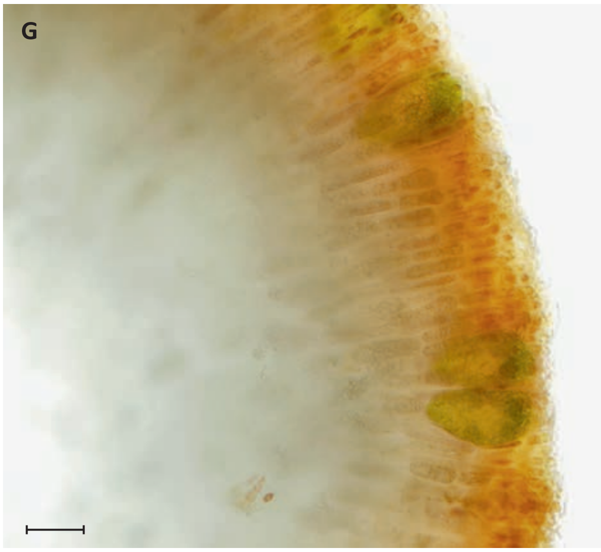
***Codiolum*-phase** is a relatively large elongate ellipsoid to ovoid cell, 28-37 µm wide and 73-81 µm long. It has a thick wall, which may have a thickened papilla in the upper end and an elongate colourless stipe-like extension at the base. Parietal plastid with many pyrenoids.

**Reproduction:** Sexual and vegetative reproduction by swarmers. Sporangia in upright thalli develop from intercalary vegetative cells in the upper part of branches, individually or in long series. They are


E: *Spongomorpha aeruginosa.* Branches with many intercalary sporangia in series (arrow). Mature sporangia, orange coloured by the red eyespots in the swarmers. Scale 20 µm.




F: *Spongomorpha aeruginosa.* Mature and empty sporangia, exit-pore with a small lid (arrow). Scale 10 µm.




G: *Spongomorpha aeruginosa.* Endophytic *Codiolum*-phases. Scale 50 µm. G-H: Between cortex filaments of Discoid Fork Weed (*Polyides rotunda*). Beach east of Holtemmen, Læsø, drift, 23.7.2013.


H: *Spongomorpha aeruginosa. Codiolum*-phase, thick wall with a papilla in the upper end. Scale 50 µm.

the same size and shape as in the vegetative condition, but the red eyespots of the swarmers turn the sporangia olive-green or brownish. Swarmers are released through a circular exit-pore with a disc-shaped lid. They are drop-shaped and contain a basal plastid and a red eyespot. The swarmers may be quadriflagellate zoospores, which develop into new bush-like offspring, or biflagellate gametes. After fertilization, the zygote develops into the unicellular *Codiolum*-phase. All the cell contents of this becomes zoospores, which germinate and develop into new upright thalli.

**Seasonal variation:** Upright thalli collected in March-September; well-developed in spring and early summer. *Codiolum*-phase collected in January and June-September.

**Habitat:** Upright thalli on stone and epiphytic on various red algae; collected by divers, 0.5 to 18 m depth, and by dredge to 31 m depth in the North Sea.

*Codiolum*-phase is endophytic and collected between cortical cells in Red Rags (*Dilsea carnosa*), Hennedy's Dark-red Crust (*Haemescharia hennedyi*) and Discoid Fork Weed (*Polyides rotunda*), 1-16 m depth.

**Resembles:** Construction similar to Tarantula Weeds (*Acrosiphonia* spp.), but smaller and has a single nucleus in each cell. Distinguished from species of Green Branched Weeds (*Cladophora*) by the rhizoids which weave the branches together.

**Comment:** Culture studies of this species from Britanny by Jónsson (1959b, 1966, 1986) and from Helgoland by Kornmann (1961c, 1972b) documented the heteromorphic life history. Jónsson (1986) also found that new upright bush-like thalli might develop from the zygote after meiotic division, similar to what he had previously found for *Acrosiphonia sonderi* (Jónsson 1969).

**References:** Jónsson (1959b, *S. lanosa*, 1962, *S. lanosa*, 1966, *S. lanosa*, 1969, 1986), Kornmann (1961c, *S. lanosa*, 1964d, 1972b).

**Order: Ulothricales · Family: Ulotrichaceae**

## *Protomonostroma undulatum*

**(Wittrock) K.L.Vinogradova**

**Appearance:** Thin oval, very soft, and delicate light green blades with a wavy margin. They become up to 21 cm in length, occasionally with rounded lobes. Basal part is narrow with rhizoids attaching the blade to the substratum.
**Structure:** Monostromatic parenchyma with diffuse growth. Vegetative cells are angular, 20-24 µm in surface view, and may occur in groups of 2-8 cells. Vegetative cells, each contains a parietal plate-shaped plastid with one pyrenoid. Cells become elongate towards the base with downward-growing rhizoids for attachment of the blade from most cells.

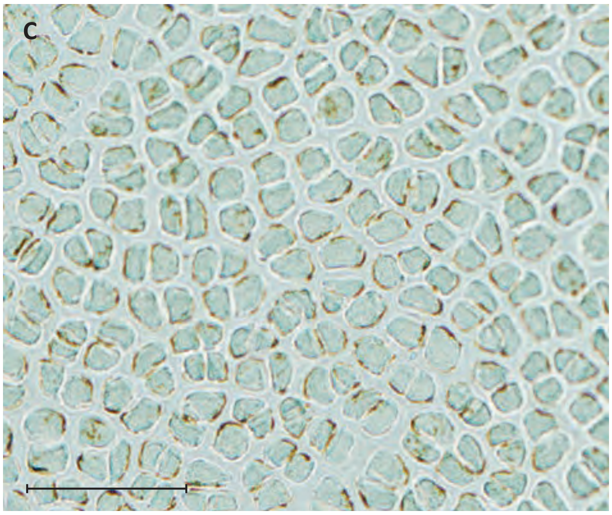
A

A: *Protomonostroma undulatum*. Oval blade with wavy margin on Wrack (*Fucus*). Hirsholm, 0.5 m, 16.4.1977. Scale 2 cm.

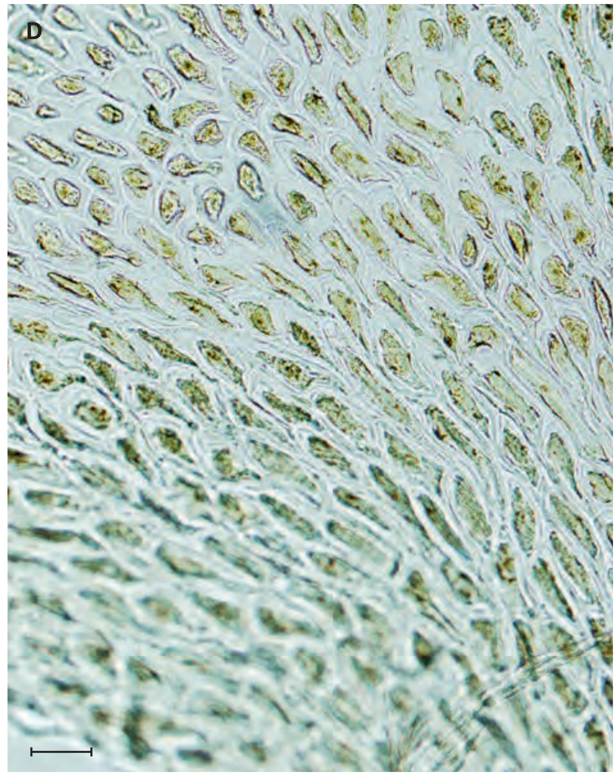
**Reproduction:** Upright blades alternate with unicellular *Codiolum*-phase. Sporangia in the blades develop from transformed vegetative cells. They are rounded and form in groups of 4 or 8 cells. The *Codiolum*-phase is pyriform or obovoid with a thick wall. It produces zoospores which germinate and develop into filaments. Monostromatic parenchyma, develop by continued longitudinal cell divisions. The heteromorphic life history was documented by culture studies by Kornmann & Sahling (1962) of the alga from Helgoland.
**Seasonal variation:** Blades recorded in spring, March-May.
**Habitat:** On boulders and epiphytic on other algae in the littoral and wave beaten zone.
**Resembles:** Deviates from One-layered Sea Lettuce (*Gayralia oxysperma*) by the wavy margin, and the lower part of blade fairly narrow. Deviates from Greville's Mattress Weed (*Monostroma grevillei*) and Limp Lettuce (*Ulvaria splendens*) by having only one pyrenoid in all vegetative cells, whereas the other two species have several pyrenoids in some of the cells.
**Comment:** First record in Danish waters, 1973 (Pedersen in Moestrup et al., 1975).
**References:** Kornmann & Sahling (1962, *Monostroma undulatum*), Pedersen in Moestrup et al. (1975, *M. undulatum*).

B

B: *Protomonostroma undulatum*. Elongate blades with typically wavy margin on Irish Moss (*Chondrus crispus*). Scale 2 cm. B-E: Hirsholm, 0.5 m, 10.5.1983. Leg.: L. Mathiesen.




C: *Protomonostroma undulatum*. Small angular, vegetative cells, upper part of blade. Scale 50 µm. C-E: Rehydrated herbarium material.





D: *Protomonostroma undulatum*. Lower part of blade, with rhizoids from elongate narrow cells. Scale 50 µm.

E: *Protomonostroma undulatum*. Cells with rhizoids. Scale 50 µm.

## *Ulothrix*

Shaggy Hair Weeds

**Appearance:** Narrow, unbranched threads up to a few centimetres in length.

**Structure:** Uniseriate unbranched filaments of cylindrical cells, with a parietal belt-shaped plastid. The plastid covers more than 180° of cell circumference in most species and has one or several pyrenoids. Growth is diffuse. Filaments attach to the substratum by the basal cell.

**Reproduction**: Vegetative and sexual reproduction from swarmers in intercalary sporangia. The sporangia develop from transformed vegetative cells and remain the same size and shape as in the vegetative condition. Sporangia often occur as several in a series. Swarmers are ovoid or spindle-shaped with flagella in the pointed front end and contain a parietal plastid with a pyrenoid and a red eyespot. Vegetative reproduction is by zoospores with 2 or 4 flagella or from spores without flagella (aplanospores). Zoospores germinate into new filamentous thalli. Vegetative reproduction also by fragments, which continue growth. Sexual reproduction by biflagellate gametes. After fertilization, zygotes germinate to become the unicellular *Codiolum*-phase. This contains many zoospores at maturity which germinate and grow into new filaments. Culture studies by Kornmann (1964b) and Lokhorst (1978), have documented the life history for Western European Shaggy Hair Weeds (*Ulothrix*).

***Codiolum*-phase** is a relatively large irregularly rounded cell, in some species have a short colourless stipe. Culture studies are necessary for reliable identification of a *Codiolum*-phase, which has only been recorded a few times in Danish waters.

**Comment:** Traditional species identification of Shaggy Hair Weeds (*Ulothrix*) is based on the dimensions of the filaments, width and height of cells, structure of cell walls and number of pyrenoids per cell. Unfortunately, there is large variation in these features, and overlap between species. Therefore, species identification is difficult. Naming of the species has furthermore been inconsistent in the literature, so a comparison of information in different references is not simple. Lokhorst (1978) made a comprehensive revision of Shaggy Hair Weeds (*Ulothrix*) in Western Europe and reported on the relationships between names. We therefore recommend his publication for further information about this subject.

**Identification key to species of *Ulothrix***

| | | |
|---|---|---|
| 1a. | Filaments have a soft, thick, smooth outer wall. Cells are short, 0.2-1 times as long as wide and contain (1-) 2-3 (-6) pyrenoids | *U. speciosa* |
| 1b. | Filaments have a thin, firm outer wall. Cells contain 1-2 (-6) pyrenoids | 2 |
| 2a. | Filaments (10-) 15-18 (-25) µm in width. Cells are 0.2-1 times as long as wide, with rounded corners. Outer wall often rough with small particles attached. Fertile filaments may be spiral-shaped. Zoosporangia contain (4-) 8-32 zoospores | *U. flacca* |
| 2b. | Cylindrical cells are 0.3-2 (-3) times as long as wide. Outer wall smooth. Grow in brackish water | 3 |
| 3a. | Filaments (4.8-) 7.6-12 (-13) µm in width. Zoosporangia with (1-) 2-4 (-8) zoospores | *U. subflaccida* |
| 3b. | Filaments (3.5-) 9.8-14 (-15.4-26) µm in width. Cells almost equal in width and length or only slightly longer than wide, often in groups of 2 or 4 cells. Zoosporangia with (2-) 4-16 (-32) zoospores | *U. implexa* |

A thorough and critical investigation of Shaggy Hair Weeds (*Ulothrix.*) in Danish waters has not yet been undertaken. The Danish checklist (Nielsen, 2005) includes 4 species, the records of which are based on random collections and floristic studies such as those in Tuborg Havn (Kristiansen, 1972), at Saltholm (Kristiansen, 1978a) and in Stege Nor (Lund, 1934). The text below is supported by information from Lokhorst (1978), but much uncertainty remains about species identification and distribution, particularly for the brackish water species *U. implexa* and *U. subflaccida*.

**References:** Kornmann (1964b), Kristiansen (1972, 1978), Lokhorst (1978), Lund (1934), Nielsen (2005), Pedersen (2011), Wille (1901).

## *Ulothrix flacca*

**(Dillwyn) Thuret**

Flabby Shaggy Hair Weed

**Appearance:** Narrow, soft threads typically 1 cm long, and up to 6 cm in length. Older threads might be spiral-shaped and appear as a wool-like cover.

**Structure:** Uniseriate unbranched filaments, (10-) 15-18 (-25) µm in width. Cells are 0.2-1 times as long as wide and develop rounded corners. The parietal belt-shaped plastid contains 1-2 (-3) pyrenoids. The firm but rough wall is typical, often with many small adherent particles. Filaments can occur parallel to each other as if pasted together. They attach to the substratum by the elongate basal cell and downward-growing rhizoids from a few other basal cells. In closely packed filaments, basal cells become irregular with short extensions.

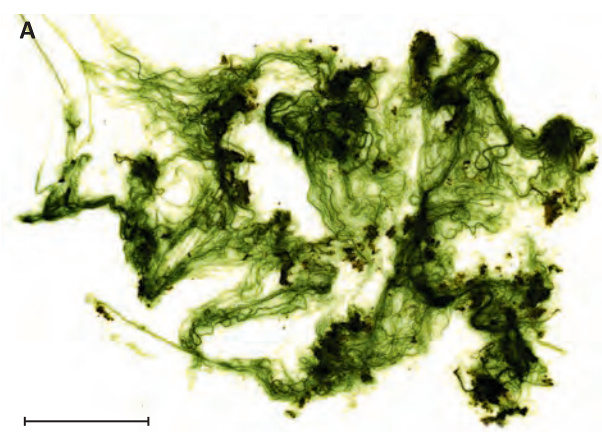
**Reproduction:** Both sexual and vegetative reproduction are known (Lokhorst, 1978). Sporangia contain (4-) 8-32 zoospores or (4-) 8-64 (-128) gametes. Aplanospores may occur, they develop like zoospores. Fertile filaments with sporangia are straight or twisted like a spiral. Vegetative reproduction also occurs from fragments which continue growth.

**Seasonal variation:** Collected in February-September, well-developed in spring.

**Habitat:** Forms a green cover on stone in the littoral and epiphytic on species of Wrack (*Fucus*), does not grow on soil. Occurs in both wave-exposed and sheltered localities.

**Comment:** Includes algae which are mentioned by Wille (1901) and Lund (1934) as *U. pseudoflacca* f. *major* Wille, *U. pseudoflacca* f. *minor* Wille and *U. consociata* Wille according to Lokhorst (1978). The alga mentioned by Wille (1901) as *U. flacca*, is similar to the modern concept of *U. speciosa*.

**References:** Kornmann (1964b, *U. pseudoflacca*), Lokhorst (1978), Lund (1934, *U. pseudoflacca*), Wille (1901, *U. pseudoflacca, U. consociata*).



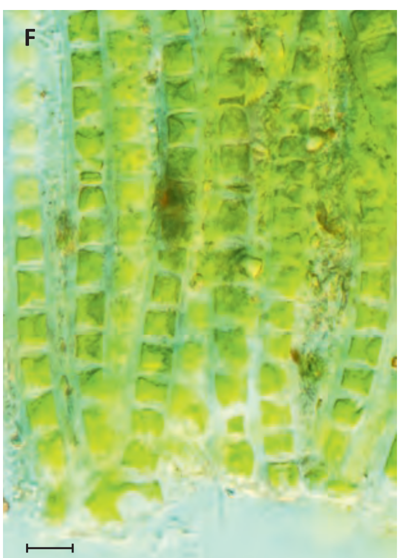

A: *Ulothrix flacca.* Narrow threads removed from a boulder and spread on paper. Lynetteløbet, Copenhagen, 0.5 m, 15.4.2004. Scale 2 cm.


B: *Ulothrix flacca.* Twisted filaments. Scale 200 µm. B, F: Vesterø Havn, Læsø, 0.1 m, 19.3.2015.

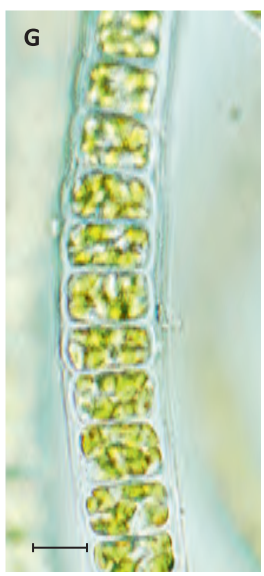

C: *Ulothrix flacca.* Uniseriate filament of vegetative cells with rounded corners. Parietal plastid with one pyrenoid, stained with potassium iodide. Scale 10 µm. C-E, G: Vesterø Havn, Læsø, 0.1 m, 14.3.2014.


D: *Ulothrix flacca.* Uniseriate filament, outer wall rough with many small particles attached. Scale 10 µm.

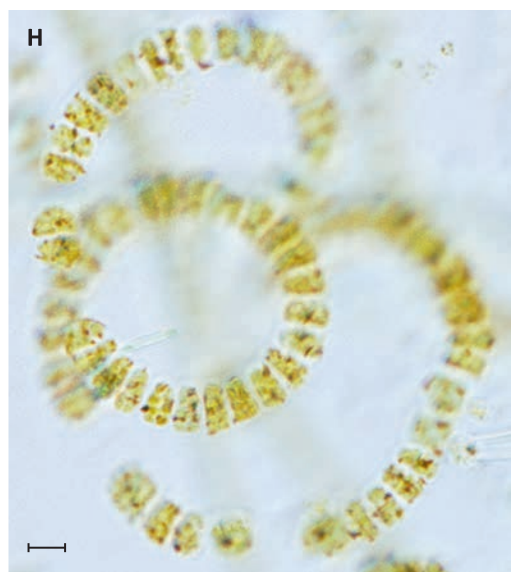

E: *Ulothrix flacca.* Basal cell and a few lower cells with downward-growing rhizoids. Scale 10 µm.




F: *Ulothrix flacca.* Basal cells of closely packed filaments.
Scale 10 µm.




G: *Ulothrix flacca.* Series of sporangia with many swarmers. Scale 10 µm.




H: *Ulothrix flacca.* Spiral-shaped fertile filament. Margretheholms Havn, Copenhagen, 0.2 m, 17.3.2004. Scale 10 µm.

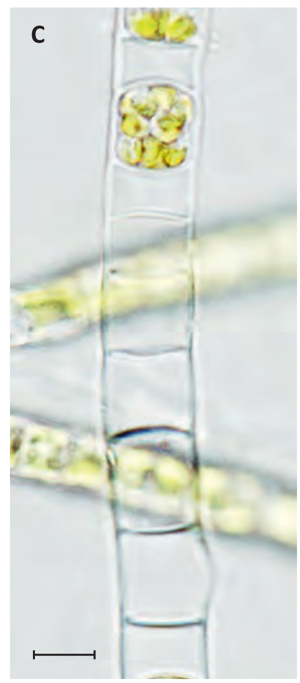
## *Ulothrix implexa*

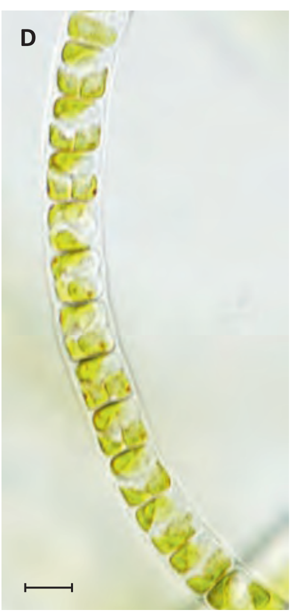
**(Kützing) Kützing**

Interwoven Shaggy Hair Weed

**Appearance:** Light-green narrow threads.
**Structure:** Filaments (3.5-) 9.8-14 (-26) µm in width and typically with a thin, firm and smooth wall. Densely connected cylindrical cells without rounded corners. Cells may occur in groups of 2 or 4 cells, and are 0.3-1.5 times as long as wide. Plastid parietal and typically shorter than the length of the cell and contains 1 (-4) pyrenoids. The basal cell develops into an elongated rhizoid and may be branched. Rhizoids may also occur on intercalary vegetative cells (Lokhorst, 1978).
**Reproduction:** Sporangia contain (2-) 4-16 (-32) zoospores. Filaments with sporangia are straight or slightly curved and become olive-green at maturity.
**Habitat:** Brackish water species. In the littoral on various hard substrata and epiphytic on other algae. Recorded on stone with *Rivularia* and *Ralfsia*, Fænø Biologiske Station, 23.4.1891, Leg.: L.K. Rosenvinge.
**References:** Lokhorst (1978).






A: *Ulothrix implexa*. Epiphytic on Dumont's Tubular Weed (*Dumontia contorta*). Lynetteløbet, Copenhagen, 0.5 m, 15.4.2004. Scale 2 cm.

B: *Ulothrix implexa*. Pairwise cylindrical cells, each with a belt-shaped plastid and one pyrenoid. Scale 10 µm. B-D: Margretheholms Havn, Copenhagen, 0.2 m, 23.2.2009.

C: *Ulothrix implexa*. Empty sporangia and a sporangium with many swarmers. Scale 10 µm.

D: *Ulothrix implexa*. Sporangia in series, each with 4 swarmers. Scale 10 µm.

# *Ulothrix speciosa*

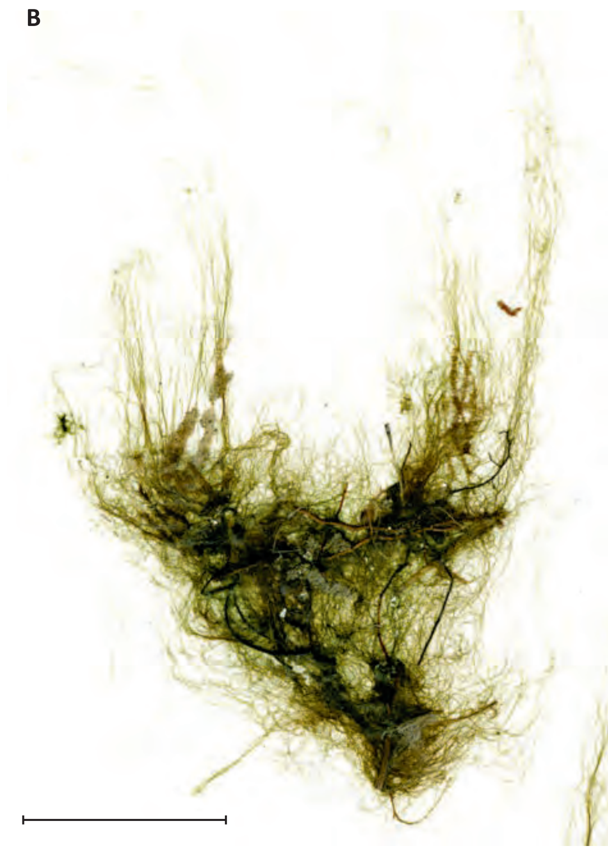
**(Carmichael) Kützing**

Showy Shaggy Hair Weed

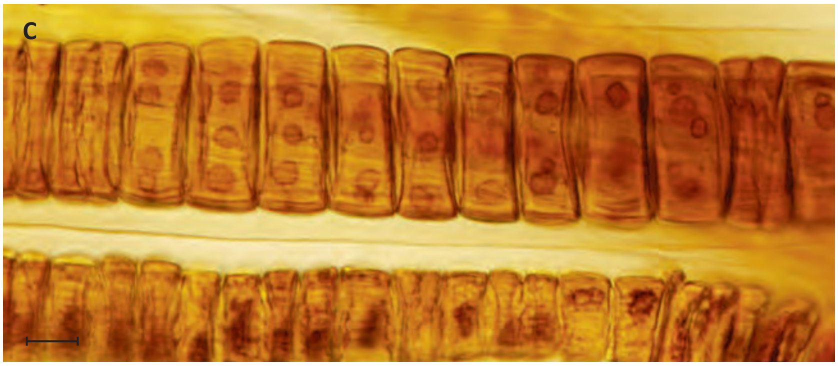
**Appearance:** Mats of narrow threads in the upper part of the littoral on boulders and also grows on soil.
**Structure:** Filaments with a thick smooth outer wall without attached particles. The wall appears double as if the cells are within a sheath. Cells tend to be in groups of 2 or 4 cells. Filaments, 20-42 µm in width with short cells, 0.2-1 times as long as wide, each containing (1-) 2-3 (-6) pyrenoids.
**Reproduction:** Fertile filaments with sporangia are spirally-twisted and brownish to orange in colour. Some sporangia contain many small, spindle-shaped swarmers, which are pale with a red eyespot. These biflagellate swarmers develop into unicellular *Codiolum*-phase without or after copulation according to Lokhorst (1978). Other sporangia are green with larger swarmers.

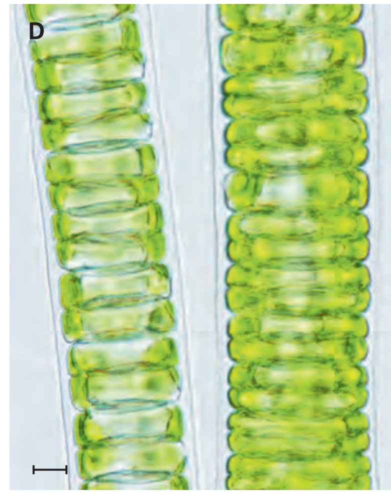
*Codiolum*-phase is elongate ellipsoid to ovoid.
**Seasonal variation**: Collected in February-July, October-September and December.
**Habitat:** On stone in the wave-beaten zone, in salt marshes on soil and epiphytic on other algae and plants.
**Comment:** The species is similar to alga mentioned as *U. flacca* by Wille (1901), and as *U. flexuosa* by Kornmann (1964b) according to Lokhorst (1978 p. 199).
**References:** John in Brodie et al. (2007), Kornmann 1964b (*U. flexuosa*, *U. speciosa*), Lokhorst (1978), Pedersen (2011), Wille (1901, *U. flacca*).


A: *Ulothrix speciosa*. Narrow threads on boulder. Photo by K.L. Krabbe. A, D-F: Lystbådehavn, Aarhus, wave-beaten-zone, 27.2.2017.




B: *Ulothrix speciosa*. Threads on drifting fragments of other algae. Scale 2 cm. B-C: Rønnerne, Frederikshavn, shallow water, 7.4.1969.






C: *Ulothrix speciosa*. Filament of short cells with 3-5 pyrenoids. Thick smooth outer-wall. Rehydrated herbarium material. Scale 10 µm.

D: *Ulothrix speciosa*. Filaments with groups of 2 or 4 cells. Scale 10 µm.

E: *Ulothrix speciosa*. Filament of short cells with 2-4 pyrenoids, stained with potassium iodide. Scale 10 µm.

F: *Ulothrix speciosa*. Spiral-shaped filaments with mature (right arrow) and empty (left arrow) sporangia. Scale 50 µm.

# *Ulothrix subflaccida*

**Wille**

Floppy Shaggy Hair Weed

**Appearance:** Very narrow threads in the littoral.

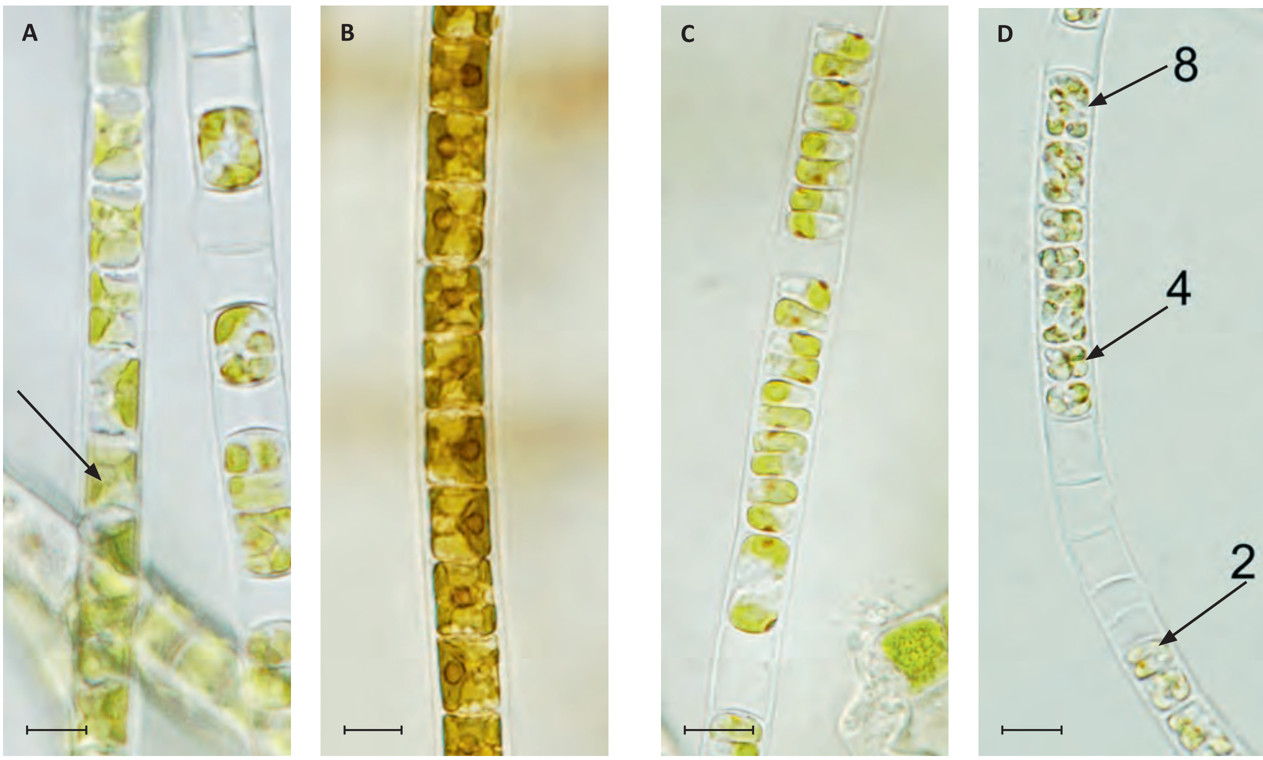
**Structure:** Filaments typically < 12 µm in width and may be (4.8-) 7.7-12.1 (-13.2 µm) according to Lokhorst (1978). Cylindrical cells, 1-2 (-3) times as long as wide with a thin smooth wall. The parietal plastids each contains 1 (-6) pyrenoids, which become smaller when the number increases.

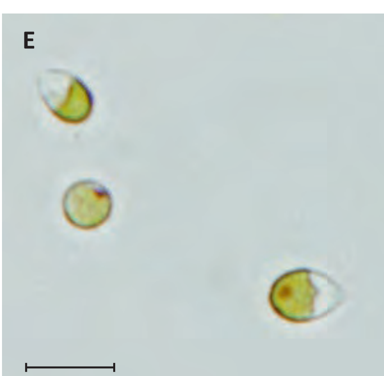
**Reproduction:** Zoosporangia contain (1-) 2-4 (-8) zoospores. Sporangia are almost same colour at maturity as the vegetative cells.

**Seasonal variation:** Recorded in February-April, July and September-October.

**Habitat:** Brackish water species, on stone in the littoral, collected between filaments of Cotton Wool Weeds (*Ectocarpus* sp.) and epiphytic on other algae and Eelgrass (*Zostera marina*).

**References:** Kristiansen (1972, 1978a), Lokhorst (1978), Lund (1934).




A: *Ulothrix subflaccida*. Vegetative and fertile filaments with relatively long cells, with one pyrenoid (arrow). Scale 10 µm. A-E: Northeastern part of Refshaleøen, Copenhagen, 0.1 m, 23.2.2009.

B: *Ulothrix subflaccida*. Vegetative filament of cylindrical cells, which are longer than wide, each contains one pyrenoid. Stained with potassium iodide. Scale 10 µm.

C: *Ulothrix subflaccida*. Filament of mature sporangia, each with 2 zoospores. Scale 10 µm.

D: *Ulothrix subflaccida*. Fertile filament, sporangia with 2, 4 or 8 zoospores. Scale 10 µm.

E: *Ulothrix subflaccida*. Swarmers with pointed front end, basal plastid and red eyespot. Scale 10 µm.

# *Urospora*

Glossy Fringe Weeds

**Appearance:** Soft unbranched threads, 5-10 (-20) cm in height. Life history comprises a unicellular *Codiolum*-phase, forming dark green velvet-like patches on stone, c. 1 mm in height.
**Structure**: Filaments are uniseriate and consist of cylindrical to barrel-shaped cells. Attached to the substratum by rhizoids from the lower cells. Growth is diffuse. Vegetative cells contain a parietal cylindrical plastid with several pyrenoids. In older cells, the plastid is perforated and may extend into the centre of the cell.
***Codiolum*-phase** is club-shaped, the lower narrow part resembles a stipe. The upper part is rounded ellipsoid and contains a parietal perforated plastid with many pyrenoids, similar to the plastid in cells of the filaments. The stipe-looking part is colourless and appears as a continuation of the wall in the upper part, and is 1-2 times as long as the upper part of the cell. The *Codiolum*-phase was previously known as *Codiolum gregarium* A.Braun.
**Reproduction:** Filaments have vegetative and sexual reproduction by swarmers. Intercalary vegetative cells transform into sporangia, more or less barrel-shaped. Development of sporangia begins in the upper end of the filaments and continues towards the base. Vegetative reproduction is by zoospores which develop into new filaments. Zoospores are elongate drop-shaped with 4 flagella at the blunt front and have a pointed rear end, each contains a parietal plastid, one pyrenoid and a red eyespot. Sexual reproduction by isogametes which are drop-shaped with 2 flagella in the pointed front end, and have a parietal plastid and a red eyespot. Zygotes develop into the unicellular sporophytic *Codiolum*-phase. At maturity all contents of the *Codiolum*-phase is transformed into zoospores, appearing similar to the zoospores of the filaments, being drop-shaped with a pointed rear end and 4 flagella in the blunt front end. They germinate into new filamentous offspring.
**Seasonal variation:** Well-developed in winter and spring.
**Habitat:** On stone in upper part of the wave-beaten zone.
**Comment:** *Codiolum*-phases of Slender Glossy Fringe Weed (*U. penicilliformis*) and Barrel-celled Glossy Fringe Weed (*U. wormskioldii*) look similar in the field. Reliable identification to species requires culture studies.
**References:** Kornmann (1961a, b).

**Identification key to species of *Urospora***

| | | |
|---|---|---|
| 1a. | Filaments (80-) 100-500 (-1200) µm in width | *U. wormskioldii* |
| 1b. | Filaments (19-) 25-35 (-57) µm in width | 2 |
| 2a. | Downward-growing rhizoids from several lower cells | *U. penicilliformis* |
| 2b. | Downward-growing rhizoids only from the basal cell | *U. neglecta* |

# *Urospora neglecta*

**(Kornmann) Lokhorst & Trask**

**Comment:** Recorded from Elsinore and Korsør by Lokhorst & Trask (1981 p. 388) based on old herbarium specimens. Probably overlooked in recent collections and confused with Slender Glossy Fringe Weed (*U. penicilliformis*). The two species look similar but *U. neglecta* develops attachment rhizoids only from the basal cell whereas Slender Glossy Fringe Weed (*U. penicilliformis*) has rhizoids from several of the lower cells.
**References:** Kornmann (1966, *Hormiscia*), Lokhorst & Trask (1981).

# *Urospora penicilliformis*

**(Roth) Areschough**

Slender Glossy Fringe Weed

**Appearance:** Narrow green threads, up to 8 cm in height. Appears as thin wet hair-like filaments, when above the water.

**Structure:** Uniseriate unbranched filaments attach to the substratum by 3-5 rhizoids from a few of the lower cells. Young filaments have cylindrical cells (19-) 25-35 µm in width and 0.5-2 times as long as wide. Older cells become barrel-shaped and have thicker walls, 32-45 (-57) µm in width and approximately as long as wide, or only slightly longer. Vegetative cells have a parietal cylindrical plastid, slightly perforated to net-shaped with many pyrenoids.

**Reproduction:** Gametangia and zoosporangia may form in the same or in different filaments. Zoospores in mature sporangia are placed with the pointed rear end towards the centre of the sporangium. They are released through a short exit-tube. Vegetative reproduction may also occur by aplanospores.

**Seasonal variation:** Filaments collected all year, well-developed in spring. *Codiolum*-phase collected in December and in spring (Kristiansen, 1972).

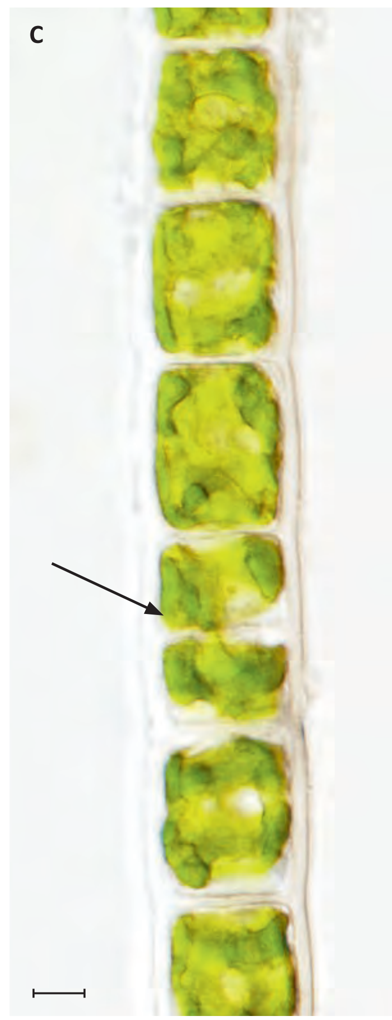
**Habitat:** In the wave-splash zone where the filaments cover boulders as a green fringe.

**References:** Kristiansen (1972), Lokhorst & Trask (1981), Wilkinson in Brodie et al., (2007).

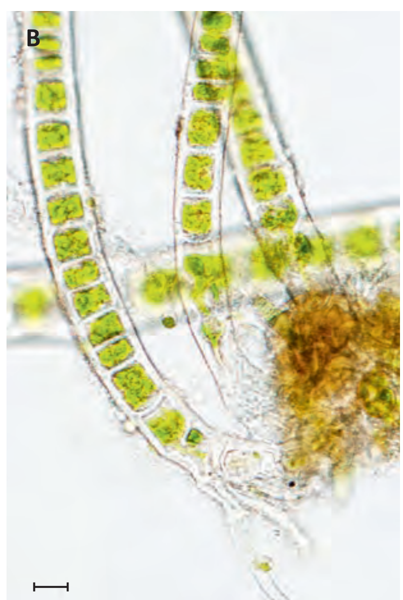
A: *Urospora penicilliformis.* Threads on herbarium paper. Margretheholms Havn, Copenhagen, wave-beaten zone, 15.4.2004. Scale 2 cm.

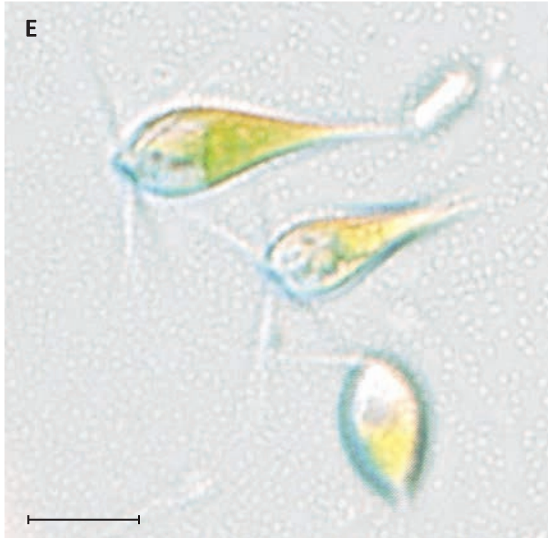
B: *Urospora penicilliformis.* Base of filament with rhizoids from several lower cells. Southeastern harbour-basin, Mosede Havn, 0.5 m, 20.5.2008. Scale 20 µm.

C: *Urospora penicilliformis.* Filament of cylindrical vegetative cells with parietal perforated plastid. Diffuse growth, 2 short new cells (arrow). Scale 10 µm. C-D: Stones circle at the Aquarium, The Blue Planet, Copenhagen, Kastrup, 15.2.2014.










D: *Urospora penicilliformis*. Fertile filament of barrel-shaped sporangia, zoospores turn the pointed tail towards the centre of the sporangium. Scale 10 µm.

E: *Urospora penicilliformis*. Zoospores with 4 flagella in blunt front and elongate pointed rear end. Eastern harbour jetty, Gilleleje, 29.5.2014. Scale 10 µm.

F: *Urospora penicilliformis*. Gametangia (left arrow) and zoosporangium (right arrow) in same filament. Upper part of bulwark at sauna, Skovshoved Havn, 27.2.2017. Scale 10 µm.

G: *Urospora penicilliformis*. *Codiolum*-phase. Sheltered side of northern harbour jetty, Frederikshavn, 0.1 m, 11.5.1975. Scale 50 µm.

# *Urospora wormskioldii*

**(Mertens) Rosenvinge**

Barrel-celled Glossy Fringe Weed

**Appearance:** Light green slightly shiny threads, 10-20 cm in height.

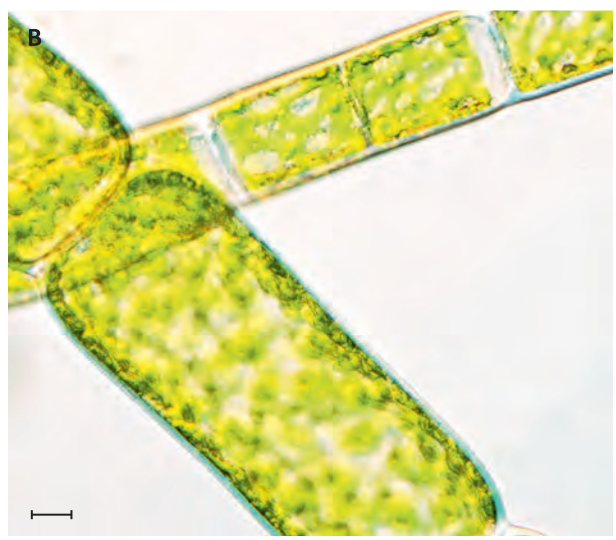
**Structure:** Uniseriate unbranched filaments, attach to substratum by rhizoids from many of the basal cells. Young cells are cylindrical, but soon become barrel-shaped with rounded cross walls. Cells (80-) 100-500 (-1200) µm in width and 1-4 times as long as wide. Vegetative cells have a parietal perforated net-shaped plastid with many pyrenoids.

**Reproduction:** Sexual reproduction with dioecious gametophytes and vegetative reproduction with zoospores or aplanospores. Sporangia are barrel-shaped or almost spherical, light to dark olive-green at maturity, and up to 1.5 mm in width. Gametes are drop-shaped with 2 flagella, and unequal in size (anisogametes). After fertilization, the zygote develops into a unicellular *Codiolum*-phase. Zoospores are drop-shaped with a pointed rear end and 4 flagella in the blunt front end. They are released through an exit-pore and grow into new filaments or into dwarf thalli dependent on physical condition such as temperature, according to culture studies by Lokhorst & Trask (1981). Dwarf thalli form zoospores or aplanospores similarly to other filaments, according to Wilkinson in Brodie et al. (2007).

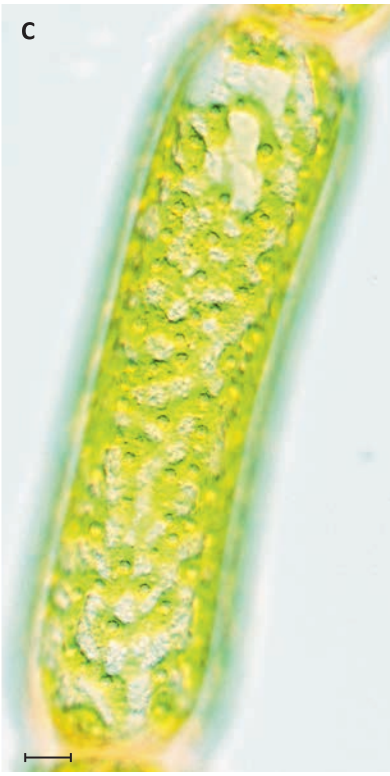
**Seasonal variation:** Well-developed in spring, collected in March-May.

**Habitat**: On solid substrata such as wooden poles and stone, where filaments make a closely packed stock, and epiphytic on coarser algae and sea grass. Low down in the wave-beaten zone to 1 m depth.


A: *Urospora wormskioldii*. Relatively thick filaments. Thyborøn, 6.4.1980. Leg. & det.: T. Christensen, Scale 2 cm.




B: *Urospora wormskioldii*. Young filament of cylindrical cells crossing an older filament of barrel-shaped cells. Scale 20 µm. B-F: Stone enclosure to the west of Vesterø Havn, Læsø, 0.3 m, 19.3.2015.



C: *Urospora wormskioldii.* Vegetative cell with parietal perforated plastid and many pyrenoids. Scale 10 µm.

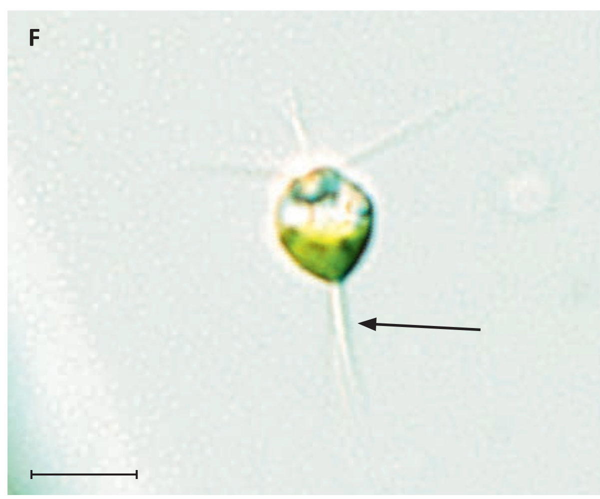
D: *Urospora wormskioldii.* Filament with two almost orange gametangia between vegetative cells. Scale 50 µm.

E: *Urospora wormskioldii.* Sporangium with zoospores. Scale 10 µm.

**Resembles:** Reminiscent of Brick Weed (*Chaetomorpha*), but filaments not as stiff as in this genus and form closely packed patches with a slightly shiny surface.

**Comment:** *Codiolum*-phases as '*Codiolum gregarium*', collected at Thyborøn developed gametophytic filaments of Barrel-celled Glossy Fringe Weed (*Urospora wormskioldii*) in culture by Lokhorst & Trask (1981, p.368).

**References:** Lokhorst & Trask (1981), Wilkinson in Brodie et al. (2007).



F: *Urospora wormskioldii.* Zoospore with pointed rear end (arrow) and 3 of 4 flagella visible in the blunt front end. Scale 10 µm.

**Order: Ulvales · Family: Bolbocoleonaceae**

## *Bolbocoleon piliferum*

**Pringsheim**

Green Onion Hair Weed

**Appearance:** Microscopic epi- or endophytes.

**Structure:** Uniseriate, creeping filaments with scattered branches on all sides. In some individuals cells are approximately cylindrical, 7-10 µm in width and 1-10 times as long as wide, in others, the cells are irregularly rounded, 25-45 µm in width. Vegetative cells contain a parietal, somewhat perforated plastid with 3-12 pyrenoids. Special small onion-shaped cells with a hair-like colourless extension (bolbocoleon-hair) occur between ordinary vegetative cells. They contain a small plastid with 1-2 pyrenoids in the lower part of the cells. Plastids have an indented margin which may resemble a fringe.

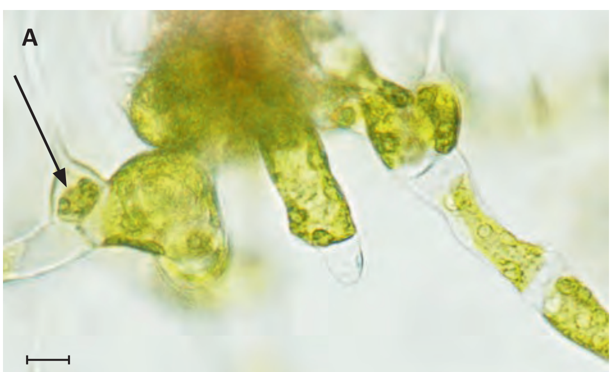
**Reproduction:** Vegetative reproduction by zoospores that develop in sporangia of transformed vegetative cells which become slightly swollen. Swarmers with 2 or 4 flagella are reported, but only quadriflagellate zoospores are recorded in Danish waters. Zoospores germinate and develop into new filaments. Young thalli studied in culture have an empty zoosopore wall and germination tube.

**Habitat:** Epiphytic, and endophytic in cell walls between surface cells of soft red and brown algae, 0.5-15 m depth.

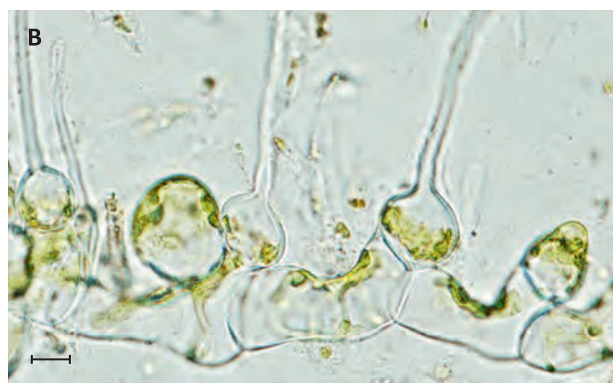
**Seasonal variation:** Collected in May, July-November.

**Comment:** Easily confused with other epi- and endophytic green algae, when bolbocoleon-hairs are absent. In such cases culture studies are necessary to confirm the identity.

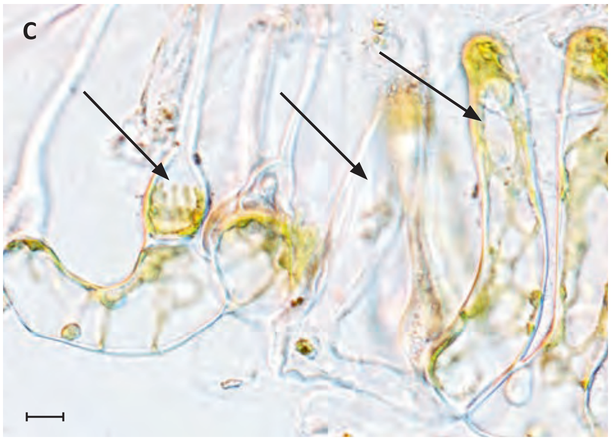
**References:** Gunnarsson & Nielsen (2016), Nielsen (1979), Nielsen et al. in Brodie et al. (2007), O'Kelly et al. (2004b), O'Kelly et al. in Brodie et al. (2007), Pringsheim (1862), South (1968).



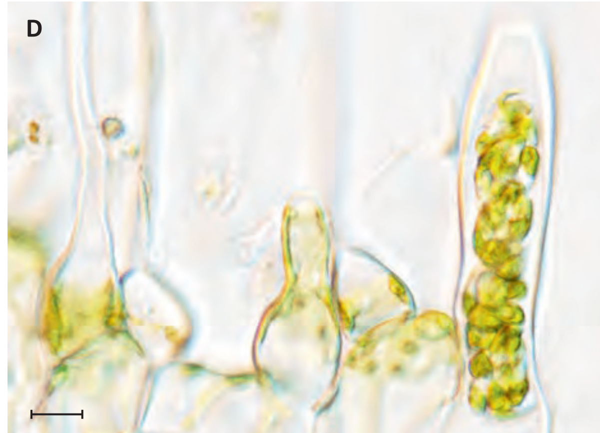

A: *Bolbocoleon piliferum*. Irregular vegetative cells with many pyrenoids and bolbocoleon-hair with 2 pyrenoids (arrow). Endophytic in Sea Noodle Worm Weed (*Nemalion multifidum*). Beach south of Vesterø Havn, Læsø, drift, 9.7.2013. Scale 10 µm.




B: *Bolbocoleon piliferum*. Creeping filament with upright bolbocoleon-hairs. Scale 10 µm. B-D: Endophytic between assimilating filaments of Punctured Ball Weed (*Leathesia marina*).




C: *Bolbocoleon piliferum.* Upright vegetative cells with perforated plastid (right arrow), empty sporangium (middle arrow) and bolbocoleon-hair with plastid which has a margin like a fringe (left arrow). Scale 10 µm.




D: *Bolbocoleon piliferum.* Mature sporangium. Scale 10 µm.

## Family: Capsosiphonaceae

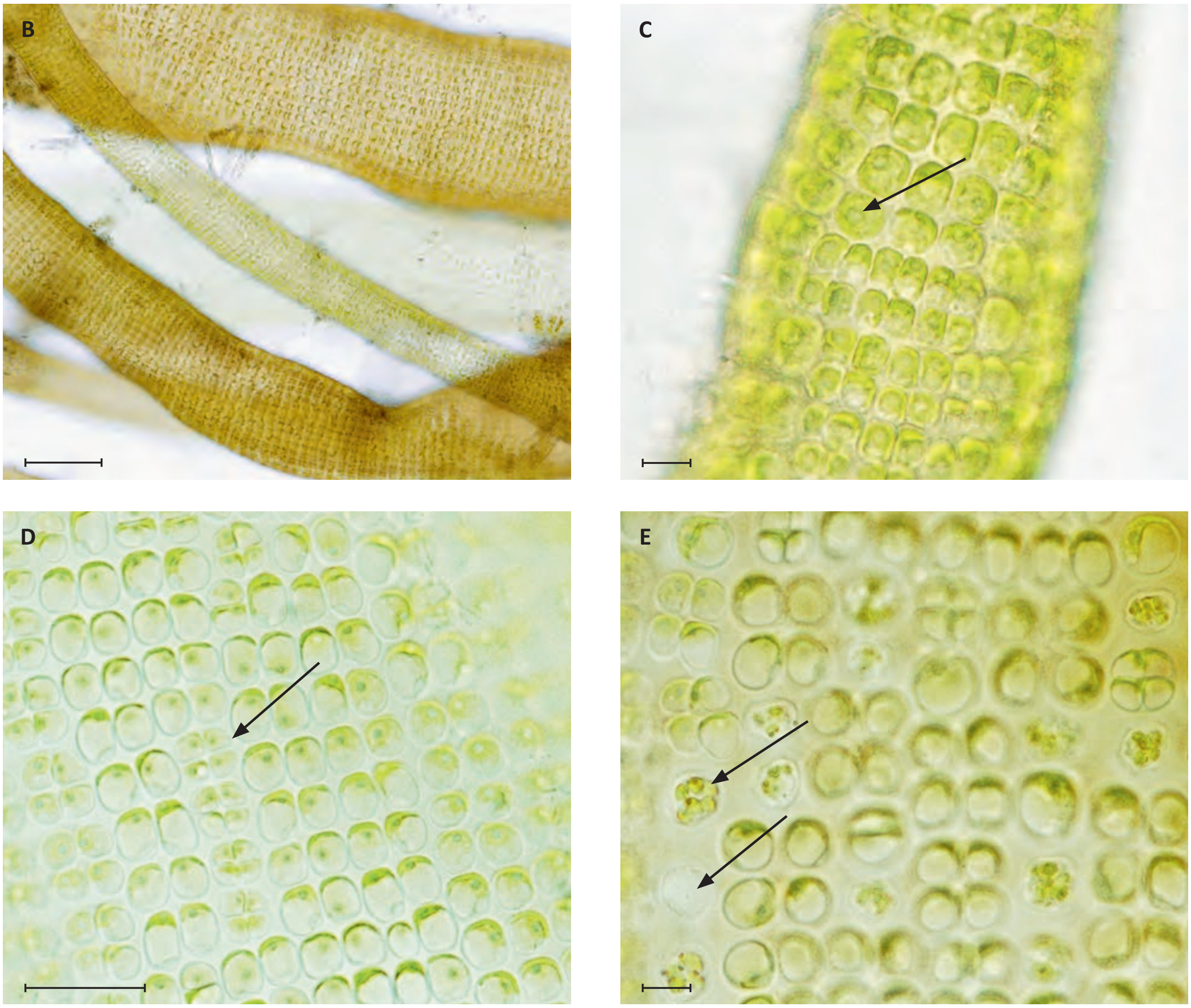
### *Capsosiphon fulvescens*

**(C.Agardh) Setchell & N.L.Gardner**

Golden Tube Weed


**Appearance:** Tube-like, olive-green to yellow-brown alga, up to 5 mm in width and 18 cm long.
**Structure:** Monostromatic tube-shaped parenchyma. Cells rounded to quadrangular with thick cell walls, arranged in distinct longitudinal and transverse rows. Diffuse growth with new cells in groups of 2 or 4 cells in a mutual outer wall. Each vegetative cell contains a parietal, plate-shaped plastid with one pyrenoid.
**Reproduction:** Vegetative reproduction by zoospores, which are drop-shaped and have a red eyespot. Sporangia develop from scattered vegetative cells in the oldest, upper part of the thallus. They are the same shape and size as in the vegetative state.
**Seasonal variation:** Collected in April, June, August-September.
**Habitat:** On stone and empty bivalve shells in shallow water at sheltered localities with a sandy bottom.
**Resembles:** Easily confused with species of Gut Weed

(*Ulva*), but distinguished by the brownish colour and the regularly arranged cells, seen microscopically.
**References:** Bliding (1963).




A: *Capsosiphon fulvescens*. Alga on empty shell of Common Cockle (*Cerastoderma edule*). Rønnerne, Frederikshavn, 29.6.1990. Scale 2 cm.

B: *Capsosiphon fulvescens*. Green and brownish tube-shaped parenchyma, of regular cell rows. Scale 100 µm. B, D: Sønder Nyland, Læsø, 0.5 m, 28.4.2016.

C: *Capsosiphon fulvescens*. Vegetative cells in longitudinal and transverse rows. A parietal, plate-shaped plastid with one pyrenoid (arrow) in each cell. C, E: Beach north of Vesterø Havn, Læsø, 23.6.2013. Scale 10 µm.

D: *Capsosiphon fulvescens*. Groups of 4 cells (arrow), after vegetative cell division. Scale 25 µm.

E: *Capsosiphon fulvescens*. Scattered sporangia in old part of thallus. Swarmers with red eyespots in mature sporangium (upper arrow) and empty sporangium (lower arrow). Scale 10 µm.

## Family: Gayraliaceae

# *Gayralia oxysperma*

**(Kützing) K.L.Vinogradova ex Scagel *et al.***

One-layered Sea Lettuce

**Appearance:** Thin, membranous blades with a bright green colour and shiny surface. Blades are rounded and attach to the substratum by rhizoids which arise from cells of a larger area in the lower part of the blade. Attached thalli, 2-4 cm in height, and drift thalli up to 20 cm in height.

**Structure:** Monostromatic parenchyma of angular to rounded cells, with thick and somewhat gelatinous cell walls. Cells in the upper part of thallus, 9-17 µm in width with a tendency to form rows in small area. Cells in the middle part are large and angular, 12-25 µm in width. Lower cells are relatively large, irregularly rounded, 20-25 µm in width and 30-40 µm in height, many of them with long colourless rhizoids, 6-10 µm in width. Rhizoids attach the thallus to the substratum. Vegetative cells contain a parietal, plate-shaped slightly lobed plastid with one pyrenoid.

**Reproduction:** Vegetative reproduction by zoospores. Upper cells of the blades transform into sporangia and become almost spherical. They contain many zoospores at maturity, which are released by decay of the sporangia walls. Zoospores are biflagellate and germinate into small, uniseriate filaments. Cells of a filament are divided both longitudinal and transversely and a small monostromatic sac is formed. This splits up and the blade develops into a monostromatic parenchyma by diffuse growth.

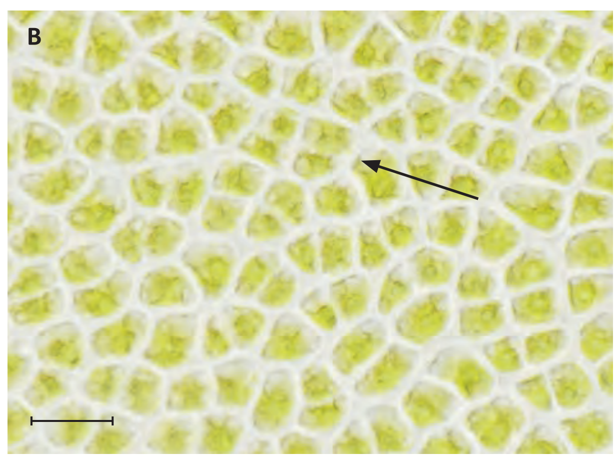
**Seasonal variation:** Collected all year.

**Habitat:** On poles in harbours and on stones in shallow water at sheltered localities in saline and brackish water.

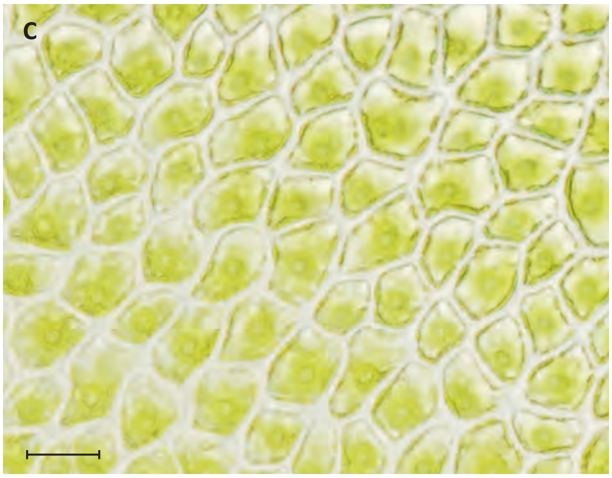
**Comment:** The life history was studied in culture by Kornmann (1964a), his studies comprised algae from Danish waters. Steinhagen et al. (2019b), who included Danish material in her studies, considered this species to be genetically similar to *Kornmannia leptoderma* (Kjellman) Bliding. Unfortunately, the *tuf*A gen sequence HQ610252.1 in Genbank with which Steinhagen compared her sequences was initially misidentified as *K. leptoderma* and later corrected to *G. oxysperma* (G. Saunders, personal communication; see also https://seaweedcanada.wordpress.com/gayralia-oxysperma-kutzing-k-l-vinogradova-ex-scagel-al-bc-a/).

**References:** Bliding (1968, *Ulvaria oxysperma*), Kornmann (1964a, *Monostroma oxyspermum*), Steinhagen et al. (2019b).

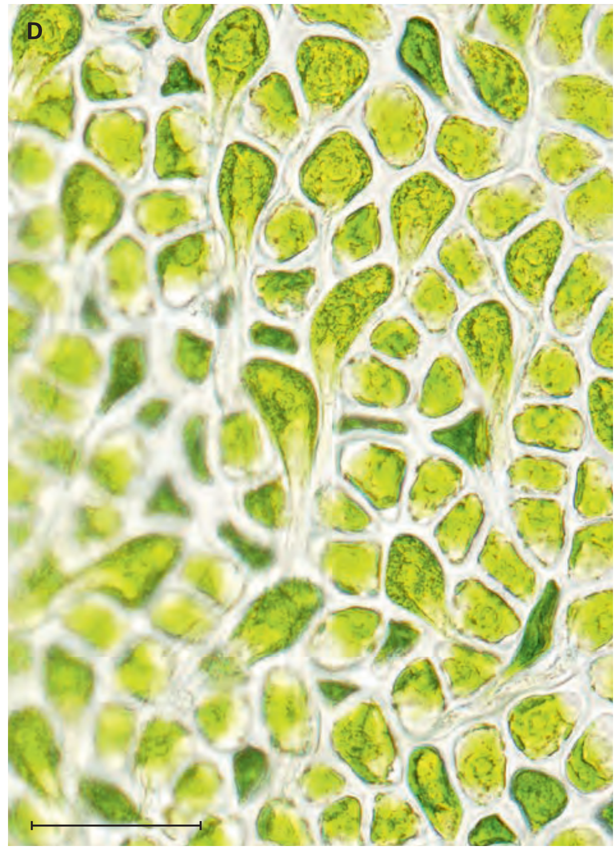

A: *Gayralia oxysperma*. Rounded membranous blades. Margretheholms Havn, Copenhagen, 15.4.2004. Scale 2 cm.



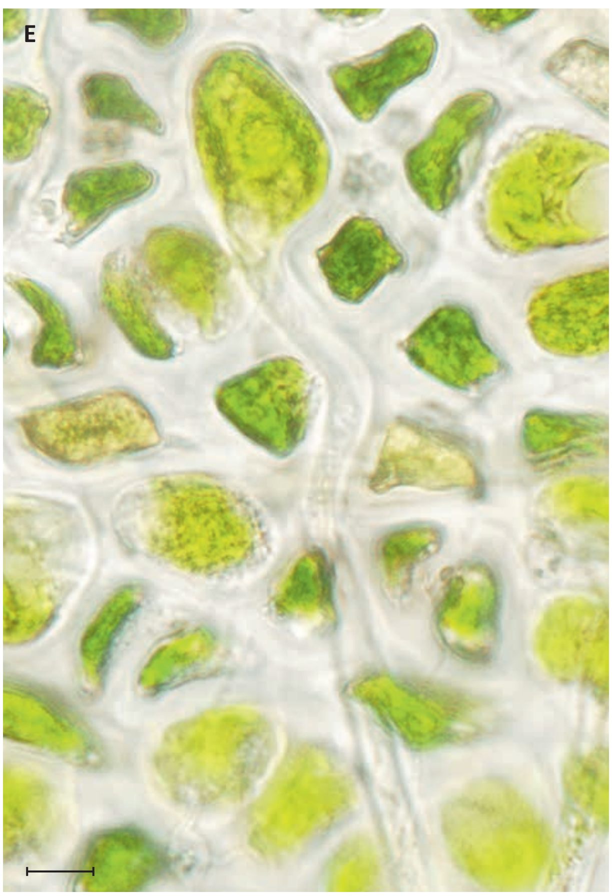

B: *Gayralia oxysperma*. Monostromatic parenchyma with diffuse growth, young cells in pairs (arrow). Scale 20 µm. B-F: Svanemøllehavn, Copenhagen, 0.5 m, 20.9.2007.



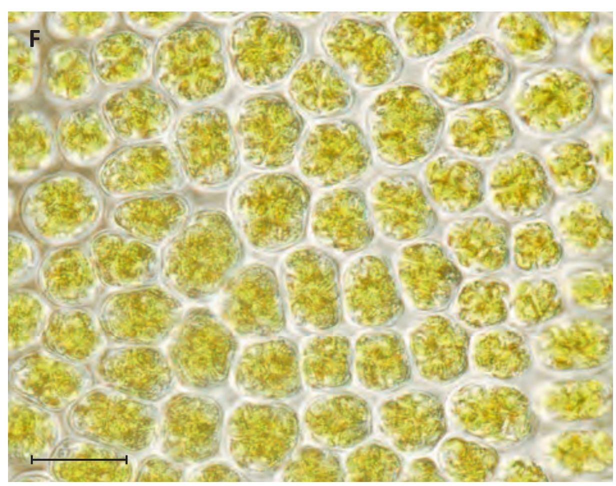

C: *Gayralia oxysperma*. Angular cells, each with a slightly lobed plastid and one pyrenoid; middle part of old blade. Scale 20 µm.




D: *Gayralia oxysperma*. Rounded cells in lower part of blade, many with long filamentous rhizoids. Scale 20 µm.




E: *Gayralia oxysperma*. Vegetative cell with rhizoid. Scale 10 µm.




F: *Gayralia oxysperma*. Rounded, mature sporangia in upper part of old blade. Scale 20 µm.

## Family: Gomontiaceae

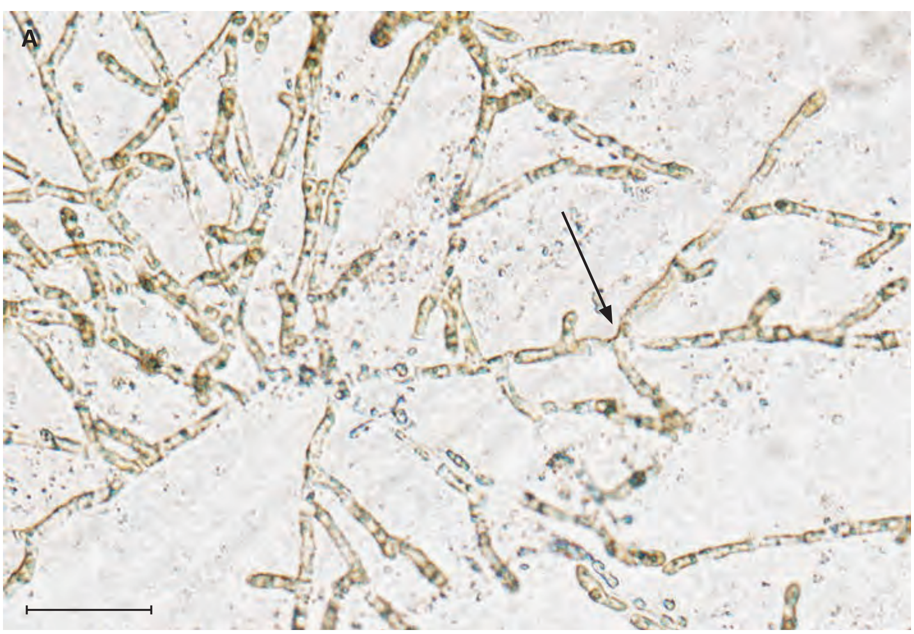
Life history comprises haploid gametophytes and diploid sporophytes. They might be isomorphic (*Eugomontia*) or heteromorphic with unicellular sporophytes (*Codiolum*-phase) and gametophytes, which are disc-shaped pseudoparenchyma (*Gomontia*) or blades (*Monostroma*).
**References:** O'Kelly et al. (2004a).

# *Eugomontia sacculata*

**Kornmann**

Green Shell Borer

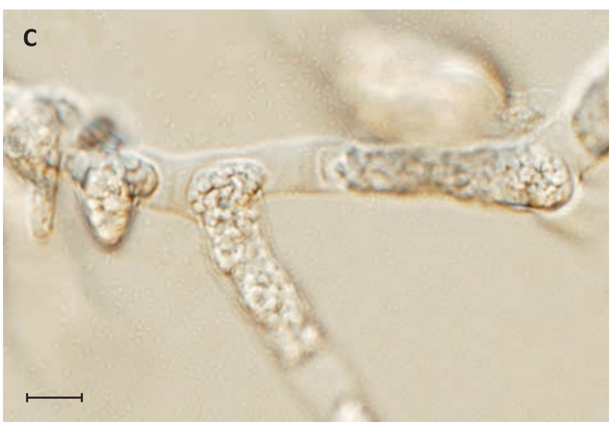
**Appearance:** Microscopic branched filaments, grow in calcified material, such as empty bivalve shells. They give the shells a bright-green colour.
**Structure:** Uniseriate filaments with scattered and opposite branches. Distal cells are cylindrical, 4.5-6.5 µm in width and 2-6 (-10) times as long as wide. Central cells are irregularly rounded. Cross walls are wide and often lamellated. Each cell contains a parietal plate-shaped, slightly lobed plastid with 1-4 pyrenoids.
**Reproduction:** Isomorphic gametophytes and sporophyte. Sporangia develop from intercalary vegetative cells, often from several consecutive cells. Gametophytes have rounded sporangia (gametangia), 20-25 µm in width, which develop in filaments outside the calcified material. Gametangia contain biflagellate gametes at maturity. Zoosporangia are relatively large, rounded, 40-60 µm in diameter, or sac-shaped, 25-40 µm in width and 60-100 µm in height. Zoospores, each



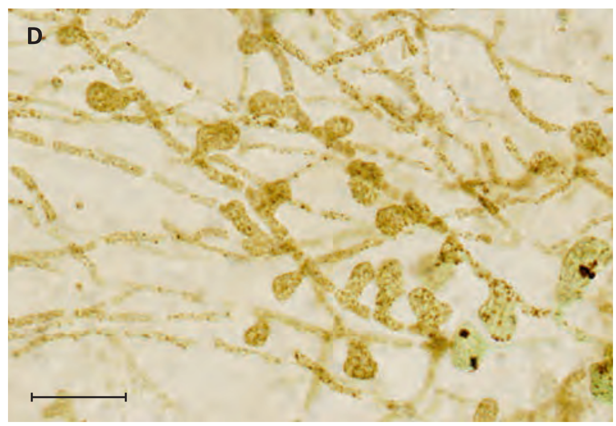

A: *Eugomontia sacculata*. Radiating filaments with scattered and a few opposite branches (arrow). Scale 50 µm. A-D: In bivalve shell, decalcified in 2 % acetic acid. A-B: Mariager Fjord, 0.2 m, 22.3.2014.

with 4 flagella are released through an exit-tube to the surface of the calcified material (Kornmann, 1960).
**Seasonal variation:** Occurs all year.
**Habitat:** Common in shells of empty bivalves, barnacles and in calcified worm tubes, 0.5-15 m depth.
**Resembles:** Twisted Hair Weed (*Phaeophila dendroides*) may appear similar when it occurs without hairs and has wide cross walls. Vegetative cells are large in Twisted Hair Weed (*P. dendroides*), and the plastid is reticulate with 6-20 pyrenoids, whereas the plastid is plate-shaped with 1-4 pyrenoids in Green Shell Borer (*E. sacculata*).
**Comment:** Considered a form of *Gomontia polyrhiza*, until culture studies by Kornmann (1959, 1960) showed them to be two independent species.
**References:** Gunnarsson & Nielsen (2016), John in Brodie et al. (2007), John and Wilkinson in Brodie et al. (2007), Kornmann (1959, 1960), Nielsen (1972).


B: *Eugomontia sacculata*. Vegetative cells with 1-3 pyrenoids and wide cross walls. Scale 10 µm.




C: *Eugomontia sacculata* Very wide cross walls. Holtemmen, Læsø, 0.2 m, summer 1971. Scale 10 µm.




D: *Eugomontia sacculata*. Sac-shaped sporangia. Nordre Rønner, Læsø, 24.5.2005. Scale 50 µm.

# *Gomontia polyrhiza*

## (Lagerheim) Bornet & Flahault

**Appearance:** Microscopic, irregular unicells, growing into calcified material such as empty bivalve shells. They may appear as tiny spots in the calcified substratum seen with the naked eye. Heteromorphic life history, in which the unicells alternate with small, discs-shaped thalli on the surface of the calcified material.

**Structure:** Unicells are rounded, spherical or irregularly sac-shaped, 100-250 µm in height and c. 150 µm in width. Several extensions to the surface of the calcified substratum may be short and rounded or conical and elongate, often with thick lamellated walls. Vegetative cells contain a parietal reticulate plastid with many pyrenoids. Disc-shaped thalli are polystromatic in centre and have short, mutually free filaments at the margin. Vegetative cells, 4-10 µm in width, each has a parietal plastid with one pyrenoid.

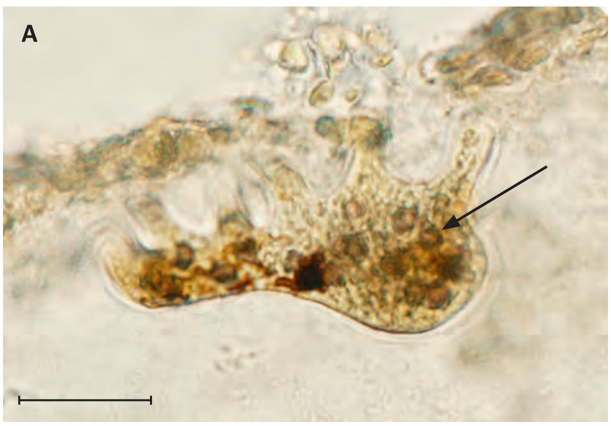
**Reproduction:** Life history comprises unicellular shell-boring sporophytes (*Codiolum*-phase) and pseudoparenchymatous disc-shaped gametophytes. Sporophytes contain a large number of zoospores at maturity, which are released through a relatively long exit-tube to the surface of the calcified substratum. Culture studies at Helgoland (Kornmann, 1959) showed zoospores to germinate into almost circular disc-shaped or irregularly formed pseudoparenchymatous gametophytes. Central cells transform into sporangia, which contain gametes at maturity. Zygotes germinate into new unicellular *Codiolum*-phase.

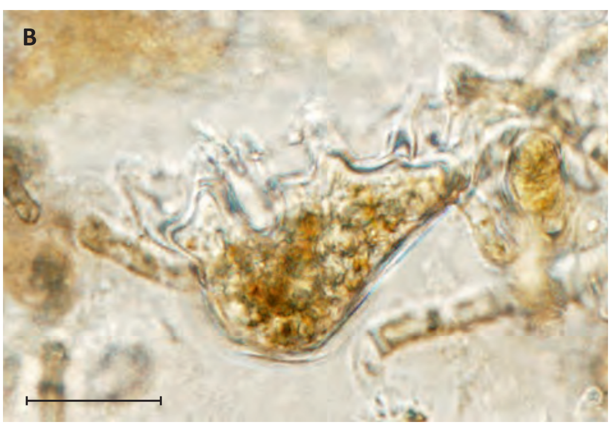
**Seasonal variation:** Shell boring *Codiolum*-phase occurs all year. In spring, small disc-shaped thalli are occasionally observed on the surface of calcified shells which contain the mature *Codiolum*-phase. These disc-shaped thalli are probably gametophytes.

**Habitat:** Unicellular *Codiolum*-phases occur in bivalve shells, barnacle shells, calcified worm tubes and other calcified material, 0.5-18 m depth.

**Resembles:** Greville's Mattress Weed (*Monostroma grevillei*) also has a unicellular shell-boring *Codiolum*-phase, but typically with a single extension to the surface of the substratum. A reliable identification depends on culture studies to verify the morphology of gametophytes.

**References:** Gunnarsson & Nielsen (2016), Kornmann (1959, *Codiolum polyrhizum*), Nielsen (1972), Nielsen & Correa (1987), Wilkinson in Brodie et al. (2007).




A: *Gomontia polyrhiza*. Unicellular sporophyte with extensions to the surface of the calcified substratum. Cell with many pyrenoids (arrow), stained with potassium iodide. Scale 25 µm. A-B: In bivalve shell, decalcified in 2 % acetic acid. Mariager, Mariager Fjord, 0.2 m, 22.3.2014.

B: *Gomontia polyrhiza*. Extensions to the surface of the calcified shell with lamellated walls. Scale 25 µm.

# *Monostroma grevillei*

**(Thuret) Wittrock**

Greville's Mattress Weed

**Appearance**: Upright light-green membranous blades. Young thalli are disc-shaped, up to 0.5 mm in diameter, with short mutually free filaments at the margin. The central part of the disc arches by continued growth and becomes sac shaped. Waves and currents in the water rupture the sac, which at first becomes cornet-shaped and later split further into several narrow lobes. The frond is typically 5-10 cm in height, but up to 30 (60) cm in very sheltered localities, where splitting happens later and is sparse. The life history is heteromorphic, blades alternate with a unicellular *Codiolum*-phase, which grows into calcified material.

**Structure**: Blades are monostromatic parenchyma with diffuse growth. Cells in central part of blade are angular and contain a parietal plate-shaped plastid with one pyrenoid. Upper cells are rounded. Cells lower down in the blade become elongate with pointed ends and contain 1-6 pyrenoids. The lowest cells have downward-growing extensions reminiscent of rhizoids, but they are within the outer wall.

***Codiolum*-phase** is spherical and up to 90 µm in width. It grows into calcified material and has a tubular extension on the surface of the substratum.

**Reproduction:** Life history comprises isomorphic dioecious gametophytic blades and a unicellular sporophyte (*Codiolum*-phase). Vegetative cells in gametophytes transform into sporangia with the same shape and size as in the vegetative condition. Development of sporangia begin in the upper part of the


A: *Monostroma grevillei*. Sac-shaped thalli. Helgenæs, Begtrup Vig, 0.5 m, 3.3.1966, Leg.: L. Mathiesen. Scale 2 cm.

B: *Monostroma grevillei*. Blade is split but still slightly cornet-shaped. Sporangia in upper part (arrow). Lynetteløbet, Copenhagen, 0.5 m, 15.4.2004. Scale 2 cm.

C: *Monostroma grevillei*. Blade split into narrow lobes. Margretheholms Havn, Copenhagen, 0.5 m, 17.3.2004. Scale 2 cm.

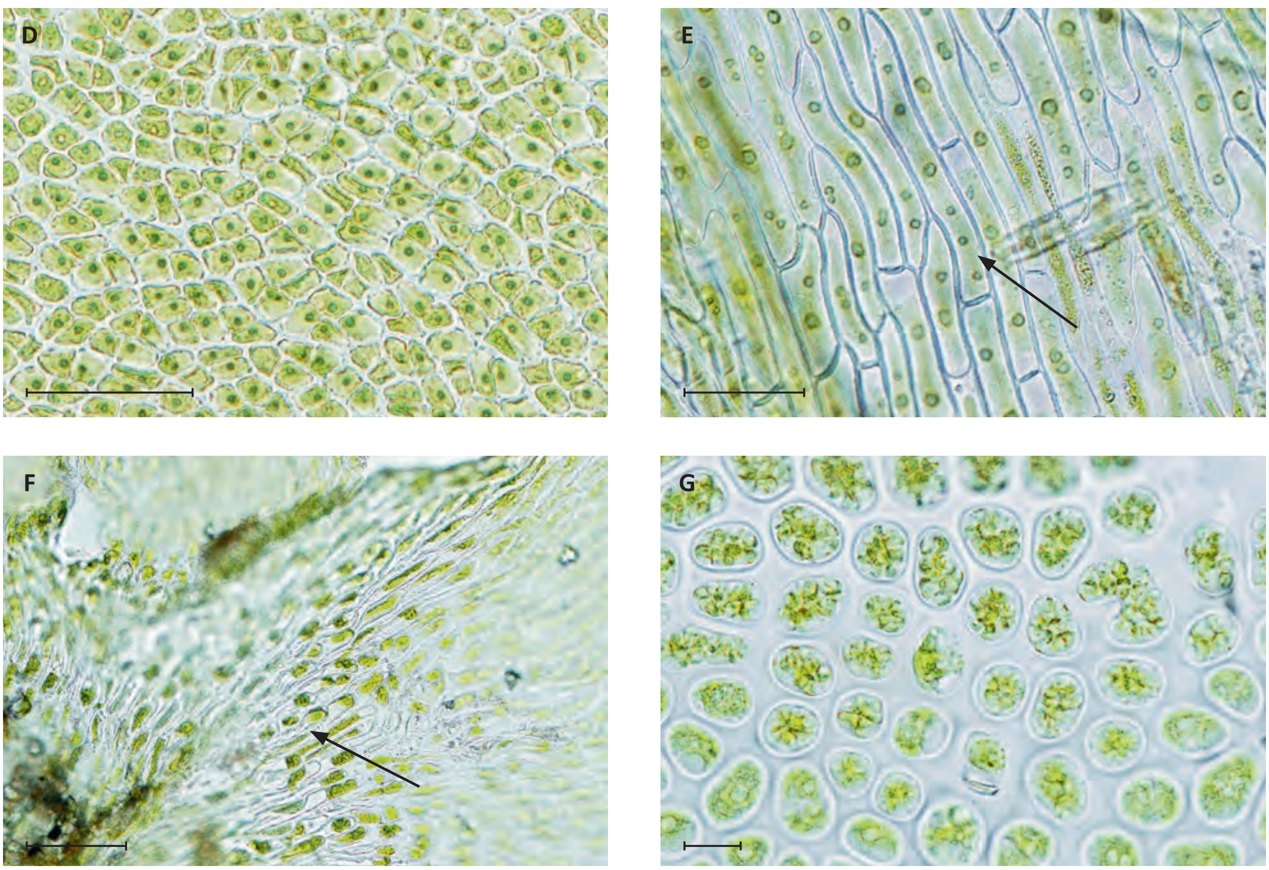
blade and continue downwards towards the base. Sporangia contain biflagellate gametes at maturity. Female gametes are larger than male gametes, which cause the upper margin in mature female thalli to become olive-green, whereas male thalli have an orange margin. Gametes swim towards the light (positively phototactic), whereas zygotes swim away from the light (negatively phototactic). The zygote develops into the unicellular *Codiolum*-phase, which at maturity is transformed into a sporangium and all contents become quadriflagellate zoospores. Zoospores are released through an exit-tube. They germinate and grow into disc-shaped gametophytes, which at temperatures of 5-6 ºC arch in the central part and by continued growth become parenchymatous monostromatic blades. The life history is known from culture studies of the algae from Helgoland (Kornmann, 1962a; Kornmann & Sahling, 1962).

**Seasonal variation:** Blades occur in winter, the first observed in October and may be present until the beginning of June. They probably do not survive temperatures above 9 ˚C according to investigations by Kristiansen in Tuborg Havn (Kristiansen, 1972). Unicellular *Codiolum*-phase is not recorded from observations in Danish waters. Disc-shaped phases known from culture studies (personal observation, RN).

**Habitat**: On stone and bivalve shells and occasionally epiphytic on Bladder Wrack (*Fucus vesiculosus*) and other algae. Common in shallow water, at harbour jetties and stones at sheltered localities, a few collections from deep waters, 0.5-11 m depth.

**Resembles:** Distinct from other green monostromatic blades by the cornet-shape, not having free rhizoids and not becoming dark-coloured by decay. Culture studies are necessary to identify the *Codiolum*-phase from that of *Gomontia polyrhiza*.

**References**: Bliding (1968), Kornmann (1962a), Kornmann & Sahling (1962, 1977), Kristiansen (1972, *Ulvopsis grevillei*), Steinhagen et al. (2019b), Wilkinson in Brodie et al. (2007).



## Family: Kornmanniaceae

## *Blidingia*

Squashed Gutweeds

**Appearance:** Uprights are tubular, in part compressed and a few centimetres in height.
**Structure:** Tubes are monostromatic parenchyma with diffuse growth. They are unbranched or sparsely branched with few small branches. Small cells with thick walls each containing a parietal plate-shaped plastid with one pyrenoid in the centre. The plastid fills the entire cell, so it appears centrally placed. Margin of plastid often indented.
**Reproduction:** Sexual or vegetative reproduction from swarmers. Sporangia develop from vegetative cells in the upper part of thallus, and remain the same shape and size as in vegetative condition. Sporangia contain many swarmers at maturity. Upper part of thallus appears pale after release of swarmers until the empty sporangia walls are worn away.
**Resembles:** Squashed Gutweeds (*Blidingia*) are distinct from small thalli of Gut Weeds (*Ulva*) by the small cells and the centrally placed plastid.
**References:** Bliding (1963), Kornmann & Sahling (1978), Steinhagen et al. (2019b, 2021), Tatewaki & Iima (1984), Woolcott et al. (2000a).

## *Blidingia marginata*

**(J.Agardh) P.J.L.Dangeard**

Squashed Ribbon Gutweed

**Appearance:** Short threads, a few centimetres long, which form a felty cover on the substratum. Threads are unbranched or have short, scattered branches in the lower part.
**Structure:** Tubular or narrow ribbon-shaped parenchyma, which arise in bunches from a disc-shaped base. Cells, 5-7 µm in width, form rows. They contain a single plastid with one central pyrenoid.
**Reproduction:** Vegetative reproduction by zoospores. Young thalli are disc-shaped, without an empty spore-wall cut off after germination.
**Seasonal variation:** Only a few collections from Danish waters, February, July and August.
**Habitat:** Collected on a harbour jetty 70 cm above the waterline and in the salt-dust zone between thalli of Stalked Green Guano Weed (*Prasiola stipitata*).
**Resembles:** The cells, occurring in rows make it distinct from Squashed Flat Gutweed (*B. minima*).
**Comment:** Probably overlooked and more frequent than the few collections in Danish waters indicate. Outside Denmark, Squashed Ribbon Gutweed (*B. marginata*) also occurs on mud and on various plants in salt marshes. It is tolerant of variations in salinity and temperature.
**References:** Maggs et al. in Brodie et al. (2007).

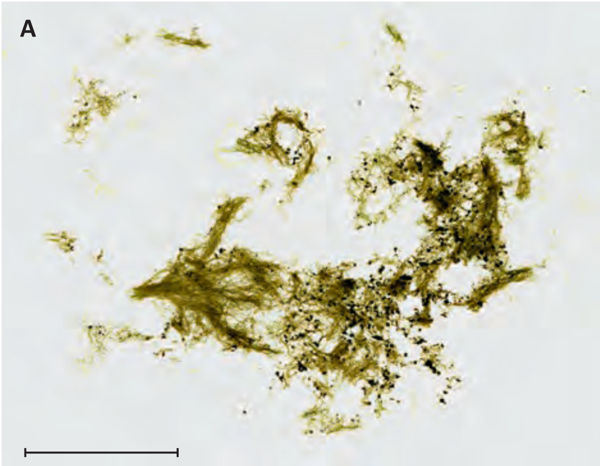
←

D: *Monostroma grevillei.* Angular cells, central part of blade, one pyrenoid per cell. Stained with potassium iodide. Scale 50 µm. D, F: Vesterø Havn, Læsø, 0.5 m, 14.3.2014.

E: *Monostroma grevillei.* Elongate cells in lower part of blade. Several pyrenoids per cell (arrow). E, G: Sønder Nyland, Læsø, 0.5 m, 28.4.2016. Scale 50 µm.

F: *Monostroma grevillei.* Basal cells with downward-growing rhizoid-like extensions (arrow). Scale 50 µm.

G: *Monostroma grevillei.* Rounded sporangia with many swarmers. Eyespots visible as dark points. Scale 10 µm.





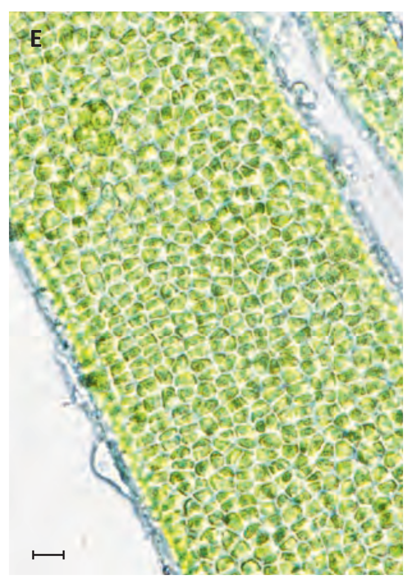
A: *Blidingia marginata*. Small filaments on herbarium paper. Scale 2 cm. A-C: Northern harbour jetty, Strandby, 70 cm above waterline, 11.8.1973. Leg.: I. Pedersen, det.: T. Christensen.

B: *Blidingia marginata*. Parenchyma of small cells in longitudinal rows. Scale 10 µm. B-C: Rehydrated herbarium material.

C: *Blidingia marginata*. Short branches. Scale 20 µm.

D-E: *Blidingia marginata*. Young (D) and slightly older (E) thalli with longitudinal cell rows. Each cell with a plastid and one central pyrenoid. Aarhus Lystbådehavn, among *Prasiola stipitata* 27.2.2017. Leg.: K.L. Krabbe. Scale 10 µm.





# *Blidingia minima*

**(Nägeli ex Kützing) Kylin**

Squashed Flat Gutweed

**Appearance:** Light-green tubular thalli, typically many together in curly carpet-like mats. Individuals typically a few centimetres in height and may be up to 10 cm.

**Structure:** Upright tubular thalli frequently several together arise from a disc-shaped base. They are monostromatic parenchyma of small rounded or angular cells, occurring irregularly in most of the frond. Cells may occur in rows in small area. Cells, 6.5-10 μm in width, each contains a plastid with one pyrenoid.

**Reproduction:** Sporangia develop from vegetative cells in the upper part of thallus. They are the same shape and size as in the vegetative condition. Swarmers may be gametes or zoospores. After the germination process, a disc-shaped almost circular alga develops. It is monostromatic initially but later becomes polystromatic in the centre. After germination of zoospores the evacuated spore-wall is cut off but only visible in few-celled young individuals. Culture studies of Squashed Flat Gutweed (*B. minima*) in Japan revealed considerable variation in the life history. The discs without uprights might be an alternative phase in a life history, where upright sporophytes alternated with disc-shaped gametophytes. There might be an alternation between isomorphic upright dioecious gametophytes and upright sporophytes. An irregular alternation between uprights and disc-shaped individuals were also observed and zoospores from upright individuals might germinate directly into new uprights.

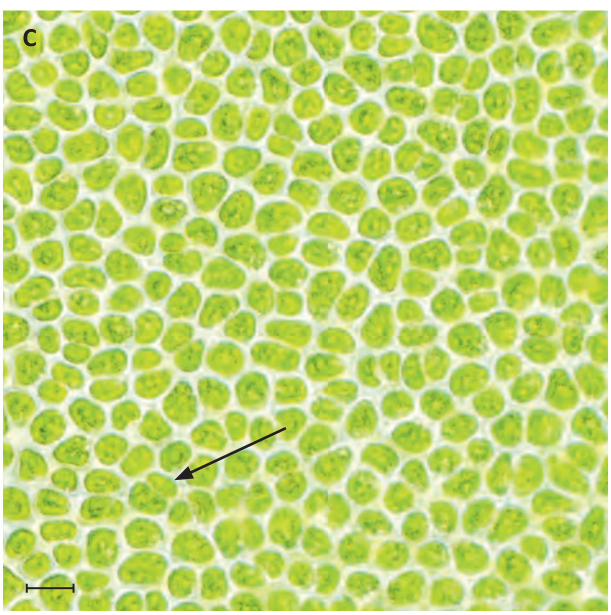
**Seasonal variation:** Occurs all year, well-developed in summer.

**Habitat:** On stone in upper part of the littoral and in the wave beaten zone.

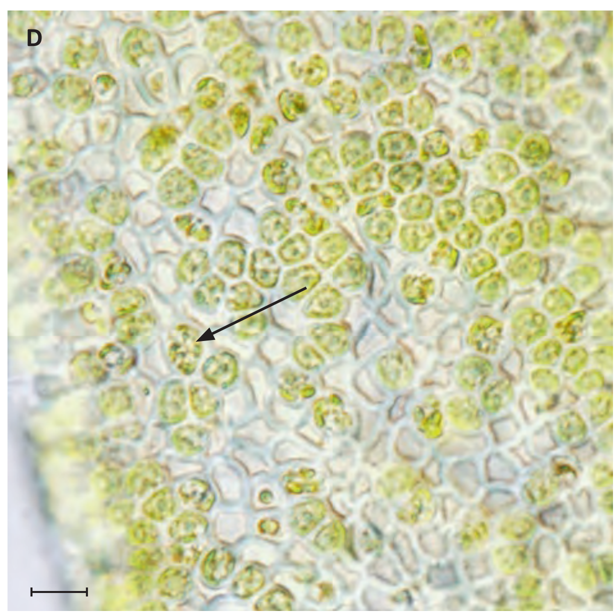
**References:** Kristiansen (1972), Tatewaki & Iima (1984).


A: *Blidingia minima*. Curly mat at the top of boulder in wave-beaten zone. Aarhus Lystbådehavn, 27.2.2017. Photo by K.L. Krabbe.


B: *Blidingia minima*. Upright slightly curved, tubular fronds with few branches. Slusen, Harbour of Copenhagen, 24.4.1998. Scale 2 cm.




C: *Blidingia minima*. Parenchyma of small, rounded cells with thick walls and diffuse growth (arrow). Plastids fill the cells, each with one pyrenoid. The Aquarium, The Blue Planet, Copenhagen, Kastrup, 15.2.2014. Scale 10 µm.




D: *Blidingia minima*. Vegetative cells, mature (arrow) and empty sporangia, upper part of frond. Hirsholm, wave-beaten zone, 1.10.2015. Leg.: K.L. Krabbe. Scale 10 µm.

## *Neostromatella monostromatica*

### M.J.Wynne, G.Furnari & R.Nielsen

**Appearance:** Microscopic spots, sometimes visible as green dots with the naked eye.

**Structure:** Monostromatic approximately circular pseudoparenchyma, 50-75 µm in diameter. Margin of mutually free short filaments of cells, c. 5 µm in width and as long as wide. In central part cells are rounded, c. 7 µm in width. Vegetative cells contain a parietal plate-shaped plastid with one pyrenoid. No hairs.

**Reproduction:** Vegetative reproduction by zoospores. Sporangia develop from vegetative cells in the middle of the disc. They are the same shape, but slightly larger than vegetative cells. Sporangia contain 4 zoospores at maturity, zoospores are released through a round pore in the upper part of the sporangium wall. Thalli with evacuated sporangia remain empty in the central part. Zoospores have 4 flagella, germinate and develop into similar offspring to the parent generation.

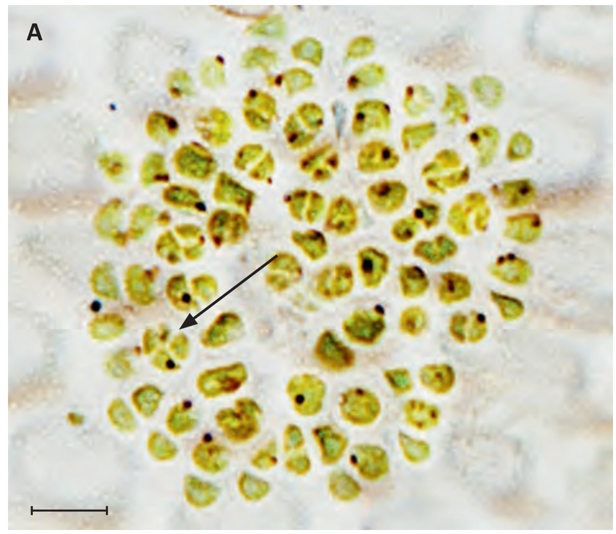
**Seasonal variation:** Collected in March-April, July-September and November.

**Habitat:** On leaves of Eelgrass (*Zostera marina*) and on bivalve shells in 0.5-8 m depth.

**Resembles:** Young Green Club Spot (*Syncoryne reinkei*), appears similar, but sporangia from centrally placed cells become club-shaped and contain many swarmers at maturity.

**Comment:** Germlings in culture consist of two unequally large cells, young individuals are approximately bilaterally symmetrical before they become circular or irregularly lumpy pseudoparenchyma (Nielsen 1988a, b).

**References:** Kornmann & Sahling (1983, *Stromatella monostromatica*), Nielsen (1988a, b, *S. monostromatica*), Wynne & Furnari (2014).




A: *Neostromatella monostromatica*. Monostromatic circular alga with margin of short mutually free filaments. Mature sporangia with 4 zoospores (arrow). Central area empty. On old leaf of Eelgrass (*Zostera marina*), Frederiksholm at Motortorpedobådshal, Holmen, Copenhagen, 0.5 m, 24.4.1998. Scale 10 µm.

## *Pseudendoclonium*

Green Grits

**Appearance:** Microscopic algae, often many together colouring the substratum green.
**Structure:** Small pseudoparenchymatous masses of rounded cells with a margin of short radiating filaments with scattered branches. Cells are cylindrical, each with a plate-shaped plastid and one pyrenoid. No hairs.
**Reproduction:** Vegetative reproduction from fragments which continue growth and by quadriflagellate zoospores, which grow into offspring similar to the former generation. Biflagellate swarmers observed in one species might be gametes, but copulation not observed. Sporangia develop from vegetative cells; they are conical or rounded and slightly larger than in the vegetative condition. In general, species can be identified according to habitat.

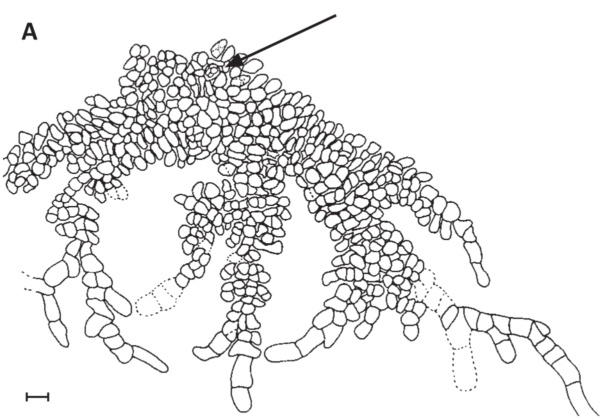
**Identification key to species of *Pseudendoclonium***

| | | |
|---|---|---|
| 1a. | In walls of the hydroid *Dynamena pumila* | *P. dynamenae* |
| 1b. | On larger algae, common on Bladder Wrack (*Fucus vesiculosus*) | *P. fucicola* |
| 1c. | On or in wood or other solid substrata in the salt-dust zone | *P. submarinum* |

## *Pseudendoclonium dynamenae*

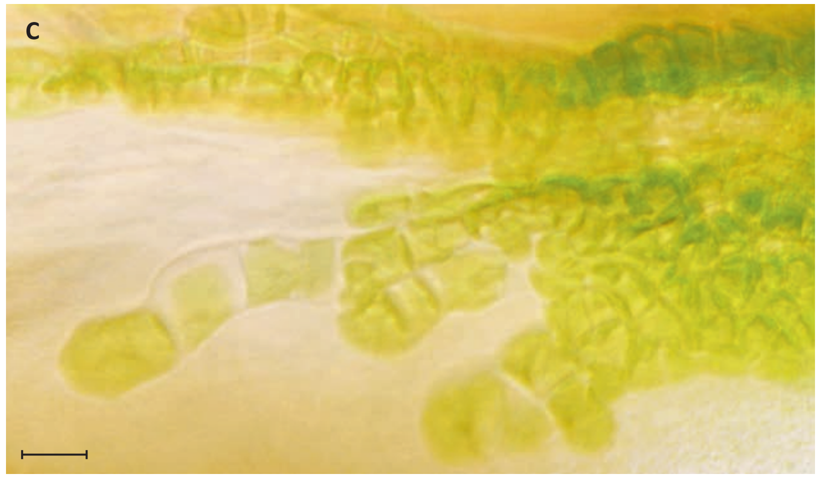
**R.Nielsen**
Hydroid Green Grit

**Appearance:** Microscopic filaments in chitin walls of hydroids, which become green in colour.




A: *Pseudendoclonium dynamenae*. Polystromatic pseudoparenchyma with margin of uniseriate filaments of large cells. Sporangia with swarmers in central part (arrow). Scale 10 µm. A-B: Sheltered side, southern harbour jetty, Hirsholm, 0.5 m, 5.1.1973.

**Structure:** Pseudoparenchymatous uneven polystromatic central area with radiating uniseriate branched filaments. Cells in the central area are rounded or slightly angular, 2-3 µm in width in surface view. Mutually free filaments at the margin consist of cylindrical cells, 4-5 µm in width and 2-4 times as long as wide. In sections of the hydroids, the central cells appear elongate with the length perpendicular to the host surface. Each vegetative cell contains a parietal plate-shaped plastid with one pyrenoid.
**Reproduction:** Sporangia develop from the upper central cells and contain 4 or 8 zoospores at maturity. Zoospores have 2 or 4 flagella. An empty spore-wall and short evacuated germination-tube occur on few-celled young filaments in culture.
**Seasonal variation:** Present all year, sporangia recorded in January and June-July.
**Habitat:** In chitin walls of the hydroid *Dynamena pumila*, which frequently grow on Egg Wrack (*Ascophyllum nodosum*). In shallow water, down to 5 m depth.
**References:** Gunnarsson & Nielsen (2016), Kornmann & Sahling (1994), Nielsen (1984), Nielsen in Brodie et al. (2007).



B: *Pseudendoclonium dynamenae*. Green coloured hydroid *Dynamena pumila* on Egg Wrack (*Ascophyllum nodosum*). Scale 2 cm.

C: Marginal filament of large cells, appears to arise from small cells in the uneven central part. Sheltered side, southern harbour jetty, Hirsholm, 0.5 m, 14.4.2015. Scale 10 µm.

**Lower illustration:**
A: *Pseudendoclonium fucicola*. Pseudoparenchyma of small cells, empty sporangium (arrow). On Bladder Wrack (*Fucus vesiculosus*). Frederikshavn, 0.3 m, 9.4.1975. Scale 100 µm.

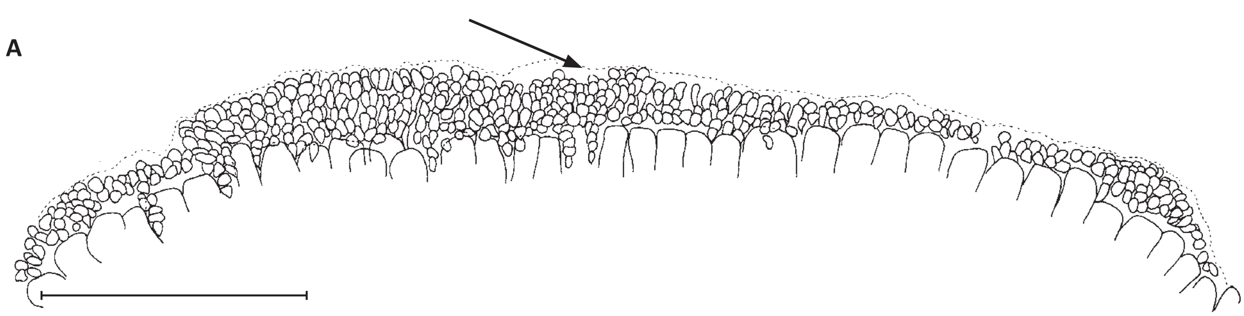
## *Pseudendoclonium fucicola*

**(Rosenvinge) R.Nielsen**

Wrack Green Grit

**Appearance:** Microscopic epiphytes, often many together and visible as a green powder on the host-alga.
**Structure:** Rounded cushion-shaped pseudoparenchyma, of densely adpressed upright filaments in central part and margin of uniseriate radiating filaments. Cells are rounded, 3.5-5 µm in width, each contains a parietal plate-shaped plastid with one pyrenoid.

**Reproduction:** Sporangia develop from the upper central cells, which become slightly larger than in the vegetative condition and develop a conical top. Swarmers with 4 flagella, or 2 flagella have been observed in culture studies.
**Seasonal variation:** Present all year.
**Habitat:** Epiphytic on species of Wrack (*Fucus*) 0.5-1 m depth.
**References:** Gunnarsson & Nielsen (2016), Nielsen (1980), Nielsen in Brodie et al. (2007).



## *Pseudendoclonium submarinum*

**Wille**

Pole Turf Green Grit

**Appearance:** Microscopic unicells, cell-clumps, or short filaments, typically several together colouring the substratum green.

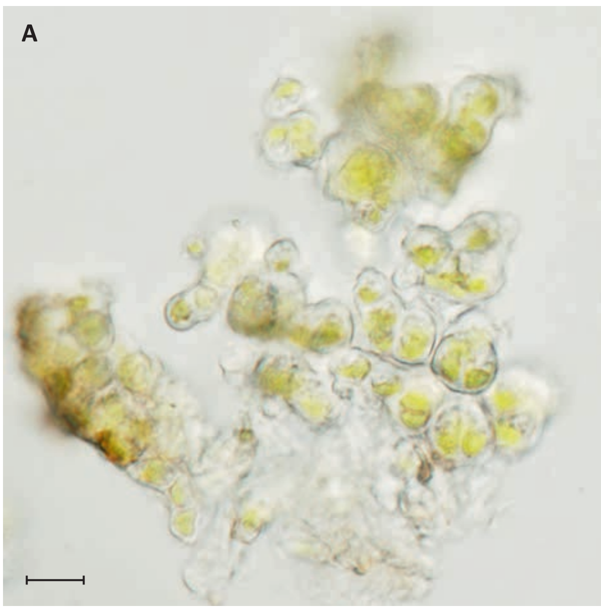
**Structure:** Unicells, few-celled filaments, cell-clumps or short filaments which may have scattered branches. Cells are rounded, up to 6-7 µm in width. Each vegetative cell contains a parietal plate-shaped plastid with one pyrenoid.

**Reproduction:** Vegetative reproduction from fragments which continue to grow and by zoospores. Sporangia develop from transformed vegetative cells, become rounded and slightly larger than in the vegetative condition. Sporangia contain a few quadriflagellate zoospores at maturity.

**Seasonal variation:** Present all year.

**Habitat:** In the salt-dust zone, on and in wooden poles and as a thin green cover on boulders and other solid substrata.

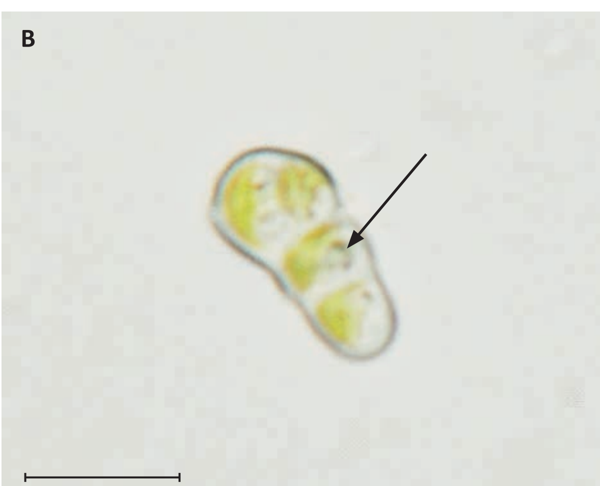
**References:** Gunnarsson & Nielsen (2016), Nielsen (1980), Nielsen in Brodie et al. (2007), Wille (1901).

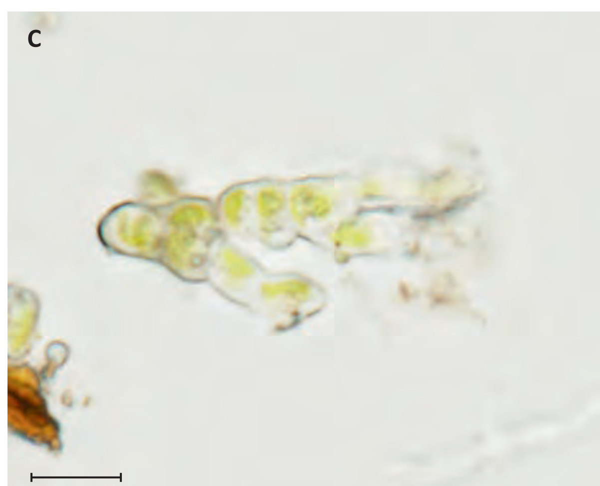



A: *Pseudendoclonium submarinum*. Cell-clumps of rounded unicells or short filaments. Scale 10 µm. A-C: On wooden pole of bulwark, southern part of Margretheholms Havn, Copenhagen, 21.9.2007.

B: *Pseudendoclonium submarinum*. Few-celled filament. Parietal plastid with one pyrenoid (arrow). Scale 10 µm.

C: *Pseudendoclonium submarinum*. Short filament with scattered branches. Scale 10 µm.



## *Tellamia contorta*

**Batters**

Snail Shell Filament

**Appearance:** Microscopic endozoic filaments, often many together colouring the host green.

**Structure:** Uniseriate filaments with scattered and opposite branches. Branches may be curved, sickle-shaped. Filaments are often mutually free in area of host, not entirely covered by the alga. Cells in such individuals are cylindrical, 1-4 times as long as wide. In areas where the substratum is completely covered by the alga, cells are rounded, lens-shaped or spherical, 2.5-4 µm in width. Vegetative cells contain a parietal plate-shaped plastid with one pyrenoid.

**Reproduction:** Vegetative reproduction by zoospores. Sporangia develop from vegetative cells and are the same shape and size as in the vegetative condition cylindrical sporangia develop a small exit-papilla, and rounded sporangia a conical top. Sporangia contain 2 or 4 zoospores at maturity.

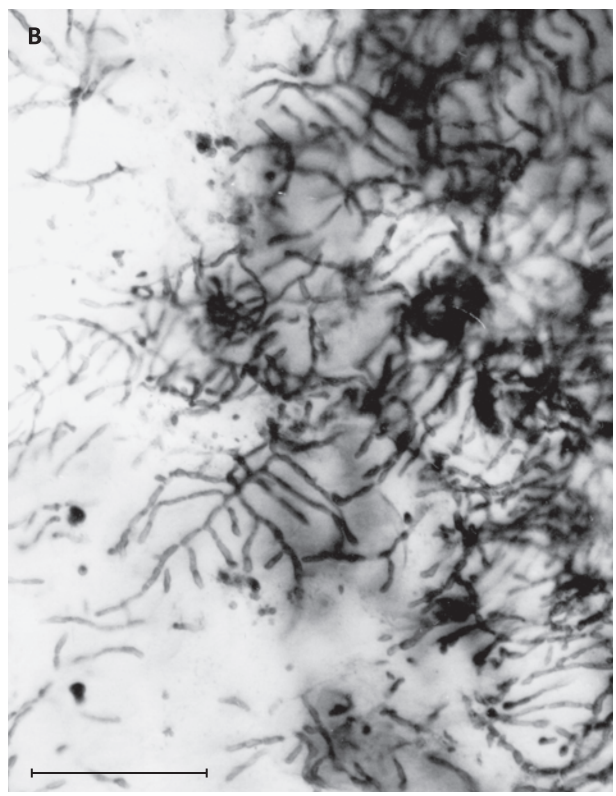
**Seasonal variation:** Present all year. Mature sporangia recorded in January, July and November.

**Habitat:** In periostracum of Flat Periwinkle (*Littorina obtusata*) and the similar *L. mariae*, 0.5-1 m depth.

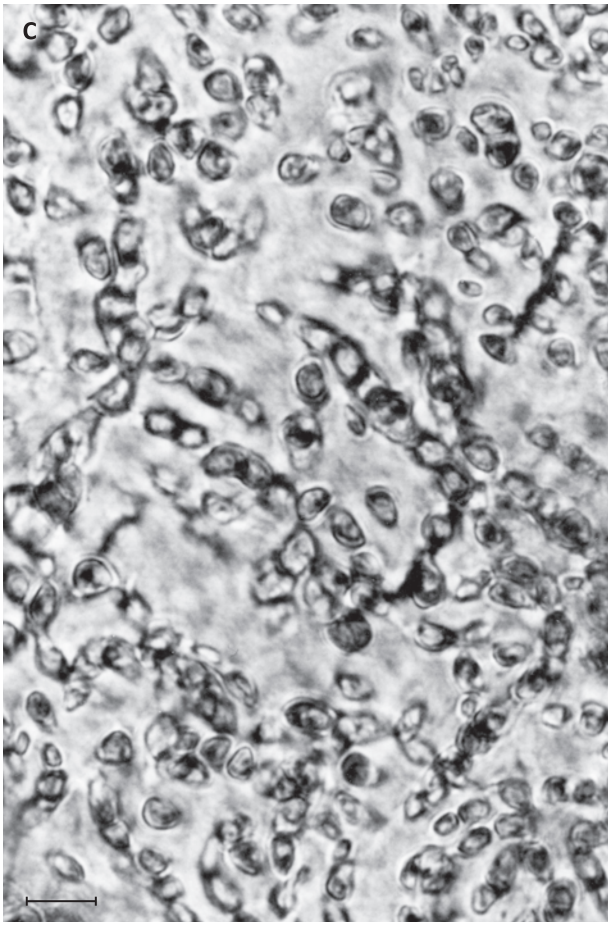
**Comment:** Originally described as two species (*T. contorta* and *T. intricata* Batters), but probably a single species according to Nielsen & McLachlan (1986) and Printz (1926).

**References:** Batters (1895a, b), Gunnarsson & Nielsen (2016), Nielsen & McLachlan (1986), Nielsen & Wilkinson in Brodie et al. (2007), Printz (1926).

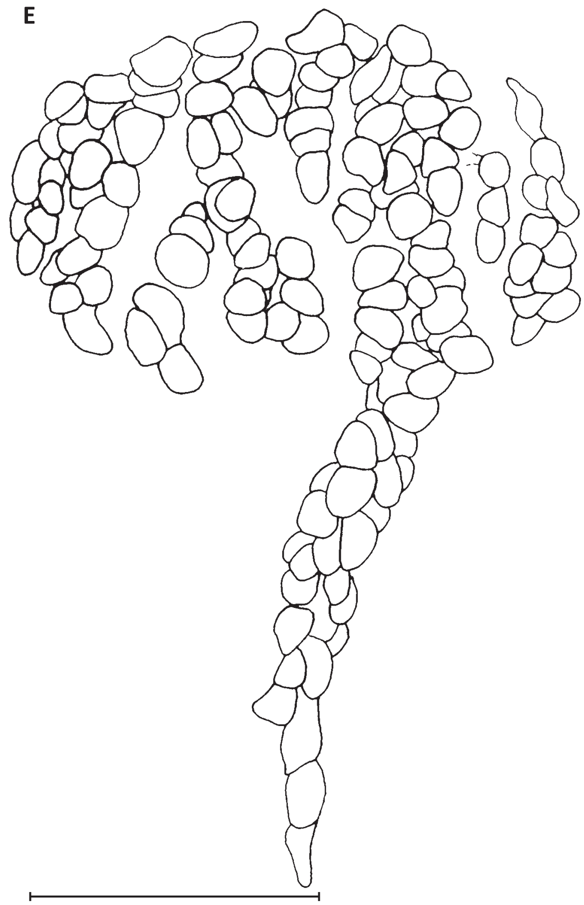

A: *Tellamia contorta*. Old part of Flat Periwinkle (*Littorina obtusata*) green coloured by the alga. Horneks Odde, Læsø, 0.5 m, 24.9.2017. Scale 0.5 cm. Photo by P. Corfixen.

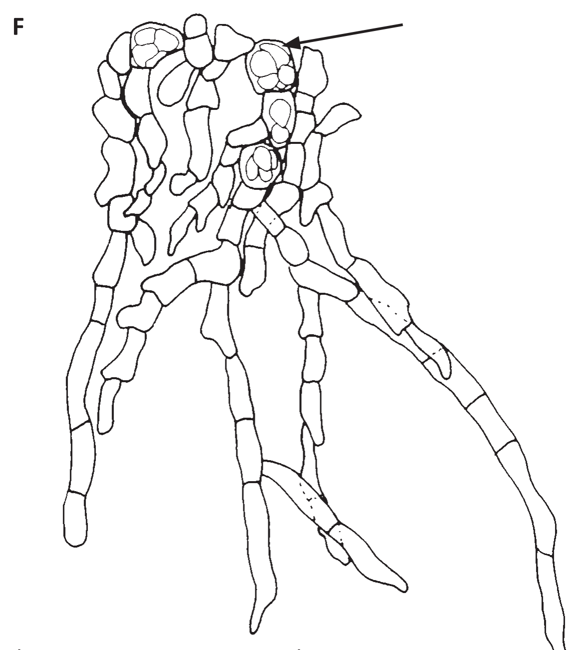



B: *Tellamia contorta*. Openly branched filaments. Scale 100 µm. A-E: In periostracum of Flat Periwinkle (*Littorina obtusata*). B-C: Deget, Frederikshavn, 0.5 m, 14.6.1974.



C: *Tellamia contorta*. Densely growing alga, lens-shaped cells. Scale 10 µm.





D: *Tellamia contorta*. Openly branched alga with scattered and opposite branches. Scale 50 µm. D-F: Hirsholm, 0.2 m, 11.1.1980.

E: *Tellamia contorta*. Densely branched alga. Scale 50 µm.

F: *Tellamia contorta*. Sporangia (arrow). Scale 50 µm.

## Family: Phaeophilaceae

# *Phaeophila dendroides*

**(P.Crouan & H.Crouan) Batters**

Twisted Hair Weed

**Appearance:** Microscopic branched filaments, growing into calcified material.

**Structure:** Uniseriate filaments with scattered and opposite branches. Cells are cylindrical, rounded or are irregular in shape. Cylindrical cells are 8-12 µm in width and 3-9 times as long as wide. Rounded and irregular cells, up to 40 µm in width, occasionally to have wide cross walls. Swellings or short cylindrical protrusions which grow towards the surface of the calcified substratum may occur on some cells. Vegetative cells contain a parietal, reticulate plastid with 6-20 pyrenoids. Characteristic spirally twisted colourless hairs occur from walls of vegetative cells (phaeophila-hair), occasionally separated from the cell by a thick wall at the base.

**Reproduction:** Vegetative reproduction by zoospores. Sporangia develop from intercalary vegetative cells, which develop a relatively long exit-tube. Zoospores are drop-shaped with 4 flagella in the pointed front end. The evacuated spore-wall and a narrow germination-tube occur on germlings in culture and are cut off from the rest of the germling.

**Seasonal variation:** Present all year.

**Habitat:** Grow into empty bivalve shells and other calcified material, 0.5-21 m depth. Very common in calcified tubes of Sinistral Spiral Tubeworm (*Spirorbis spirorbis*) growing on species of Wrack (*Fucus*). Twisted Hair Weed (*P. dendroides*) is only recorded as shell-boring in Danish waters. In other areas it also occurs epi- and endophytically in larger algae.

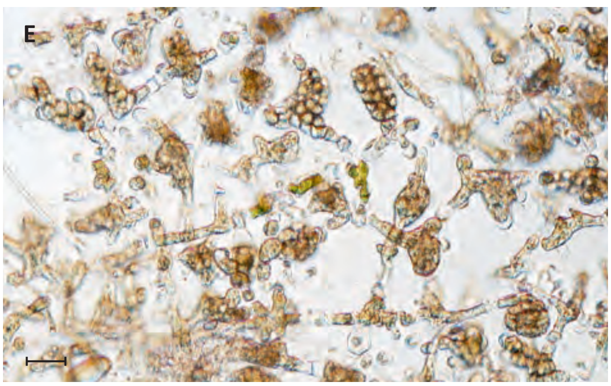
**Resembles:** Occasionally similar to Green Shell Borer (*Eugomontia sacculata*) when hairs are absent. The two species are distinct from each other by the shape of the plastids and number of pyrenoids, plate-shaped with 1-4 pyrenoids in Green Shell Borer (*Eugomontia sacculata*).

**References:** Chappell et al. (1990), Correa et al. (1988), Gunnarsson & Nielsen (2016), Kylin (1935), Nielsen (1972), Nielsen in Brodie et al. (2007), O'Kelly et al. (2004c).


A: *Phaeophila dendroides.* Branched filaments with upright phaeophila-hairs (arrow). Scale 20 µm. A-E: In calcified tube of *Spirorbis spirobis* on Bladder Wrack (*Fucus vesiculosus*). Decalcified in 2 % acetic acid. Beach north of Vesterø Havn, Læsø, 0.2 m, 2.9.2017.


B: *Phaeophila dendroides.* Vegetative cells with protrusions towards the surface of the calcified tube, twisted phaeophila-hairs. Scale 10 µm.






C: *Phaeophila dendroides*. Scattered and opposite (arrow) branches. Scale 10 µm.

D: *Phaeophila dendroides*. Twisted phaeophila-hair in the middle of the opposite branching in fig. C. Scale 10 µm.

E: *Phaeophila dendroides*. Irregular sporangia. Scale 20 µm.

## Family: Ulvaceae

### *Ochlochaete hystrix*

**Thwaites ex Harvey**

Stiff Hair Green Weed

**Appearance:** Microscopic filaments or pseudoparenchyma.

**Structure:** Uniseriate filaments, mutually free or confluent to disc-shaped circular or clustered pseudoparenchyma. Free filaments have scattered branches, and consist of cylindrical cells, c. 5 µm in width and 3-7 times as long as wide. Cells in disc-shaped or irregularly clustered thalli are rounded to ovoid, 7.5-12 µm in width. Vegetative cells contain a parietal lobed plastid with 1 (-3) pyrenoids. Colourless, coarse straight hairs arise from walls of vegetative cells (ochlochaete-hair), and are very characteristic when they arise from the narrow end of ovoid cells.

**Reproduction:** Vegetative reproduction by swarmers with 2 or 4 flagella and probably both kinds may function as zoospores. Sporangia develop from vegetative cells, which keep the same shape and size when ovoid. In other cases, the sporangia become slightly larger than the vegetative cells and develop a relatively long neck or exit tube. Sporangia contain many swarmers at maturity.

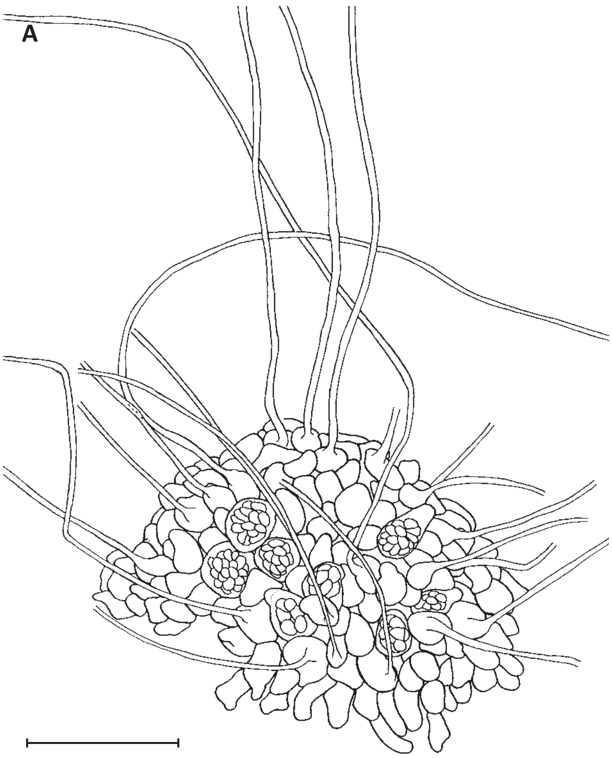
**Seasonal variation:** Collected in March-November.

**Habitat:** Epiphytic on various algae and sea grasses and grows on mollusc shells and stone which may be soft to touch when many hairs are present, 0.5-13 m depth.

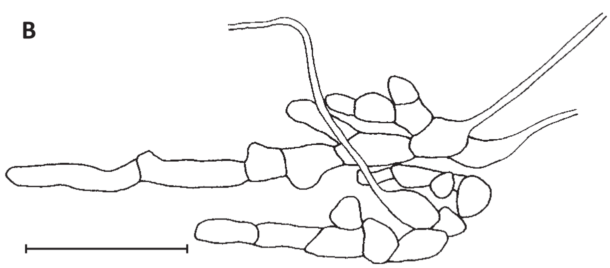
**Resembles:** Hairs may appear similar to bolbocoleon-hairs. The number of pyrenoids per cell is distinctive, Green Onion Hair Weed (*Bolbocoleon piliferum*) has many pyrenoids in vegetative cells, whereas Stiff Hair Green Weed (*O. hystrix*) has 1 (-3) pyrenoids per cell.

**Comment:** Probably more frequent in brackish water than in water with a higher salinity.

**References:** Nielsen (1978), Nielsen in Brodie et al. (2007), O'Kelly et al. (2004c), Wærn (1952, *Ochlochaete ferox*).

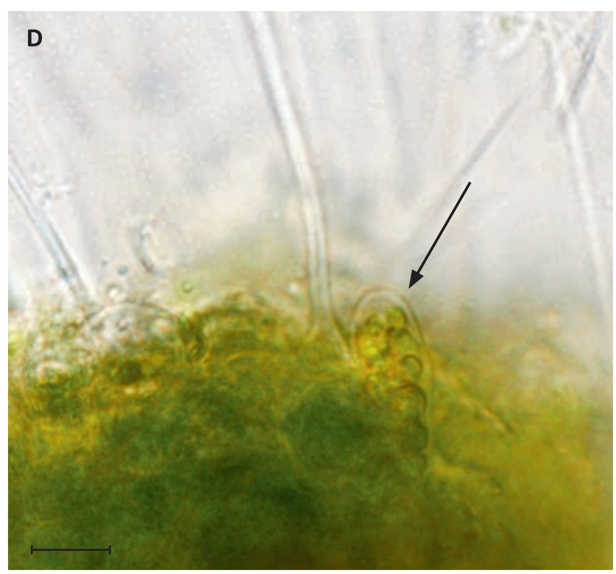



A: *Ochlochaete hystrix*. Disc-shaped alga with ochlochaete-hairs and ovoid sporangia. Scale 50 µm. A-B: On empty bivalve shell with other small green algae, Ajstrup, Mariager Fjord, 0.5 m, 29.9.1979.




B: *Ochlochaete hystrix*. Branches of cylindrical cells and ochlochaete-hairs in ovoid cells. Scale 50 µm.


C: *Ochlochaete hystrix*. Rounded cells with ochlochaete-hairs. Vegetative cell with one pyrenoid (arrow).
Scale 10 µm. C-D: On bivalve shell. Sydstranden, Dragør, 0.5 m, 13.8.2017.




D: *Ochlochaete hystrix*. Ochlochaete-hairs and sporangium (arrow). Scale 10 µm.

## *Percursaria percursa*

**(C.Agardh) Rosenvinge**

Running Thread Weed or Twin Thread Weed

**Appearance:** Thin, light-green unbranched threads, occur as entangled masses.

**Structure:** Filamentous alga of quadrangular cells in two regular rows, with pairwise cells. Thallus is thus a narrow monostromatic parenchyma, 25-30 µm in width. Diffuse growth, cells continue to grow next to each other in pairs and the frond appears as a uniseriate cell row when seen from the narrow side. Thallus not attached to the substratum. Vegetative cells, 1-2.5 times as long as wide, each contains a parietal plate-shaped plastid with 1-3 pyrenoids. The plastid only fills approximately half of the cell length, so cells appear pale.

**Reproduction:** Sporangia develop from vegetative cells and contain many swarmers. At maturity sporangia develop a small exit-papilla. Kornmann (1956) studied the alga from Sild in culture and observed that swarmers in contact with a solid substratum germinated and developed into small discs from which the upright parenchyma arose.

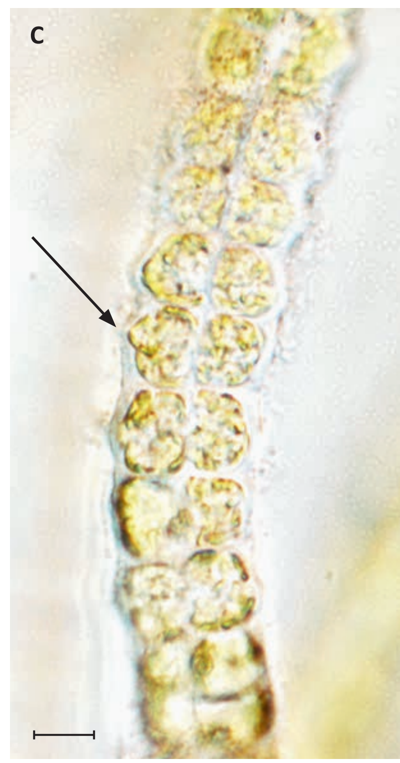
**Seasonal variation:** Collected in May-October; sporangia recorded in June.

**Habitat:** Light-green cover on soil in salt marshes, commonly together with Rooting Green Thread Weed (*Rhizoclonium riparium*), or large masses of narrow threads in shallow water at sheltered sandy beaches, that become dry at low water.

**References:** Kornmann (1956), Maggs & Kelly in Brodie et al. (2007), Steinhagen et al. (2019b).


A: *Percursaria percursa.* Narrow threads spread on herbarium paper. Dammen north of the jetty, Nordre Rønner, Læsø, 0.2 m, 8.8.2005. Scale 2 cm.


B: *Percursaria percursa.* Parenchyma of paired cells in two rows, each cell contains a narrow parietal plastid and 1-3 pyrenoids. Scale 10 µm. B-C: Sheltered area, beach north of Vesterø Havn, Læsø, 23.6.2013.




C: *Percursaria percursa.* Sporangia with small exit-papilla (arrow), many swarmers, eyespots visible as dark points. Scale 10 µm.

## *Ruthnielsenia tenuis*

**(Kylin) C.J.O'Kelly, B.Wysor & W.K.Bellows**

Ruth's Weed

**Appearance:** Microscopic, branched filaments. Growing into calcified material.

**Structure:** Uniseriate filaments with scattered branches, cells cylindrical to irregularly rounded. Cylindrical cells, 3-7.5 µm in width and 5-10 times as long as wide. Vegetative cells each contains a parietal plastid with 1-3 pyrenoids. Tiny colourless hairs arise from vegetative cells.

**Reproduction:** Vegetative reproduction by zoospores. Sporangia develop from rounded cells and develop a conical top with a small exit-papilla. Zoospores germinate into germlings of narrow cylindrical cells that grow into filamentous thalli.

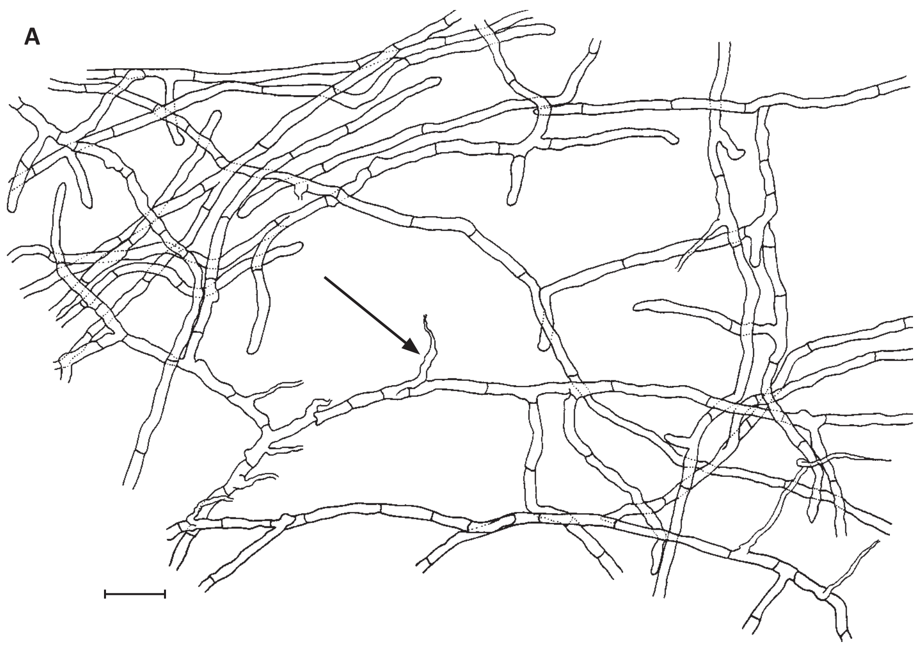
**Seasonal variation:** All year, collected in May-July and September.

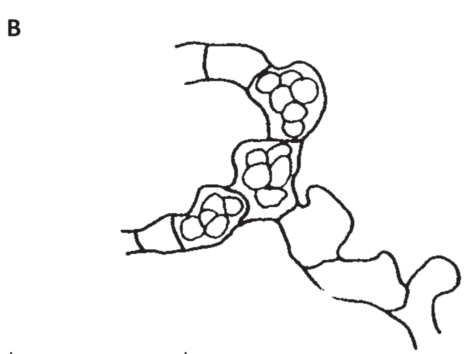
**Habitat:** In empty bivalve shells, 0.2-8 m depth.

**Resembles:** *Ulvella testarum* (Kylin) R.Nielsen, C.J.O'Kelly & B.Wysor looks similar but without hairs, and young few celled thalli consist of relatively short wide cells, whereas young thalli in *R. tenuis* consist of relatively narrow cylindrical cells. *Ulvella testarum* is described from the Swedish west coast but not recorded in Danish waters.

**References:** Kylin (1935, *Entocladia tenuis*), Nielsen (1972, *Phaeophila tenuis*), Nielsen in Brodie et al. (2007), O'Kelly et al. (2004c).

A: *Ruthnielsenia tenuis.* Filaments with scattered branches and upright hairs (arrow). Scale 25 µm. A-B: In empty bivalve shell, decalcified in 2 % acetic acid and mounted in glycerol. Ajstrup, Mariager Fjord, 29.9.1978.




B: *Ruthnielsenia tenuis.* Sporangia. Scale 25 µm.

## *Ulva*

Gut Weeds, Sea Lettuces

**Appearance:** Thallus, tubular with or without branches, or a flat membranous rounded or elongate blade. Tubular thalli are more or less compressed or almost flat, but at least with a tubular stipe. Blades regular or split into rounded lobes.

**Structure:** Parenchymatous thalli with diffuse growth. The tubular thalli in the Gut Weeds (*Ulva* spp.) have cavities surrounded by a monostromatic parenchyma, becoming distromatic in compressed area, but the two cell-layers can be separated. In the Sea Lettuces (*Ulva* spp.) the tubular part typically becomes compressed and the flat distromatic blade develops, with the two cell layers densely connected. However, morphology can vary considerably within species.

Cells are rounded, irregularly angular or cylindrical, appearing rectangular in surface view. Cells irregularly placed or in longitudinal and/or transverse rows. Vegetative cells each contains a parietal plate-shaped plastid, with regular, lobed or dentate margin, with one or several pyrenoids. The plastid fills the whole cell in some species but only part of the cell in others. It occurs in the upper part of the cell as a small cap (cap-shaped plastid) in a few of the species. The plastid moves around within the cell according to the direction of light and may be in one side or fill the whole cell. Young individuals attach by creeping filaments with scattered branches, later also by rhizoids from cells in the lower part of the frond. Creeping filaments may be confluent to an attachment disc.

**Reproduction:** Both sexual and vegetative reproduction with isomorphic generations. Sporangia develop in the upper part of the frond from vegetative cells and keep the same shape and size as in the vegetative condition. Swarmers are drop-shaped with a plate-shaped plastid, one pyrenoid and a red eyespot. They have 2 or 4 equally long flagella in the pointed front end. Gametes have 2 flagella, whereas zoospores have 2 or 4 flagella. Fertile part of thallus becomes dark green, yellow green to orange-yellow because the red eyespots of the many swarmers within the sporangia more or less dominate the colour. A basal cell and a uniseriate filament form during the germination process, and the filament becomes tubular by continued growth. The basal cell divides and develops into the uniseriate filaments which attach the thallus to the substratum.

**Seasonal variation:** Species of Gut Weeds, Sea Lettuces (*Ulva* spp.) present all year, well-developed in summer.

**Habitat:** On stone and epiphytic. In wave-exposed localities there is a small carpet of Squashed Flat Gutweed (*Blidingia minima*) in the wave-beaten zone, tubular Gut Weeds species (*Ulva* spp.) in the littoral and below this Windowed Sea Lettuce (*U. fenestrata*) occurs. This species does not tolerate desiccation and in most Danish localities Windowed Sea Lettuce (*U. fenestrata*) is sublittoral but may occur higher up in the littoral on very exposed shores.

**Resembles:** Squashed Flat Gutweed (*B. minima*) is distinct from species of Gut Weeds (*Ulva* spp.) by the much smaller cells and the plastid, which fills the cell, and one centrally placed pyrenoid.

**Comment:** Tubular species were previously referred to *Enteromorpha* and species of blades to *Ulva*. Molecular analysis has shown that each of these two genera is not monophyletic, so today they are in one genus under the oldest name (*Ulva*). We have chosen to keep the traditional popular names Gut Weeds and Sea Lettuce.

Petersen (1939) undertook comprehensive studies of Gut Weeds (as *Enteromorpha* spp.) in Danish waters. For identification he used the outer shape, size and branching pattern, shape of cells and their arrangement. His studies resulted in the material being grouped into many subspecies. Unfortunately, Petersen (1939) did not mention the shape of plastid and number of pyrenoids, and modern methods were not available, Petersen's work is therefore a very preliminary analyses of Gut Weeds (*Ulva* spp.) and their distribution in Danish waters.

Gut Weed (*U. intestinalis*) and Thread or Tape Weed (*U. compressa*) were studied and compared in culture by Larsen (1981), these studies are the only ones using modern methods in studies of *Ulva* from Danish waters. In other European areas, Bliding (1963, 1968) and Koeman & Hoek (1980, 1982a, b, 1984) made very detailed investigations including culture studies. Later, molecular studies confirmed most of their species concepts and in addition revealed new species (Hayden & Waaland (2002), Hayden et al. (2003), Kirkendale et al. (2013) Kraft et al. (2010).

The collection of *Ulva* spp. in the algal herbarium, Natural History Museum of Denmark has not been reviewed in recent years, and collections from recent years are not very comprehensive. It is expected that genetic investigations of species of Gut Weeds and Sea Lettuces (*Ulva* spp.) in Danish waters will change the understanding of the individual species and probably increase the number of species recorded compared to those listed in this book whose identification is entirely based on morphological features. As with the studies of this group along the German coasts of the North and Baltic Seas (Steinhagen et al., 2019a, b), there are many uncertainties in respect to species identification. The maps for species distribution in this group therefore need revision.

**References:** Bliding (1963, 1968), Hayden & Waaland (2002), Hayden et al. (2003), Kirkendale et al. (2013), Koeman (1985), Koeman & Hoek (1980, 1982a, b, 1984), Kraft et al. (2010), Larsen (1981, 1988), Maggs et al. in Brodie et al. (2007), Mares et al. (2011), Petersen (1939), Steinhagen et al. (2019a, b).

**Identification key to species of *Ulva***

| | | |
|---|---|---|
| 1a. | Tubular, filamentous or membranous blade with hollow stipe and hollow edge of the blade | 2 |
| 1b. | Membranous distromatic blade, with the two cell layers densely connected | 11 |
| 2a. | Rounded cells with one pyrenoid and cap-shaped plastid | 3 |
| 2b. | Cylindrical or irregularly angular cells, one or several pyrenoids, parietal plate-shaped plastid | 5 |
| 3a. | Unbranched (may have branches in brackish water localities) with irregularly placed cells | 4 |
| 3b. | Branched flat frond, minor area with cells in rows | *U. compressa* |
| 4a. | Tubular, often swollen and ruffled. Cells, 10-16 µm in width | *U. intestinalis* |
| 4b. | Narrow, ribbon shaped. Cells, 7-12 µm in width | *U. intestinaloides* |
| 5a. | Large angular cells, 14-25 (-40-50) µm in width, 1-5 pyrenoids | 6 |
| 5b. | Cylindrical cells, 1-3 pyrenoids | 7 |
| 6a. | Branched tubes or narrow ribbon-shaped thallus. Cells in longitudinal rows. Plastids of sister-cells, after cell divisions are typically along opposite walls | *U. clathrata* |
| 6b. | Delicate bush-like thallus reminiscent of *Cladophora*, cells in longitudinal and transverse rows, apical branches uniseriate | *U. paradoxa* |

| | | |
|---|---|---|
| 7a. | Unbranched thallus. Cells in regular longitudinal and transverse rows, one pyrenoid per cell | 8 |
| 7b. | Unbranched or branched thallus. Cells in irregular longitudinal rows and short transverse rows | 10 |
| 8a. | Tangled thin, unattached threads, in sheltered localities with sandy bottom | *U. torta* |
| 8b. | Upright fronds | 9 |
| 9a. | Tubular or ribbon-shaped fronds, lower part narrow and twisted as a spiral | *U. simplex* |
| 9b. | Flat membranous blade or ribbon-shaped, with hollow stipe and margin. Fronds may be elongate and wavy as a frill | *U. linza* |
| 10a. | Cells rectangular in surface view, most cells twice as long as wide, new cells cut off by oblique walls, cells contain (1-) 2 (-4) pyrenoids | *U. flexuosa* |
| 10b. | Many cells almost quadrangular in surface view, one large pyrenoid | *U. prolifera* |
| 11a. | Plastid fills whole cell in surface view or to one side. Lower part of blade with margin of small cells. Does not occur in brackish water | *U. fenestrata* |
| 11b. | Plastid cap-shaped, placed in upper part of cell. No margin of small cells, occurs in brackish water | *U. curvata* |

## *Ulva clathrata*

**(Roth) C.Agardh**

Spiky Tendrils

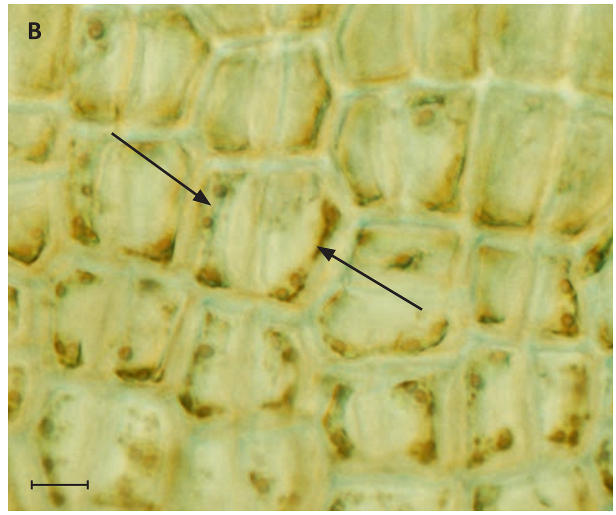
**Appearance:** Ribbon-shaped, tubular or approximately thread-like branched fronds with a distinct main axis, and often many small branches. Fronds, up to 30 cm long.

**Structure:** Cells in young algae rectangular in rows. Cells in older thalli irregularly angular, 14-25 µm in width. In lower part occasionally up to 40-50 µm in width (Bliding, 1963). Plastid, thin, plate-shaped occasionally with a lobed margin, typically placed in one side of the cell. After cell division, plastids are in opposite sides in the two daughter cells. Each cell contains (1-) 3-5 pyrenoids, a few in the youngest cells and several in older cells in the lower part of the frond.

**Seasonal variation:** Collected in June-October.

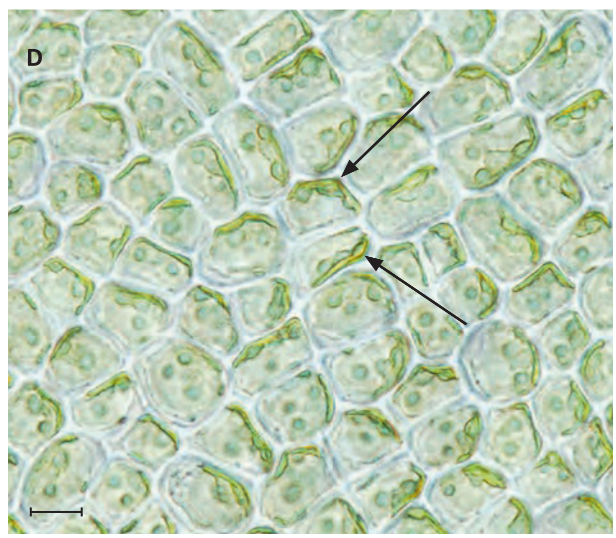
**Habitat:** On stone and epiphytic on Bladder Wrack (*Fucus vesiculosus*), 0.5-4 m depth.

**References:** Bliding (1963, *Enteromorpha clathrata*), Blomster et al. (1999, *E. muscoides*), Koeman & Hoek (1984, *E. clathrata*), Maggs et al. in Brodie et al. (2007).


A: *Ulva clathrata*. Well-developed frond with main axis and branches on all sides. Scale 2 cm. A, B: Just north of the jetty, Nordre Rønner, Læsø, shallow water, 8.8.2005.

B: *Ulva clathrata*. Series of vegetative cells, each with 3-4 pyrenoid. Sister-cells with plastids in opposite sides (arrows). Stained with potassium iodide. Scale 10 µm.

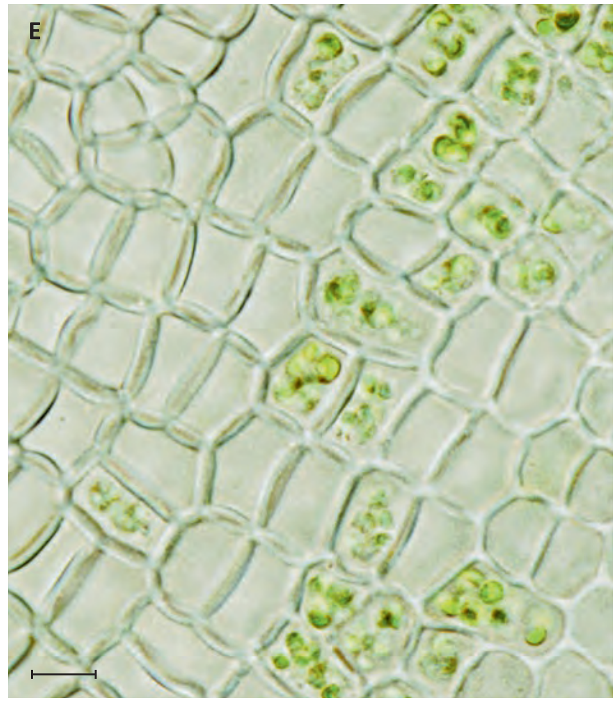

C: *Ulva clathrata*. Much branched frond with narrow branches. Scale 2 cm. C-E: Bløden Hale, Læsø, 0.2 m, 22.8.2016.

D: *Ulva clathrata*. Vegetative irregularly angular cells with 1-4 pyrenoids. Sister-cells with plastids in opposite sides (arrows). Scale 10 µm.

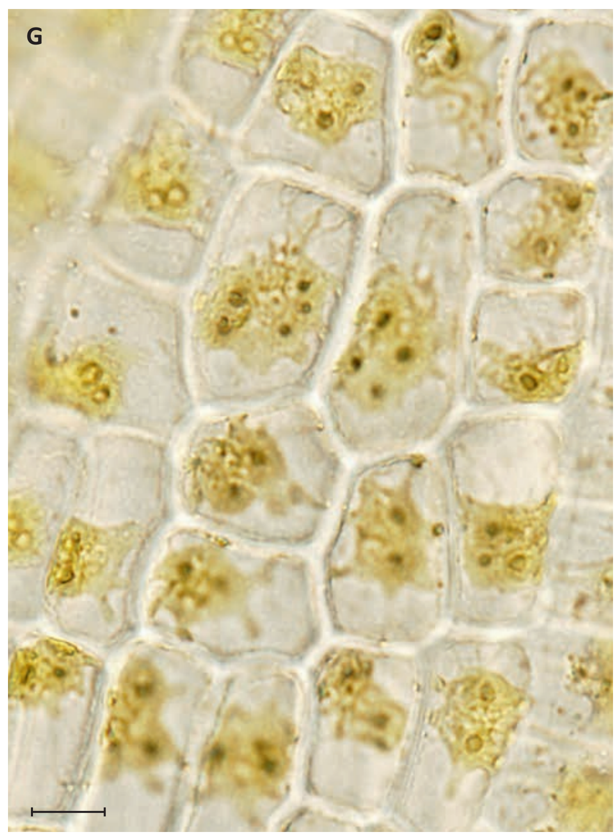
E: *Ulva clathrata.* Mature and empty sporangia, upper part of a branch. Scale 10 µm.

F: *Ulva clathrata.* Frond of narrow branches. Scale 1 cm.
F-G: Rønnerne, Frederikshavn, 0.2 m, 22.9.2017.

G: *Ulva clathrata.* Centrally placed plastids with 2-5 pyrenoids. Stained with potassium iodide. Scale 10 µm.







# *Ulva compressa*

**Linnaeus**

Thread or Tape Weed

**Appearance:** Frond with scattered branches or almost unbranched, typically short branches at the lower part of main axis. Branches are compressed (flat) and increasing in width towards the apex.

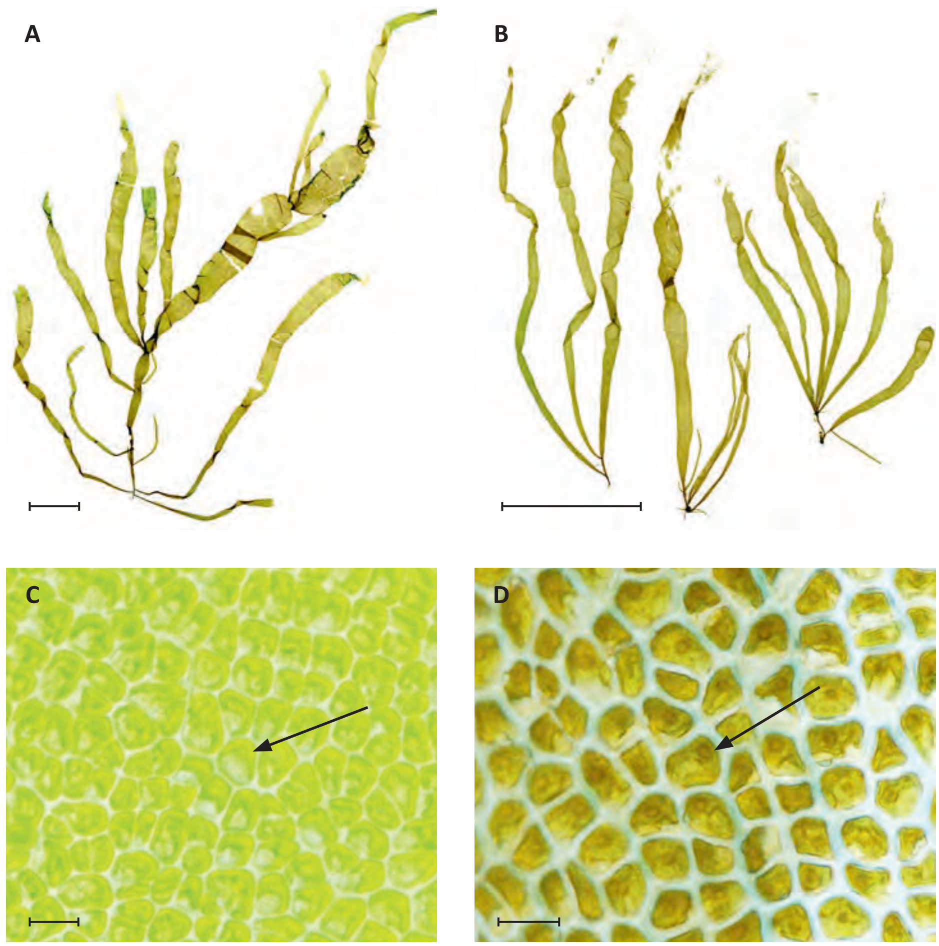
**Structure:** Plastids are in the upper part of cells (cap-shaped), with one pyrenoid. Cells are rounded and irregularly placed or form circles around a central cell, 12-16 (-30) µm in width. In small areas, the cells may form rows, such cells being rectangular with rounded corners, 7.5-14 µm in width and 14.3-15.3 µm in height.

**Seasonal variation:** Collected in January, March-November.

**Habitat:** On stone and boulders in shallow water, 0.5-4 m depth. Resistant to wave exposure. Does not grow in brackish water with salinity < 9 according to Koeman & Hoek (1982a).

**Resembles:** Gut Weed (*U. intestinalis*) also has cap-shaped plastids with one pyrenoid, but is typically hollow and unbranched, but may have branches in localities with brackish water or changing salinity. Frond of Tape Weed (*U. compressa*) typically flat and branched and does not grow in brackish water with salinity < 9. The two species may be separated by the irregularly placed cells in Gut Weed (*U. intestinalis*) as opposed to small areas with cell-rows in Tape Weed (*U. compressa*).

**References:** Bliding (1963, *Enteromorpha compressa*), Blomster et al. (1998, *E. compressa*), Koeman & Hoek (1982a, *E. compressa*), Larsen (1981, *E. compressa*), Maggs et al. in Brodie et al. (2007), Steinhagen et al. (2019a, b).




A: *Ulva compressa*. Scattered branches become wider towards the apex. South-eastern shore, Nordre Rønner, Læsø, 0.2 m, 15.8.2005. Scale 2 cm.

B: *Ulva compressa*. Only a few branches from lower part of main axis, upper part of branches with sporangia. Head of southern harbour jetty, exposed side, Hirsholm, 0.5 m, 4.7.1984. Scale 2 cm.

C, D: *Ulva compressa*. Cap-shaped plastid with one pyrenoid (arrows) per cell. Small area with cell-rows. Distal end of the old northern harbour jetty, Frederikshavn, 0.1 m, 28.3.2017. Scale 10 µm. D: Stained with potassium iodide.

# *Ulva curvata*

## (Kützing) De-Toni

**Appearance:** Light-green or yellow-green elongate or broad oval blades. A short hollow stipe occurs in the lower margin. Blades, up to 35 cm in length and 14 cm in width, are smooth and feels slightly thick and soft to touch.

**Structure:** Blades distromatic of two densely connected cell layers. Cells irregularly quadrangular, 10.5-20 µm in width and 14.5-20 µm in height, in surface view. Cells in small areas are in series which might be straight or curved. Each vegetative cell contains a cap-shaped plastid with a slightly lobed margin and 1 (-2) pyrenoids. Dark rhizoidal cells occur in the lower part of the blade. These cells have narrow rhizoids extending downwards between the two cell layers. No special small cells at the blade margin.

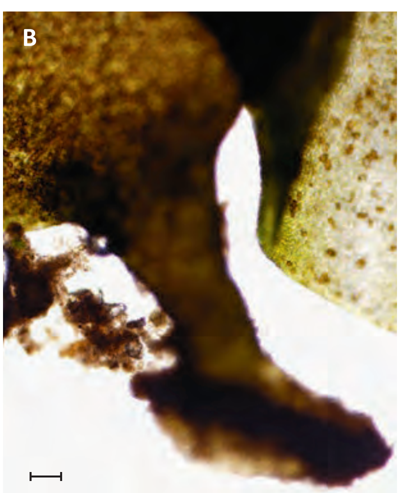
**Reproduction:** Sporangia with biflagellate swarmers, 6-6.5 µm in length and 3-4 µm in width, observed in the alga from the Sound. In alga from France sexual reproduction with small male and larger female gametes was reported by Bliding (1968).

**Seasonal variation:** Collected in August-September, sporangia recorded in September.

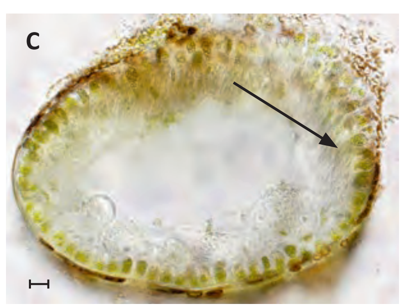
**Habitat:** On rhizomes of Eelgrass (*Zostera marina*), empty shells of Blue Mussel (*Mytilus edulis*) and small stones, 0-1 m depth. Sheltered beach with shallow water and bottom of sand and clay.

**Resembles:** Different from Windowed Sea Lettuce (*U. fenestrata*) by the cap-shaped plastid and not having

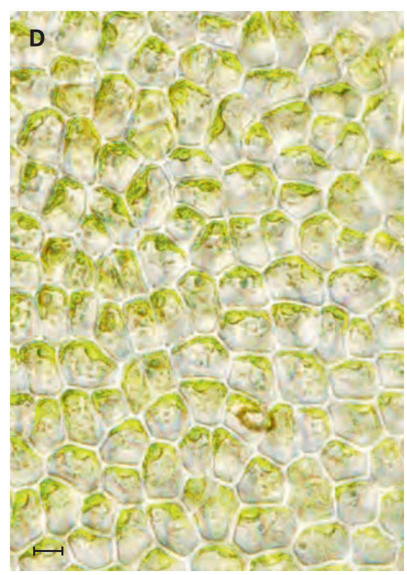

A: *Ulva curvata.* Light yellow-green blade, stipe displaced from the middle of the basal margin. Scale 2 cm. A-H: Sydstranden, Dragør, The Sound, 0.2 m, 13.8.2017.




B: *Ulva curvata.* Oblique stipe. Scale 100 µm.




C: *Ulva curvata.* Hollow stipe with downward-growing rhizoids (arrow), oblique transverse section. Scale 20 µm.

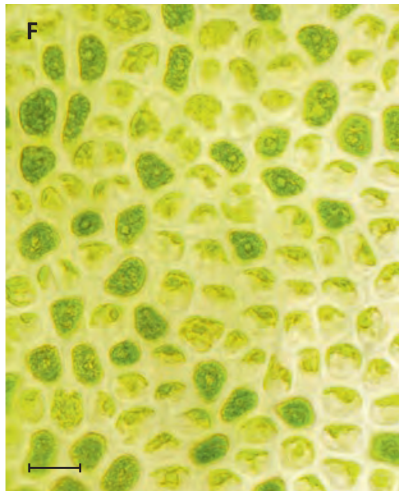



D: *Ulva curvata.* Vegetative cells. Cap-shaped plastid with one pyrenoid. Scale 10 µm.

a margin of small cells in lower part of blades. The plastid in Windowed Sea Lettuce (*U. fenestrata*) fills the whole cell wall or is lateral in the cell.

**References:** Bliding (1968), Hoek (1962), Koeman & Hoek (1980), Kornmann & Sahling (1977).


E: *Ulva curvata*. Distromatic blade, transverse section. Scale 10 µm.

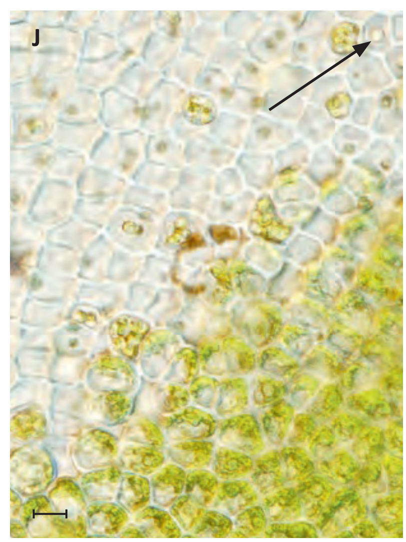



F: *Ulva curvata*. Dark green rhizoidal cells between ordinary vegetative cells. Scale 20 µm.


G: *Ulva curvata*. Long rhizoids in lower part of blade, oblique longitudinal section. Scale 20 µm.


H: *Ulva curvata*. Rhizoids between the two cell layers, lower part of blade, longitudinal section. Scale 20 µm.


I: *Ulva curvata*. Fertile blade with mature and empty sporangia in upper part. Scale 2 cm. I-J: Sydstranden, Dragør, The Sound, 0.2 m, 12.9.2017.




J: *Ulva curvata*. Vegetative cells, mature and empty sporangia with exit-pore (arrow). Scale 10 µm.

## *Ulva fenestrata*

**Postels & Ruprecht**

Windowed Sea Lettuce

**Appearance:** Membranous blades with consistency like a plastic bag. A basal disc supports an inconspicuous compact stipe. Shape of blades varies from rounded to elongate or almost triangular, and blades may be split into large lobes. Among the lager individuals in the algal herbarium, Natural History Museum of Denmark, is an elongate individual, 95 cm in height and 11 cm in width and another rounded individual, 35 cm in height and 23 cm in width, both with an attachment disc. Unattached drifting individuals can continue growth, and in sheltered nutrient rich localities become several square metres. Blades of both attached and drifting fronds often have holes made by grazing snails and small crustaceans.

**Structure:** Distromatic with the two cell layers closely connected. Cells are irregularly rounded, 10.3-15.7 µm in width. Vegetative cells contain a plate-shaped lobed plastid with one pyrenoid. The position of the plastid depends on light direction and intensity; the plastid may fill the whole cell, when seen in surface view or be displaced to one side in strong light. A margin of small cells occurs in the lower part of blades and forms a narrow "wing". Many rhizoidal cells turn the basal part of blades dark. These cells are approximately twice as large as other vegetative cells and contain several pyrenoids. The rhizoids grow in between the two cell layers of the frond and contribute to keeping them together. Rhizoids also make up the major part of the stipe.

**Reproduction:** Sexual reproduction with dioecious gametophytes and vegetative reproduction by zoospores. Swarmers are drop-shaped and have a red eyespot. The unequally large anisogametes have 2 flagella, whereas zoospores have 4 flagella. Sporangia form in the upper part of blades become a different colour from the rest of the frond. Female gametes and zoospores are the same size and develop in sporangia which give blades a dark olive-green margin. Sporangia with smaller male gametes make the margin orange yellow. Following fertilization, zygotes develop into a diploid blade in which zoospores form after meiosis. Zoospores germinate and develop into male and female gametophytes (Hoek et al., 1995).

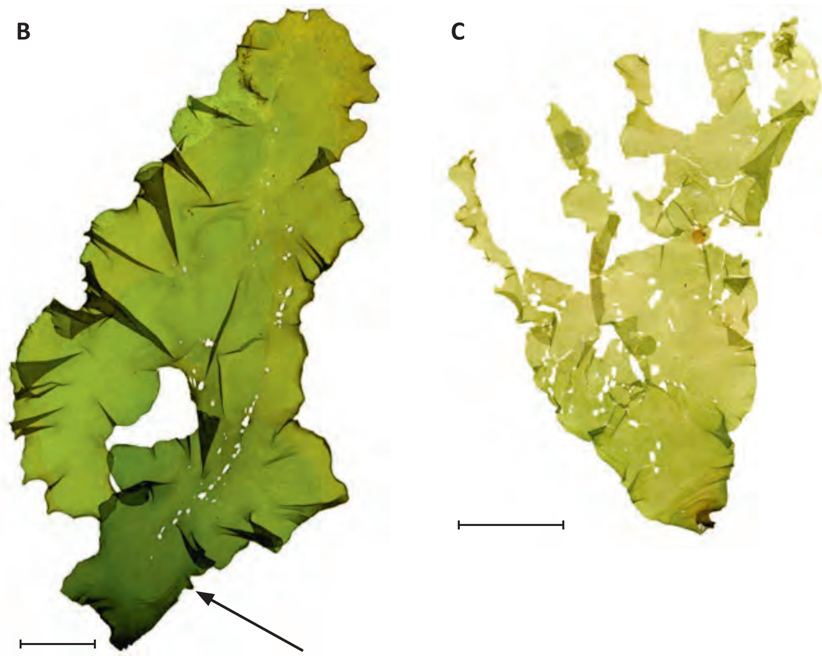
**Seasonal variation:** Present all year, well-developed in summer.

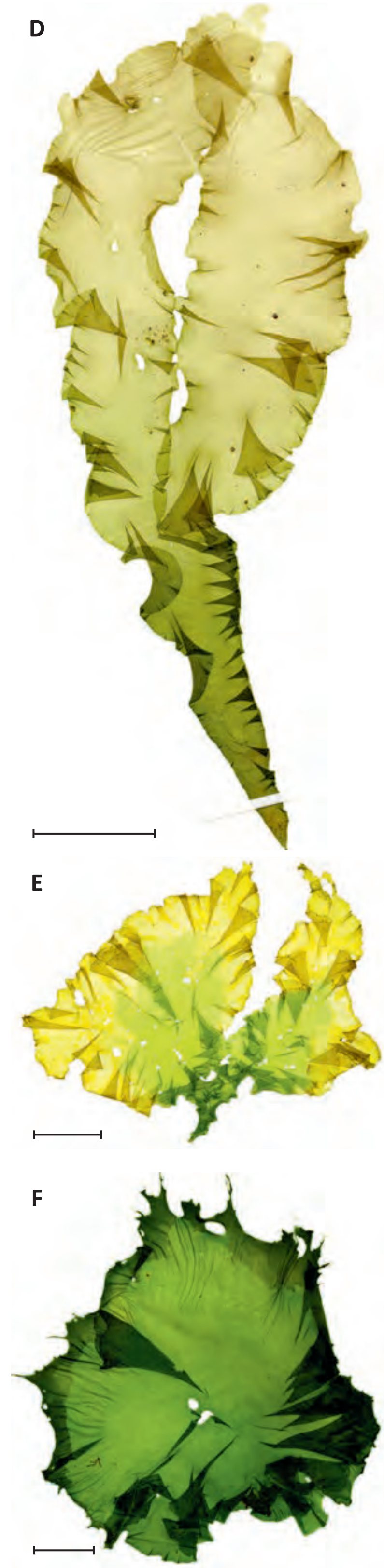
**Habitat:** On solid substrata and epiphytic, 0-8 m depth. Very tolerant of eutrophication and develops into masses of drifting algae in sheltered nutrient rich localities.

**Resembles:** Doubled Ribbon Weed (*U. linza*) might look similar but has a hollow stipe and is hollow along the margin of blades, whereas Windowed Sea Lettuce (*U. fenestrata*) is flat to the base and at the margin. The two cell layers of the blade are strongly connected in Windowed Sea Lettuce (*U. fenestrata*), whereas the compressed parts can be separated by preparations in Doubled Ribbon Weed (*U. linza*).

**Comment:** Copulation between small male gametes and larger female gametes, can easily be observed at home with a microscope. Fertile algae with orange coloured margins and others with olive-green margins can be collected and taken home in separate containers without water, but with a lid to avoid evaporation. At home, small fragments of orange-yellow and olive-green margins can be placed in a drop of seawater in the same slide-preparation, and it will be possible to observe the copulation by looking at the slide under


A: *Ulva fenestrata*. Broad blade with two lobes, base at arrow. Scale 2 cm. A-B: Hanklit, Thisted Bredning, 0.5 m, 19.8.2008.




B: *Ulva fenestrata*. Elongate blade with base at arrow. Scale 2 cm.

C: *Ulva fenestrata*. Triangular blade, split into several lobes, small holes made by grazing animals. Lighthouse, Fornæs, 0.5 m, 24.6.1980. Leg.: L. Mathiesen. Scale 2 cm.

D: *Ulva fenestrata*. Elongate, triangular blade split into 2 lobes. Gjerrild, 1 m, 12.7.1990. Leg.: K. Nielsen. Scale 2 cm.

E: *Ulva fenestrata*. Blade with two lobes and orange-yellow margin, male. Beach south of Vesterø Havn, Læsø, drift, 3.6.2017. Scale 2 cm.

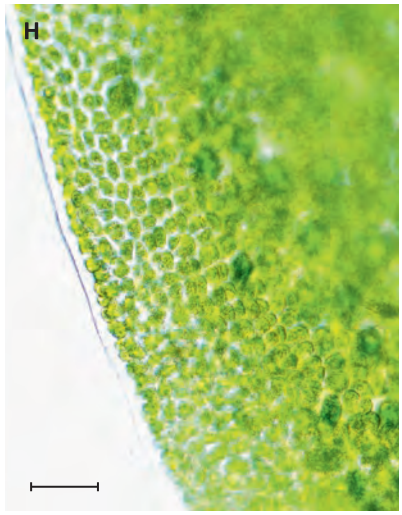
F: *Ulva fenestrata*. Almost circular blade with dark olive-green margin, sporangia with female gametes or zoospores. Vesterø Havn, Læsø, 0.5 m, 11.8.2015. Scale 2 cm.

the microscope. Remember that those blades with an olive-green margin might contain zoospores, so to obtain the wanted result, it is best to collect several specimens with an olive-green margin and repeat the copulation experiment if the first attempt is unsuccessful.

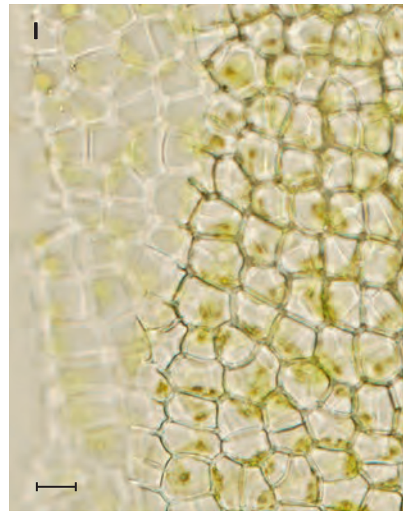
Previously, the name *U. lactuca* L. was in common use for this species in the North Atlantic. *Ulva fenestrata* was reinstated after molecular investigations of type material by Hughey et al. (2019).

**References:** Bliding (1968), Hoek et al. (1995), Hughey et al. (2019), Koeman (1985), Koeman & Hoek (1980), Loughnane et al. (2008), Maggs et al. in Brodie et al. (2007); all as *U. lactuca*.


G: *Ulva fenestrata*. Lower part of blade with dark green rhizoidal cells and narrow margin of small cells (arrow). Short compact stipe. Scale 100 µm. G-H: Northern harbour jetty, Vesterø Havn, Læsø, 0.5 m, 5.6.2017.

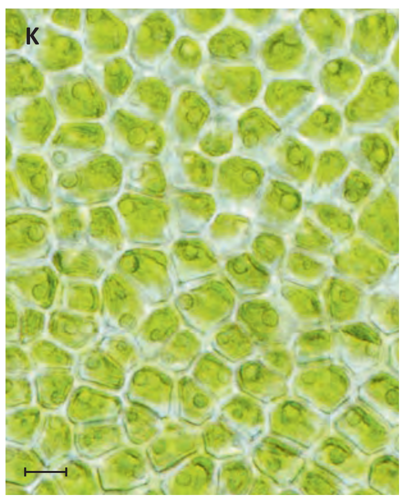



H: *Ulva fenestrata*. Lower part of blade with margin of small cells. Scale 10 µm.

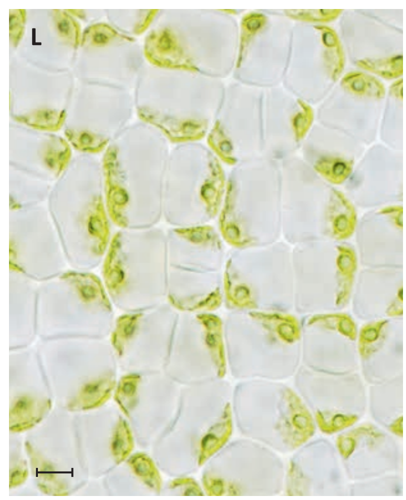



I: *Ulva fenestrata*. Blade torn apart so that the two cell layers became visible. Scale 20 µm. I, L: Sønder Nyland, Læsø, 0.5 m, 22.6.2013.


J: *Ulva fenestrata*. Distromatic blade, plastids along outer cell walls. Transverse section. Scale 20 µm. J-K: Mariager, Mariager Fjord, 0.5 m, 22.3.2014.




K: *Ulva fenestrata*. Parenchyma of rounded cells. Plastids fill the cells just below the outer cell wall. One large pyrenoid per cell. Scale 20 µm.




L: *Ulva fenestrata*. Cells with plastids displaced to side walls. Scale 10 µm.

# *Ulva flexuosa*

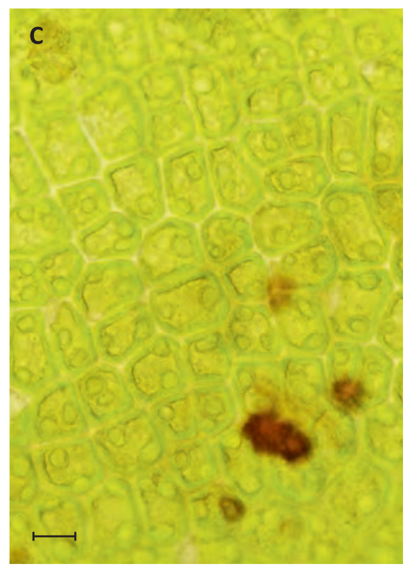
**Wulfen**

Flexuous Gut Weed

**Appearance:** Much branched alga, main axis with branches on all sides along the entire length. The branches are tubular, thread-like or ribbon-shaped.
**Structure:** Cells are typically rectangular, twice as long as wide and form longitudinal and short transverse rows. Cells in central part of fronds are 12.5-21 (-30) µm in width. New cells are cut off by oblique walls after cell divisions. Plastid typically in the middle of the cell along the lateral outer cell wall or slightly displaced towards the upper part, typically with two middle-sized pyrenoids, but may have 1-4 pyrenoids. The apical part of branches is uniseriate.
**Seasonal variation:** Collected in May-November.
**Habitat:** On stone in the middle of the littoral, 0-1 m depth.
**Resembles:** Spiky Tendrils (*U. clathrata*) may look similar as both species are much branched. A distinguishing character is the larger, irregularly angular cells in the older part of Spiky Tendrils (*U. clathrata*). Proliferous Gut Weed (*U. prolifera*) may also look similar but has rectangular cells with one large pyrenoid.
**References:** Bliding (1963, *Enteromorpha flexuosa),* Koeman & Hoek (1984, *E. flexuosa),* Maggs et al. in Brodie et al. (2007), Mares et al. (2011).

A: *Ulva flexuosa.* Main axis with branches on all sides along the whole length. Bay with sandy bottom, southwestern part of Deget, Frederikshavn, 0.2 m, 16.8.1977. Leg. & det.: J. Larsen. Scale 2 cm.

B: *Ulva flexuosa.* Quadrangular cells in rows. Scale 20 µm. B-C: Northern part of Teglværkshavnen, Copenhagen, 1 m, 27.11.2007.



C: *Ulva flexuosa.* Rectangular cells with oblique corners and 2 pyrenoids in several cells. Scale 10 µm.

# *Ulva intestinalis*

**Linnaeus**

Gut Weed

**Appearance:** Tubular unbranched fronds, often ruffled and irregularly swollen by air in the cavity. Gradual transition from the narrow stipe-looking lower part to the wider upper part. Fronds, up to 8 cm in width and 50 cm in height. Individuals with branches occur in brackish water according to Blomster et al. (1998).

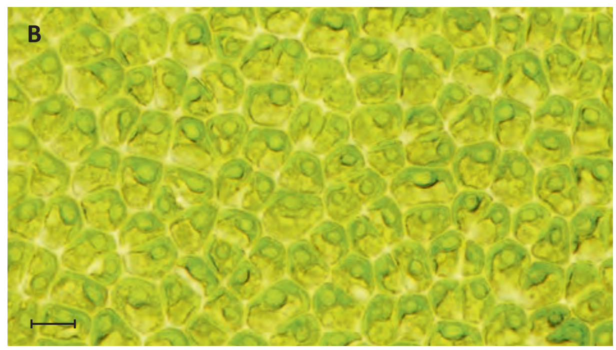
**Structure:** Cells are rounded and irregularly arranged, 10-16 μm in width. Each cell contains a cap-shaped plastid with one pyrenoid.

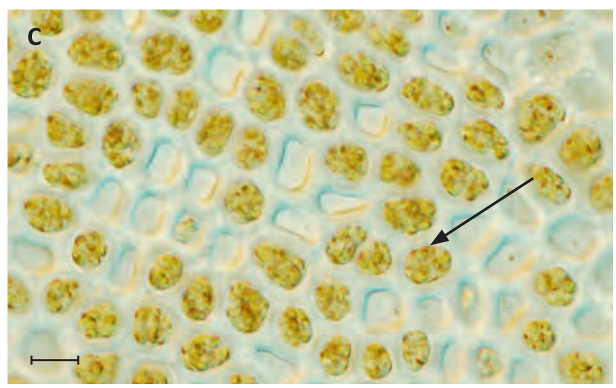
**Seasonal variation:** Present all year, well-developed in summer.

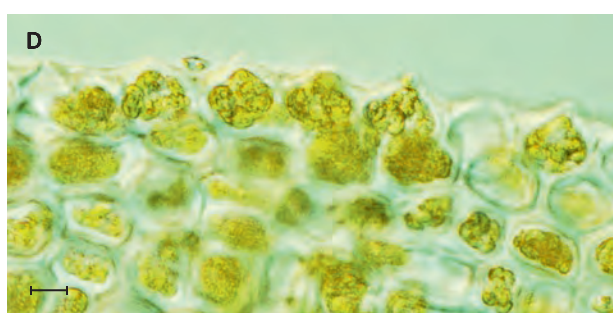
**Habitat:** On stone and epiphytic on Bladder Wrack (*Fucus vesiculosus*), 0.1-4 m depth. Unattached fronds develop into masses in shallow water at sheltered, nutrient rich localities.

**Resembles:** Thread or Tap Weed (*U. compressa*) may look similar, but has small areas where cells form series.

**References:** Bliding (1963, *Enteromorpha intestinalis*), Blomster et al. (1998, *E. intestinalis*), Koeman & Hoek (1982a, *E. intestinalis*), Maggs et al. in Brodie et al. (2007).


A: *Ulva intestinalis*. Unbranched, irregularly swollen and ruffled algae. South of the heating plant Østhavnen, Copenhagen, 21.9.2017. Scale 2 cm.

B: *Ulva intestinalis*. Rounded irregularly arranged cells, cap-shaped plastid with one big pyrenoid. Pramrenden, Langelinie, Copenhagen, 0.2 m, 20.9.2007. Scale 10 μm.

C: *Ulva intestinalis*. Mature and empty sporangia. Swarmers with red eyespots (arrow). Scale 10 μm. C-D: Margretheholms Havn, Copenhagen, 0.3 m, 18.7.2013.

D: *Ulva intestinalis*. Sporangia with small exit-papilla, seen in profile. Scale 10 μm.

## *Ulva intestinaloides*

**(Koeman & Hoek) Hayden, Blomster, Maggs, P.C.Silva, Stanhope & Waaland**

Strap Gut Weed

**Appearance:** Ribbon-shaped fronds, 0.1 cm in width and 10 cm in height.

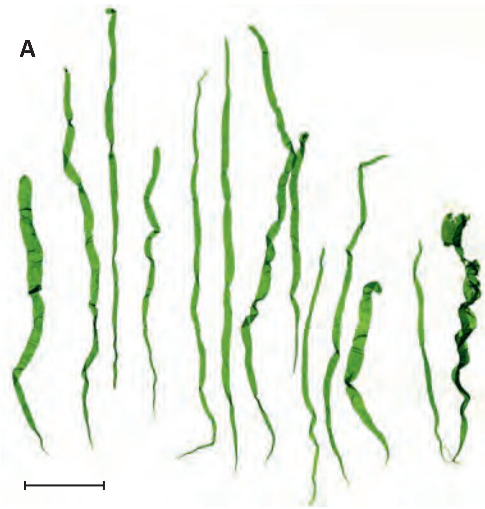
**Structure:** Small rounded cells irregularly arranged. Cells, just above the base, 8-12 µm in width and 7-12 µm in height; in middle of frond, 8-11.5 µm in width and 7-12 µm in height, and upper cells, 7-10 µm in width and 7-11.5 µm in height. Cap-shaped plastid with one pyrenoid.

**Seasonal variation:** Only a single collection from Danish waters, March 2017, with sporangia.

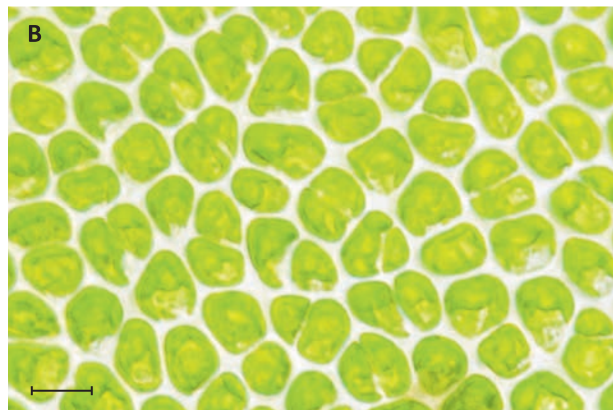
**Habitat:** On stone at outlet from a stream.

**Resembles:** Gut Weed (*U. intestinalis*) may look similar with the cap-shaped plastid, but tubular as opposed to the flat Strap Gut Weed (*U. intestinaloides*). Thread or Tap Weed (*U. compressa*) may also look similar, but typically branched and cells forming series in small areas.

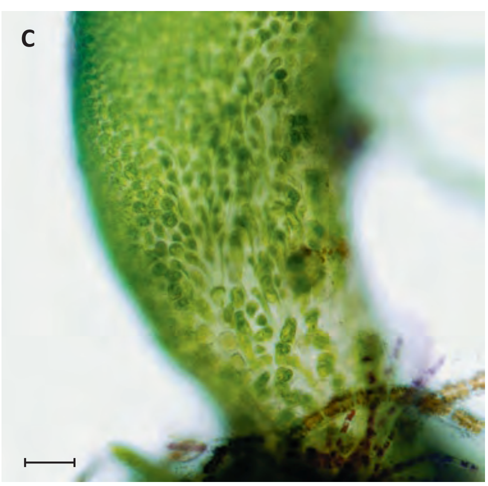
**References:** Koeman & Hoek (1982a, *Enteromorpha intestinaloides*), Maggs et al. in Brodie et al. (2007).



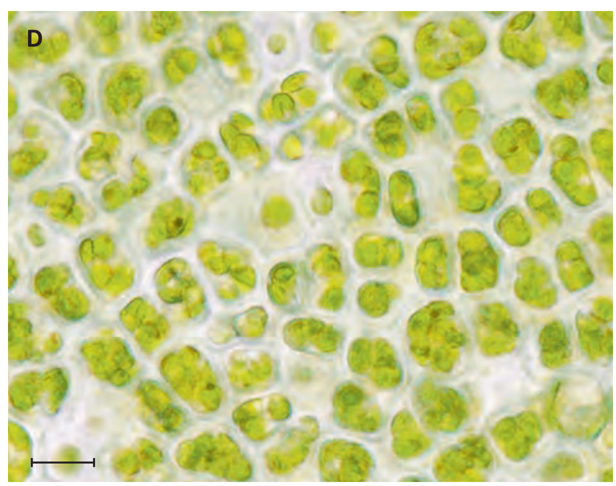

A: *Ulva intestinaloides.* Small, ribbon-shaped fronds. Scale 2 cm. A-D: Outlet from the stream, Studstrup, 3 m away from sea, 19.3.2017. Leg.: K.L. Krabbe.




B: *Ulva intestinaloides.* Vegetative cells, each with a cap-shaped plastid and one pyrenoid, just above the base of the frond. Scale 10 µm.




C: *Ulva intestinaloides.* Base with rhizoidal cells. Scale 50 µm.




D: *Ulva intestinaloides.* Mature and empty sporangia. Scale 10 µm.

# *Ulva linza*

**Linnaeus**

Doubled Ribbon Weed

**Appearance:** Flat, unbranched blade with a hollow stipe, which may have a gradual or distinct transition to the blade. Blades, up to 8 cm in width and 20 cm in height, occasionally appearing as a spirally twisted upright which may be up to 30 cm in height; or blades may be smaller and ribbon shaped. Blades are flat with a cavity at the margin.

**Structure:** Cells are cylindrical and form longitudinal and transverse rows. In surface view cells are quadrangular, 15 µm in width or rectangular, 14 µm in width and 21 µm in height. The parietal plastid fills the cell and contains 1 (-2) pyrenoids.

**Seasonal variation:** Present all year, collected in February-December, well-developed in summer.

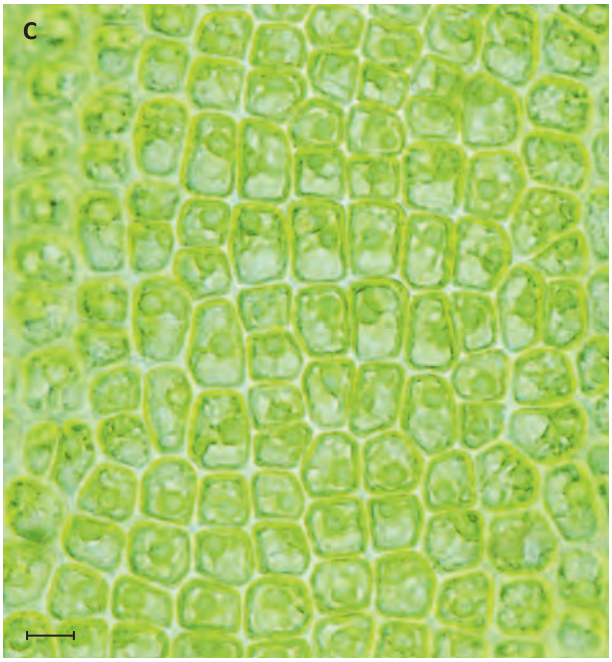
**Habitat:** On stone, common at 0-3 m depth and occasionally collected to 8 m depth.

**Comment:** The taxonomic status of *U. linza* and *U. prolifera* is still uncertain (Cui et al., 2018 and Hayden et al., 2003).

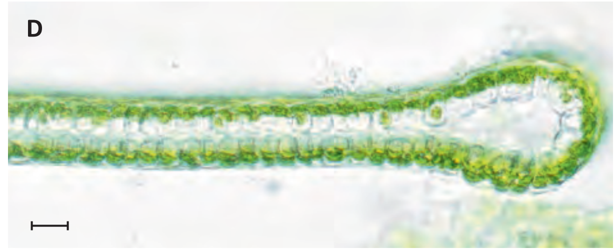
**References:** Bliding (1963, *Enteromorpha linza*), Koeman (1985 *E. linza*), Koeman & Hoek (1984, *E. linza*), Maggs et al. in Brodie et al. (2007).

A

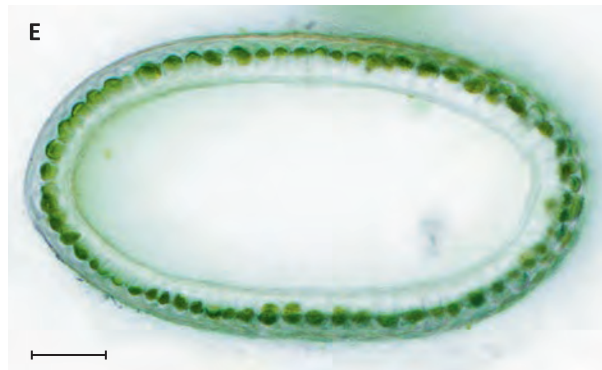
B



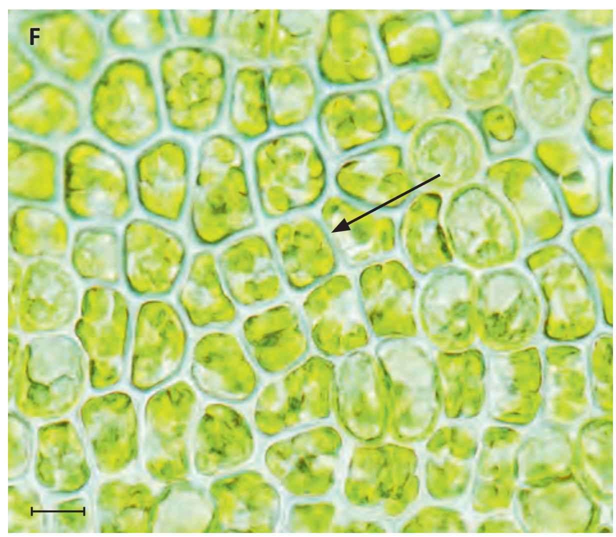

C: *Ulva linza*. Cells in longitudinal and transverse rows. Plastid fills the cell, one pyrenoid. Scale 10 µm. C, F: Basal part of northern harbour jetty, Østerby Havn, Læsø, 0.1 m, 1.4.2017.




D: *Ulva linza*. Margin of blade with cavity, transverse section. Scale 10 µm.




E: *Ulva linza*. Tubular stipe, transverse section. Scale 50 µm.




F: *Ulva linza*. Sporangia (arrow), upper part of blade. Scale 10 µm.

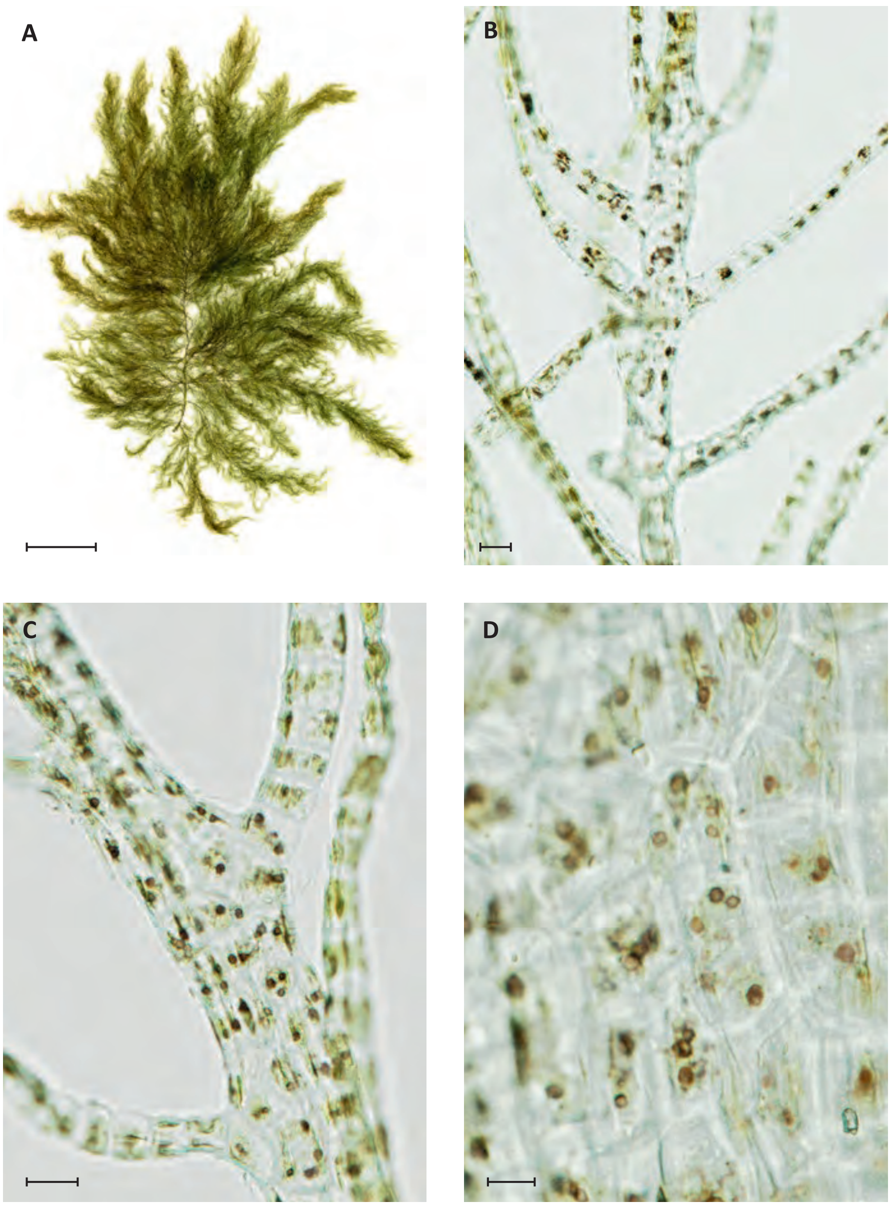
A: *Ulva linza*. Flat unbranched blade with a tubular stipe. Scale 2 cm. A, D-E: Old northern harbour jetty, Frederikshavn, 0.1 m, 28.3.2017.

B: *Ulva linza*. Shape a spirally twisted upright. Strandby, 11.6.1952. Leg.: T. Christensen. Scale 2 cm.

# *Ulva paradoxa*

## C.Agardh

**Appearance:** Delicate, bush-like alga with repeated branching, c. 15 cm in height. A distinct main axis and reminiscent of Green Branched Weeds (*Cladophora*).
**Structure:** Branching scattered, occasionally a few opposite branches. The distal part of branches is uniseriate. Cells in longitudinal and transverse rows are relatively large, 15-25 µm in width. Plate-shaped plastid with a dentate margin and 1-4 pyrenoids.
**Seasonal variation:** Collected in May-August.
**Habitat:** Recent collections on small stone and empty bivalve shells, in shallow water at sheltered localities with sandy bottom, 0.5-3 m depth. In older collections by dredge, recorded from 8 m depth at Læsø Trindel.
**References:** Bliding (1963, *Enteromorpha flexuosa* ssp. *paradoxa*), Mares et al. (2011, *U. flexuosa* ssp. *paradoxa*).




A: *Ulva paradoxa*. Delicate branched alga with distinct main axis. Rønnerne, Frederikshavn, 0.2 m, 11.7.1984. Scale 2 cm.

B: *Ulva paradoxa*. Main axis with uniseriate branches on all sides. Scale 20 µm. B-D: Kølpen, Hirsholmene, 3 m by dredge, 16.6.1997. Rehydrated herbarium material stained with potassium iodide.

C: *Ulva paradoxa*. Cells in rows. Scale 20 µm.

D: *Ulva paradoxa*. Cells with 1-4 pyrenoids. Scale 10 µm.

# *Ulva prolifera*

**O.F.Müller**

Proliferous Gut Weed

**Appearance:** Morphology variable, the thallus might be ribbon-shaped with sparse branches, c. 20 cm in height and 0.5 cm in width, or much branched with narrow branches, less than 1 mm in width, arising on all sides from all along the main axis.

**Structure:** Cells are quadrangular to rectangular in surface view, (6-) 9-13 µm in width and 9-18 µm in height, and form longitudinal and transverse rows. After cell division, the two equally large daughter cells typically occur in pairs. Plastid parietal or in the middle of the cell with one big centrally placed pyrenoid, or two pyrenoids just before cell division.

**Seasonal variation:** Collected in February-December.

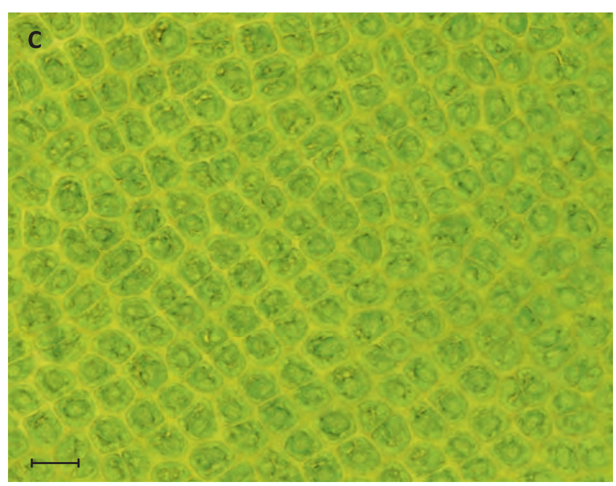
**Habitat:** In shallow water and a few collections recorded at 9 m depth.

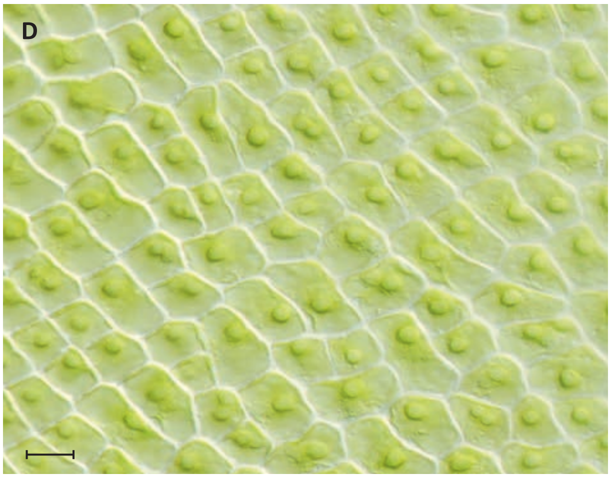
**Comment:** *Ulva procera* (K.Ahlner) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope & Waaland is considered a synonym of *U. prolifera* in agreement with Cui et al. (2018) and Leskinen & Pamilo (1997 as *Enteromorpha ahlneriana*).

**References:** Bliding (1963, *Enteromorpha prolifera*), Cui et al. (2018), Koeman & Hoek (1982b, *E. prolifera*), Maggs et al. in Brodie et al. (2007).

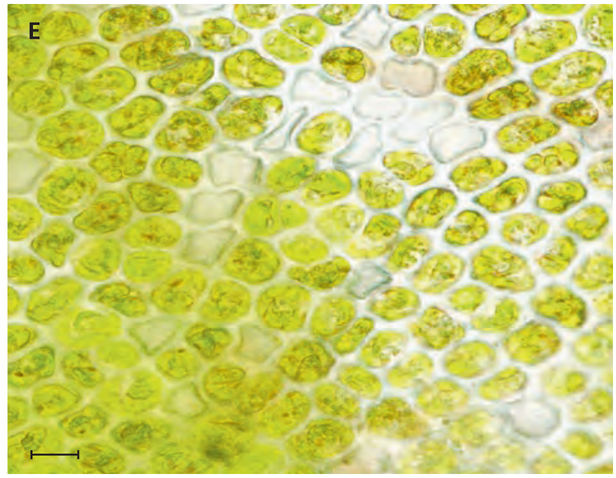


A: *Ulva prolifera.* Unbranched, ribbon-shaped individuals. Pramrenden, Langelinie, Copenhagen, 0.5 m, 24.4.1993. Scale 2 cm.
B: *Ulva prolifera.* Main axis with branches all along the length.
B, D: Quintus, Holmen, Copenhagen, 0.5 m, 21.9.2007. Scale 2 cm.
C: *Ulva prolifera.* Rows of quadrangular cells, each with one big pyrenoid. Scale 10 µm. C, E: Just north of Sluseholmen, Copenhagen, 0.5 m, 27.11.2007.






D: *Ulva prolifera*. Rows of rectangular cells, each with one large pyrenoid. Scale 10 µm.




E: *Ulva prolifera*. Mature and empty sporangia, upper part of frond. Scale 10 µm.

## *Ulva simplex*

**(K.L.Vinogradova) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope & Waaland**

**Appearance:** Unbranched tubular alga, c. 0.2 cm in width and 8 cm in height, gradually tapering towards the spirally twisted base.

**Structure:** Small to middle-sized cells in rows. Cells are rectangular in surface view, with rounded corners, 5-6.5 µm in width and 8.5-11.5 µm in height. Plastid in middle of cell with one pyrenoid.

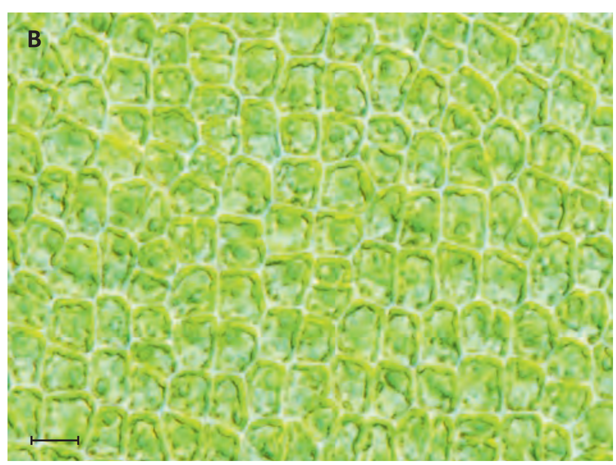
**Seasonal variation**: Collected in May and August-September.

**Habitat:** On small stones at sheltered localities with sandy bottom, 0.1-0.5 m depth.

**Comment:** This species is regarded as a synonym of *Ulva prolifera*. However, as the morphology of material referred to *U. simplex* in Danish waters is morphologically distinct, this species is retained here pending further investigations.

**References:** Bliding (1963, *Enteromorpha prolifera* Typus I), Cui et al. (2018), Koeman & Hoek (1982b, *E. simplex*).


A: *Ulva simplex*. Tubular algae with spirally twisted base. Nordre Rønner, Læsø, 0.5 m, 15.8.2005. Scale 2 cm.




B: *Ulva simplex*. Rows of cells, each with one big pyrenoid. Rønnerne, Frederikshavn, 0.2 m, 22.9.2017. Scale 10 µm.

# *Ulva torta*

**(Mertens) Trevisan**

Twisted Gut Weed

**Appearance:** Narrow entangled unbranched threads.
**Structure:** Threads, 25-50 µm in width (Bliding, 1963), consist of cylindrical cells in 3-12 longitudinal rows round a central cavity, 12-15 µm in width. Cells in surface view are rectangular, 5.5-8 µm in width and 8-10.5 µm in height. Parietal plastid along middle of outer cell wall with one pyrenoid.
**Seasonal variation:** Recorded in April and June.
**Habitat:** Unattached in shallow water at sheltered localities with sandy bottom.
**References:** Bliding (1963, *Enteromorpha torta*), Koeman & Hoek (1982b, *E. torta*), Maggs et al. in Brodie et al. (2007).


A: *Ulva torta*. Entangled threads. Scale 2 cm. A-B: Rønnerne, Frederikshavn, 0.1 m, 28.6.1997.

B: *Ulva torta*. Longitudinal rows of vegetative cells with one pyrenoid. Rehydrated herbarium material, stained with potassium iodide. Scale 10 µm.

## *Ulvaria splendens*

**(Ruprecht) K.L.Vinogradova**

Limp Lettuce

**Appearance:** Membranous green blades, turning dark-brown when decaying. They often occur as drift and grow up to 30 cm in length. Attached blades are smaller with a characteristic hollow stipe, 1-2 mm in height.

**Structure:** Monostromatic parenchyma with diffuse growth. Cells angular, 11.5-25 µm in width, with a parietal plate-shaped plastid and 1-7 pyrenoids. Marginal cells are relatively large with a thick outer wall.

**Reproduction:** Life history is known from culture studies of Bliding (1968). Sexual and vegetative reproduction by swarmers. Sporangia develop from vegetative cells and are the same shape and size as in the vegetative condition. Swarmers are released through a round pore in the cell wall at maturity. A short filament develops after the germination process and turns into a small tube by continued growth. The lower part becomes the stipe in the adult thallus. The upper part of the tube gets wider and becomes a small sac which splits and continues growth into the monostromatic blade.

**Seasonal variation:** Present all year, collected in January-December.

**Habitat:** On stone and other solid substrata in sheltered area, particularly in fiords, where Limp Lettuce (*Ulvaria splendens*) often occurs drift at shallow water. Collected by divers to 5 m depth and by dredge to 13 m depth. Apparently it has disappeared from the harbour of Frederikshavn, where collections in the algal herbarium, Natural History Museum of Denmark document its presence in 1927. There are no later collections, although many observations and collections were made in Frederikshavn.

**Resembles:** Differs from other membranous monostromatic blades, such as One-layered Sea Lettuce (*Gayralia oxysperma*) and Greville's Mattress Weed (*Monostroma grevillei*) by the dark-brown decaying spots or blades, the small tubular stipe and the large marginal cells.

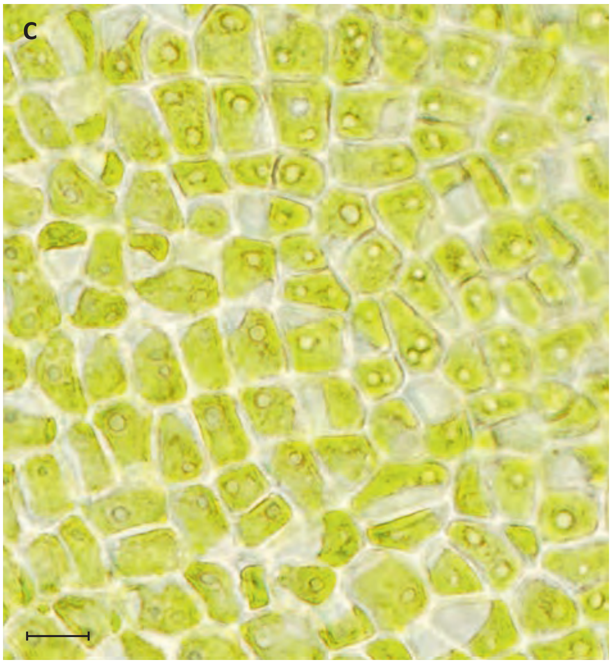
**References:** Bliding (1968, *U. obscura* var. *blyttii*), Wilkinson in Brodie et al. (2007, *U. fusca*).

A

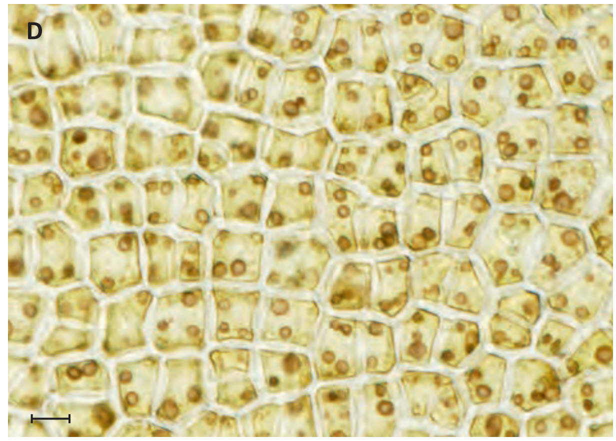
B

A: *Ulvaria splendens.* Drift alga, with decaying dark-brown spots. Ajstrup, Mariager Fjord, 0.5 m, 29.9.1979. Scale 2 cm.

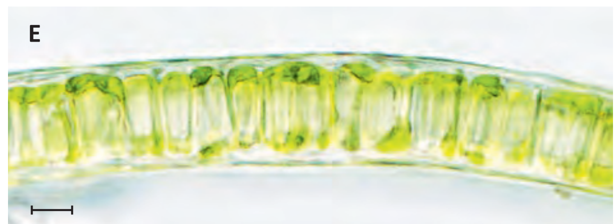
B: *Ulvaria splendens.* Small alga with stipe. Southern boat-harbour, Frederikshavn, 1.8.1922. Scale 2 cm.



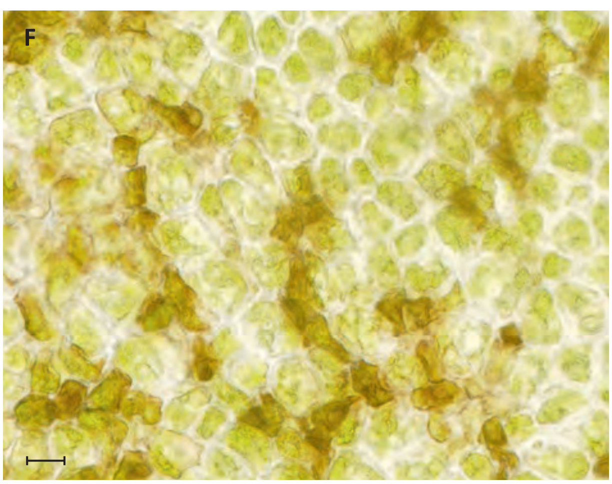
C: *Ulvaria splendens.* Parenchyma, young cells with 1-2 pyrenoids, stained with potassium iodide. Scale 10 µm. C, E-G: Mariager, Mariager Fjord, 0.2 m, 22.3.2014.



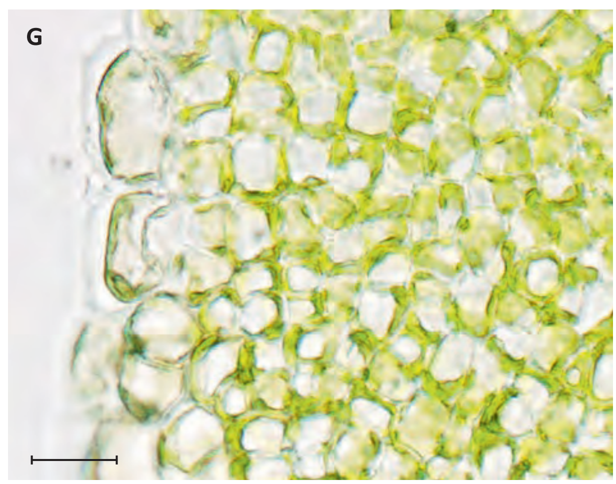
D: *Ulvaria splendens.* Older cells with 1-4 pyrenoids. Rehydrated herbarium material, stained with potassium iodide. Nordre Røse, The Sound, 13 m, 25.4.1934. Scale 10 µm.



E: *Ulvaria splendens.* Monostromatic parenchyma, transverse section. Scale 10 µm.



F: *Ulvaria splendens.* Parenchyma with fresh green and brownish decaying cells. Scale 10 µm.



G: *Ulvaria splendens.* Blade with large marginal cells. Scale 10 µm.

**Family: Ulvellaceae**

## *Epicladia*

Green Puzzles

Microscopic, uniseriate filaments, with scattered branches, confluent to pseudoparenchyma. No hairs. Vegetative reproduction by zoospores, which germinate and grow into alga similar to the parent generation.

**Identification key to species of *Epicladia***

| | | |
|---|---|---|
| 1a. | Endophytic in epidermal cells of *Zostera marina* | *E. perforans* |
| 1b. | Endozoic | 2 |
| 2a. | In chitin wall of *Flustra* or *Securiflustra* | *E. flustrae* |
| 2b. | In chitin wall of *Alcyonidium hirsutum* | *E. phillipsii* |

## *Epicladia flustrae*

**Reinke**

Flustra's Green Puzzle

**Appearance:** Microscopic, branched filaments, giving the host a green colour.

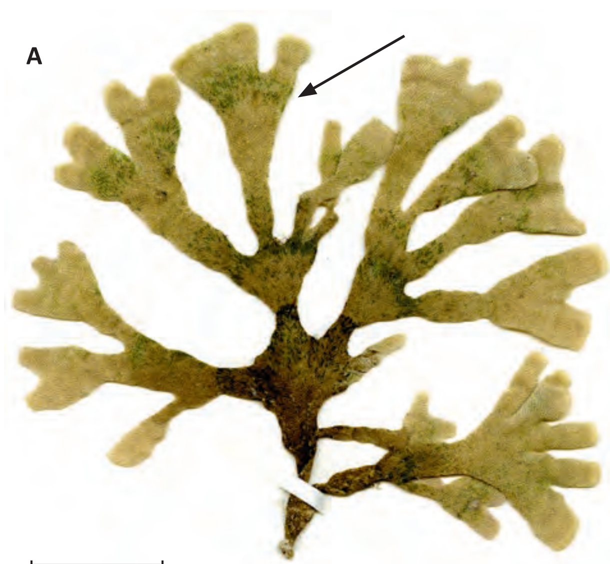
**Structure:** Uniseriate, filaments with scattered branches, confluent to a monostromatic pseudoparenchyma, with mutually free filaments at the margin. Peripheral cells are cylindrical, 3.5-5 µm in width and 2-4 times as long as wide. Central cells are rounded, 10-15 µm in diameter. Vegetative cells each contains a parietal plastid with one pyrenoid.

**Reproduction:** Vegetative reproduction by zoospores. Sporangia develop from central cells and are the same shape and size as in the vegetative condition. Zoospores with 4 flagella are released through an exit-pore, which may be on a small papilla.

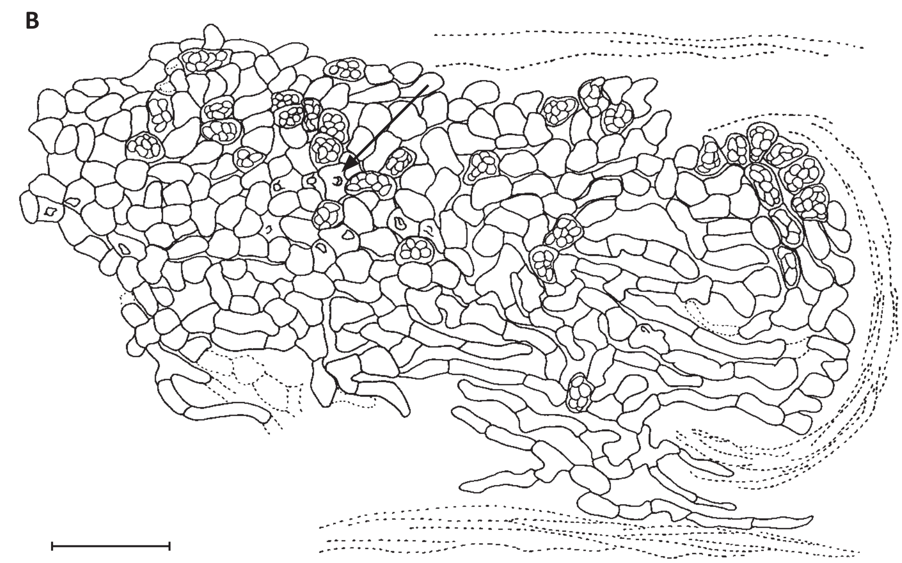
**Seasonal variation:** Present all year, collected in March-November.

**Habitat:** In chitin-walls of the bryozoan Horn Wrack (*Flustra foliacea*) and the bryozoan *Securiflustra securifrons*, 5-17 m depth.

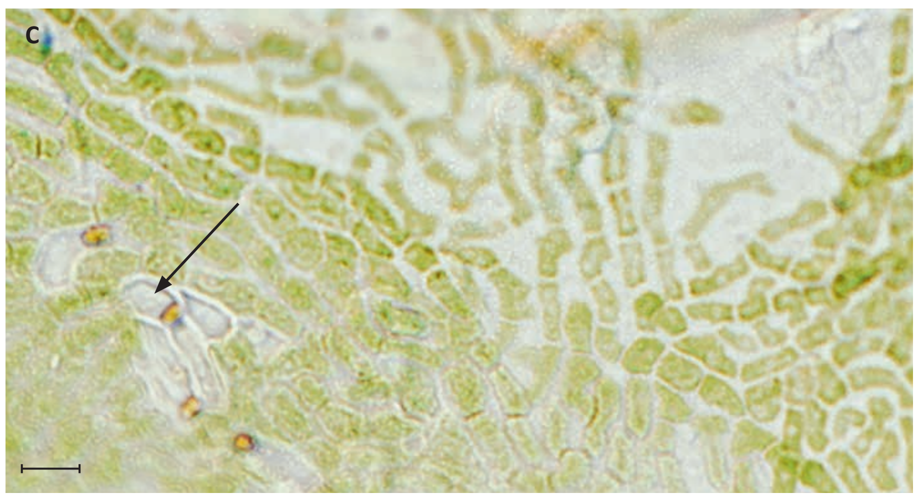
**References:** Gunnarsson & Nielsen (2016), Nielsen (1984), Nielsen in Brodie et al. (2007).




A: *Epicladia flustrae*. Green spots (arrow) in the bryozoan Horn Wrack (*Flustra foliacea*). Vejrø, 15 m, 12.8.1992. Scale 2 cm.




B: *Epicladia flustrae*. Mature sporangia with zoospores and empty sporangia with exit-pores (arrow). In chitin wall (dot and dash lines) of the bryozoan *Securiflustra securifrons*. Herthas Flak, 28.5.1978. Scale 25 µm.




C: *Epicladia flustrae*. A few empty sporangia (arrow). In chitin wall of the bryozoan Horn Wrack (*Flustra foliacea*) Munkegrunde, 11 m, 4.8.1994. Scale 10 µm.

## *Epicladia perforans*

**(Huber) R.Nielsen**

Eelgrass's Green Puzzle

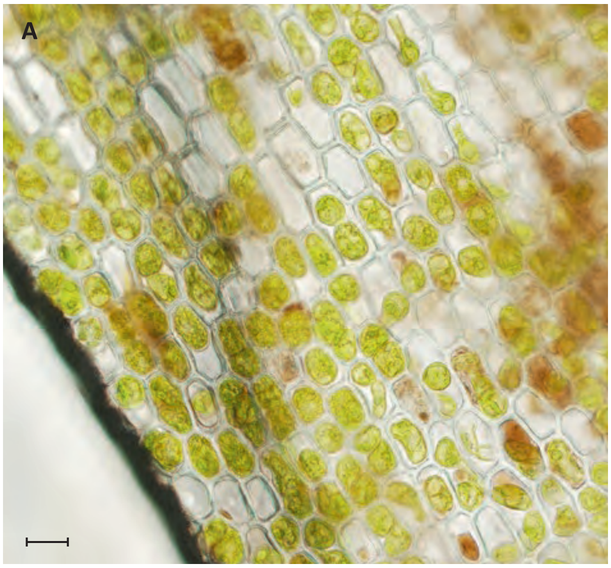
**Appearance:** Microscopic, branched filaments.

**Structure:** Uniseriate filaments, with scattered sparse branches, filling the surface cells (epidermal cells) of host plant. Most cells are round ellipsoid to spherical, 10-15 µm in diameter. Distal cells of filaments are cylindrical, 4-6 µm in width and 1.5-3 times as long as wide. Vegetative cells, each contains a parietal plate-shaped plastid with one pyrenoid.

**Reproduction:** Vegetative reproduction by zoospores. Sporangia develop from rounded vegetative cells and are the same shape and size as in the vegetative condition. At maturity, zoospores with 4 flagella are released through a circular pore. The alga, studied in culture has large, spherical sporangia. They contain 16 zoospores at maturity, which are released through a short exit tube. Zoospores germinate and grow into new filamentous thalli. The evacuated zoo-

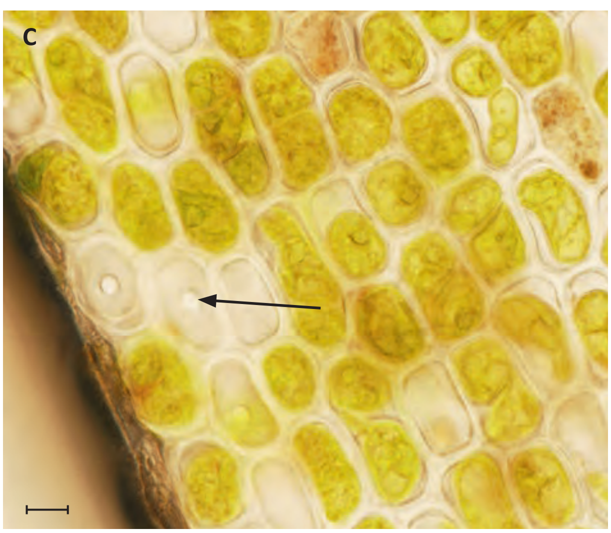
spore-wall and germination-tube are visible in very young individuals.
**Seasonal variation:** Well-developed in late summer and autumn, collected in May and August-November.

**Habitat:** Endophytic in epidermal cells of decaying drift leaves of Eelgrass (*Zostera marina*), 0.5-4 m depth.
**References:** Huber (1892), Nielsen (1980), Nielsen in Brodie et al. (2007).

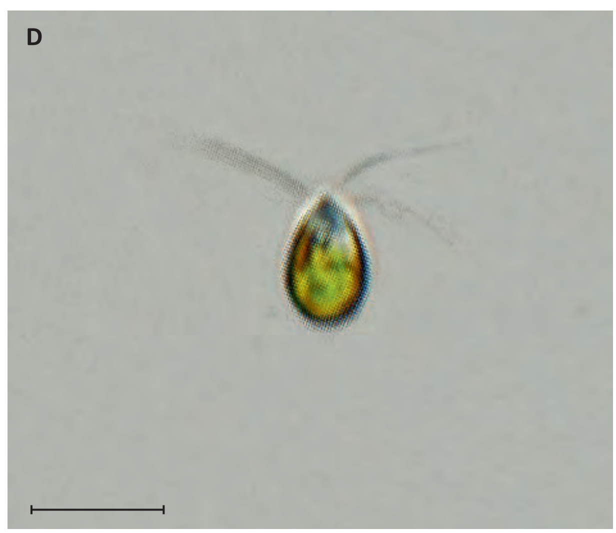



A: *Epicladia perforans.* Filaments in epidermal cells of decaying leave of Eelgrass (*Zostera marina*). Scale 20 µm. A-D: Northern part of Teglværkshavnen, Copenhagen, 1 m, 27.11.2007.


B: *Epicladia perforans.* Filaments with scattered branches growing through several host cells. Cylindrical and rounded vegetative cells, each with one pyrenoid. Scale 10 µm.




C: *Epicladia perforans.* Mature sporangia, red eyespot in swarmers visible as dark points. Empty sporangia with exit-pore (arrow). Scale 10 µm.



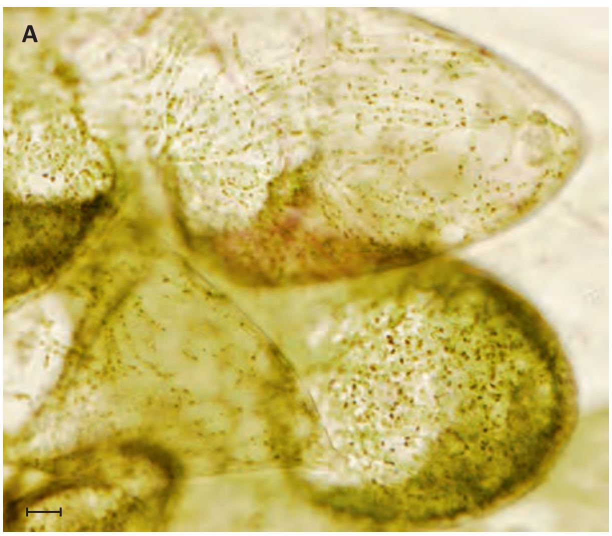

D: *Epicladia perforans.* Zoospore with red eyespot, and 3 of 4 flagella visible in the pointed front end. Scale 10 µm.

## *Epicladia phillipsii*

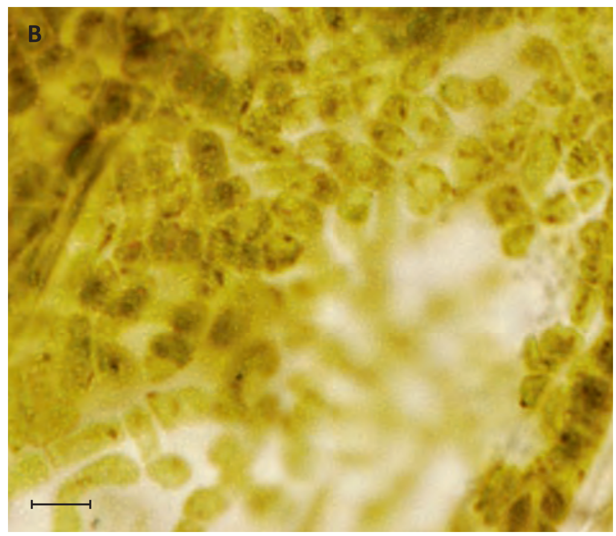
**(Batters) R.Nielsen**

Alcyonidium's Green Puzzle

**Appearance:** Microscopic, branched filaments, giving the host a dark green colour.
**Structure:** Filaments with scattered branches. Branching in the distal part of the alga fairly open with filaments of long narrow cells, 3.5-5 µm in width and 2-6 times as long as wide. Filaments in the older central part of thallus are confluent to a monostromatic pseudoparenchyma of rounded almost isodiametric cells, 6-9 µm in diameter. Vegetative cells contain a parietal plastid with one pyrenoid.
**Reproduction:** Vegetative reproduction by zoospores. Sporangia develop from rounded cells in pseudoparenchymatous area. Swarmers with 2 or 4 flagella are released through a circular pore in the sporangia walls.
**Seasonal variation:** Present all year, collected in January-March, May, July-September and November.
**Habitat:** In chitin wall of the bryozoan *Alcyonidium hirsutum*, 3-15 m depth.
**References:** Nielsen (1984), Nielsen in Brodie et al. (2007).



A: *Epicladia phillipsii.* Openly branched distal filaments and pseudoparenchyma. Hatter Barn, 9 m, 18.9.1993. Scale 20 µm. A-B: In chitin wall of the bryozoan *Alcyonidium hirsutum*.



B: *Epicladia phillipsii.* Pseudoparenchyma of short cells. Stålhage, Hirsholm, 3 m, 3.2.1996. Scale 10 µm.

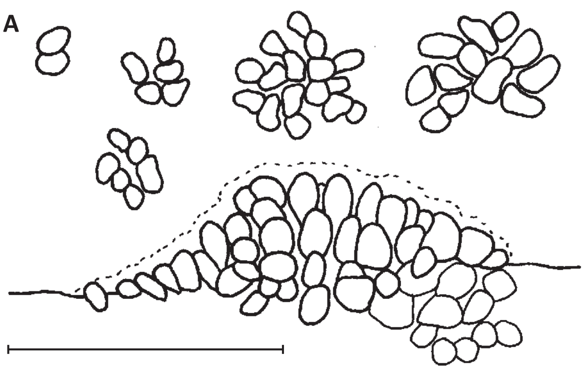
## *Syncoryne reinkei*

**R.Nielsen & P.M.Pedersen**

Green Club Spot

**Appearance:** Microscopic, epiphytic disc-like alga.
**Structure:** Monostromatic small discs, c. 125 µm in diameter, with mutually free cells at the margin. Peripheral cells are 5-7 µm in width. Cells in central part arch and become club-shaped, 6-13 µm in width and c. 20 µm in height. Vegetative cells contain a parietal plate-shaped plastid with one pyrenoid. Central cells have the plastid in the upper part of cell.
**Reproduction:** Club-shaped central cells develop into sporangia of the same shape as in the vegetative condition. They contain many zoospores at maturity, these are released by decay of the upper sporangium wall. Zoospores with 4 flagella, germinate and develop into similar individuals to the parent generation. Circular germlings are characteristic, consisting of two semi-circular cells.
**Seasonal variation:** Present all year, collected in January-July.
**Habitat:** Epiphytic on larger algae, often on basal part of Pitcher Siphon Weed (*Polysiphonia stricta*), Purple Felt Weed (*Rhodochorton purpureum*) and Stiff Little Felt Weed (*Sphaceloderma caespitulum*), 0.5-1.5 m depth.
**Resembles:** *Neostromatella monostromatica* may look similar but has no club-shaped cells.
**References:** Gunnarsson & Nielsen (2016), Nielsen in Brodie et al. (2007), Nielsen & Pedersen (1977).

A



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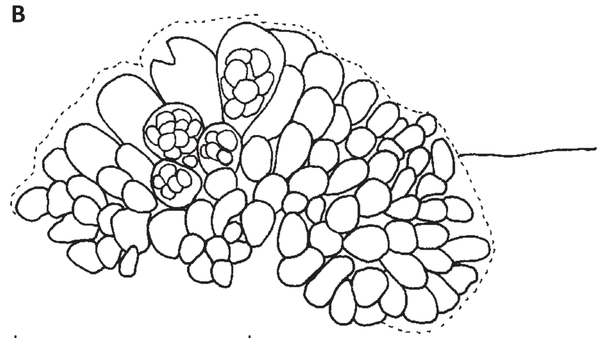

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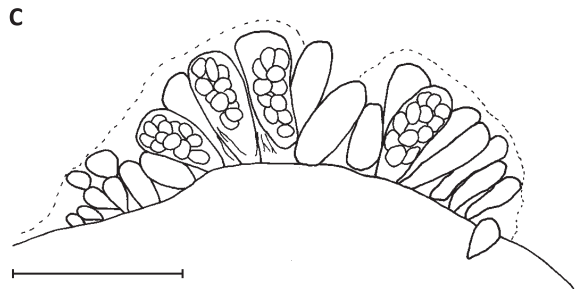


A: *Syncoryne reinkei.* Vegetative young and older specimens. Scale 50 µm. A-C: On Pitcher Siphon Weed (*Polysiphonia stricta*), Kystpromenaden, Aarhus Havn, 0.5 m, 5.3.1975.

B: *Syncoryne reinkei*. Mature and empty sporangia. Scale 50 µm.

C: *Syncoryne reinkei*. Club-shaped sporangia, longitudinal section. Scale 50 µm.

## *Ulvella*

**Appearance:** Microscopic filaments, mutually free or forming pseudoparenchymatous alga, rarely up to millimetre large.

**Structure:** Filaments may be mutually free or confluent to pseudoparenchyma, which may be irregularly cell masses or disc-shaped with furcate marginal cells. Some species have relatively wide upright filaments with narrower filaments at the base (heterotrichous). The growth-forms are seldom visible in field collected specimens but develop in culture.

Vegetative cells contain a parietal, plate-shaped, lobed and often slightly perforated plastid with one or several pyrenoids. Colourless hairs with a small bulbous base develop in many species. They are separated from the carrying vegetative cell by a wall (acrochaete-hair). Hairs are terminal on branches in some species whereas they develop on intercalary cells in other species. They are not always present but may develop on individuals in culture. This usually happens when the alga growing vigourously in nutrient rich culture-media is transferred into seawater without addition of nutrients, or when grown in strong light.

**Reproduction:** Vegetative or sexual reproduction by swarmers which develop in sporangia formed from transformed vegetative cells. Sporangia keep the same shape as in the vegetative condition or develop a conical top or exit papilla. They develop from cells similar to those carrying acrochaete-hairs. Swarmers are drop-shaped with a red eyespot and have flagella at the pointed front end. Gametes are of different sizes (anisogametes) and have 2 flagella. Male gametes are small and pale, without plastids. Female gametes are larger and have a basal plastid with one pyrenoid. Swarmers with 2 flagella may also be zoospores, whereas swarmers with 3 or 4 flagella are always zoospores. After the germination process, spores remain part of the germlings in some species, whereas an evacuated spore-wall and germination-tube occur in those of other species.

**Habitat:** On mollusc shells, wood, stone and other solid substrata, and epi- or endophytic in larger algae and plants or epi- or endozoic in animals.

**Comment:** Small green algae are common in nature, but specific characters are not always present for a reliable identification, among such are *Ulvella*-species. Therefore, it is often necessary to study the species in culture, where species-specific features develop to obtain a reliable identification. Most important characters are growth form, size, number of pyrenoids per cell, occurrence of hairs and their position, size and shape of sporangia and germination process with or without development of an evacuated spore-wall and germination-tube. A crude culture will in many cases be sufficient for identification. To obtain such, a fragment of the alga possibly with a small part of the substratum, is placed in a petri-dish with nutrient enriched sterile seawater. Petri-dishes are maintained in a culture room with temperature, light-intervals and light-intensity adjusted to the conditions at the collection locality. When a culture room is not available, the dishes can be placed on a window-sill, preferably in a north-facing window where temperature variations are restricted as opposed to a south-facing sunny window, and a fine alternative to a fancy culture room.

The genus was revised, after molecular studies of the plastid gen *tuf*A and includes species previously referred to *Acrochaete*, *Entocladia*, *Pringsheimiella* and *Ulvella* (Nielsen et al., 2013).

**References:** Nielsen et al. in Brodie et al. (2007, *Acrochaete*, *Pringsheimiella*, *Ulvella*), Nielsen et al. (2013).

### Identification key to species of *Ulvella*

The key is based on the appearance of algae in nature, where the occurrence on specific host is often species-specific, although it is necessary to also undertake culture studies for reliable identification of some species.

| | | |
|---|---|---|
| 1a. | Disc-shaped epiphytes with furcate marginal cells | 2 |
| 1b. | Branched filaments or clumps of a few cells | 3 |
| 2a. | Monostromatic, marginal cells 2-3 times as long as wide | *U. scutata* |
| 2b. | Central area polystromatic, and wide monostromatic marginal part with cells, 3-6 times as long as wide | *U. setchellii* |
| 3a. | Epi- or endophytic in *Chondrus crispus* | 4 |
| 3b. | Filaments on or in other algae or substrata | 5 |
| 4a. | Endophyte, narrow filaments, growing in the medulla of host | *U. operculata* |
| 4b. | Epiphyte of branched filaments and pseudoparenchymatous central area growing into the cortex of host | *U. heteroclada* |
| 5a. | Filaments with scattered and opposite branches, in outer cell wall of *Chylocladia verticillata*. Cells, 2-4 µm in width and 10-15 times as long as wide | *U. inflata* |
| 5b. | On other substrata, culture studies often necessary for reliable identification | 6 |
| 6a. | Relatively coarse alga on or in large brown algae. Culture studies necessary for reliable identification of species | On *Fucus* spp.: *U. parasitica* and *U. repens*. On *Chorda filum*: *U. pseudorepens* and *U. repens* |
| 6b. | Smaller, on or in various host algae | 7 |
| 7a. | Filaments with scattered branches, in filamentous brown algae, such as *Ectocarpus* spp., *Elachista fucicola* and *Pylaiella littoralis*. Distal cylindrical cells, 4-5 µm wide and (1-) 2-3 times as long as wide | *U. wittrockii* |
| 7b. | Cylindrical vegetative cells with 1-3 pyrenoids | *U. heteroclada, U. leptochaete* |
| 7c. | Cylindrical vegetative cells with 1 (-2) pyrenoids | *U. pachypes* (only known from culture studies), *U. ramulosa* on *Chaetomorpha linum*, *U. heteroclada* and *U. viridis* on various host-algae. |

## *Ulvella heteroclada*

### (Correa & R.Nielsen) R.Nielsen, C.J.O'Kelly & B.Wysor

**Appearance:** Microscopic, radiating epi- and endophytic filaments.

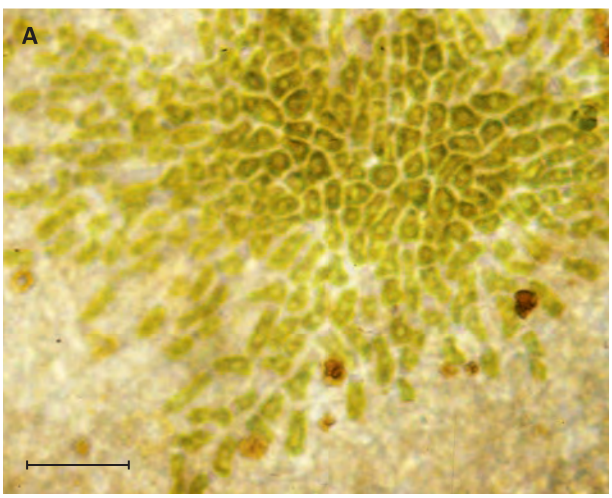
**Structure:** Microscopic, epiphytic pseudoparenchyma. Radiating short epiphytic filaments at the margin and a clustered central area from which short filaments become endophytic between cortical cells of the host. Radiating filaments consist of cylindrical cells, 4-5 µm in width and 3-10 times as long as wide. Central cells are almost isodiametric, 9-11 µm in diameter. Vegetative cells contain a parietal plastid with 1-2 pyrenoids.

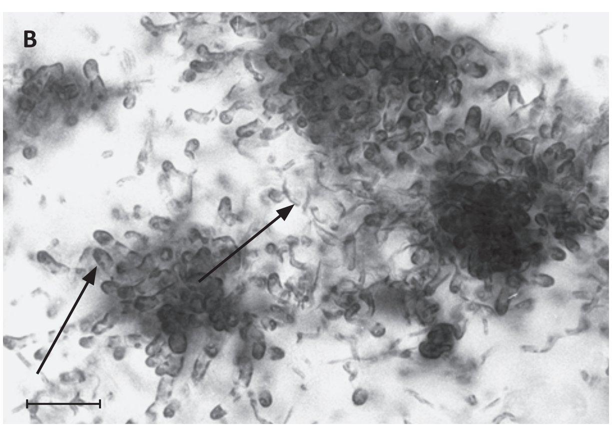
**Culture studies:** Young thalli, which develop in contact with a solid substratum, consist of radiating filaments, confluent to a pseudoparenchymatous layer in the central part. Relatively broad upright filaments arise from the central part in slightly old thalli (heterotrichous). Unattached thalli are also heterotrichous. They form tufts of relatively wide filaments which have narrow filaments at base. Cells in broad filaments have 1-3 (-4) pyrenoids, and in the narrow filaments 1-2 pyrenoids. Acrochaete-hairs are apical on broad filaments. Sporangia form from apical cells of the broad filaments and develop an elongate cylindrical shape. The spore remains part of the germling and young alga after the germination process.

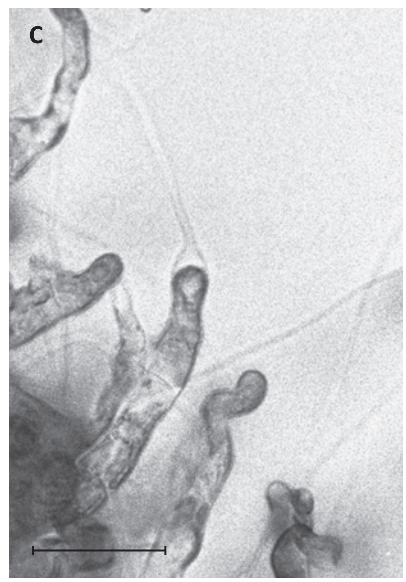
**Seasonal variation:** Present all year, collected in January, March-June, August-October and December.

**Habitat:** On Irish Moss (*Chondrus crispus*), 0.5-15 m depth.

**References:** Correa et al. (1988, *Acrochaete heteroclada*), Gunnarsson & Nielsen (2016), Nielsen et al. in Brodie et al. (2007, *A. heteroclada*), Nielsen et al. (2013).




A: *Ulvella heteroclada*. Pseudoparenchyma with mutually free branched filaments at the margin. On Irish Moss (*Chondrus crispus*), bay of harbour, Hirsholm, 0.75 m, 28.12.1985. Scale 50 µm.

B: *Ulvella heteroclada*. The alga in culture, upright relative broad filaments (left arrow) and narrow basal filaments (right arrow). Scale 50 µm. B-C: Original culture from type locality, Peggy Cove, Nova Scotia, Canada, 30.5.1985. Leg.: J. Correa.

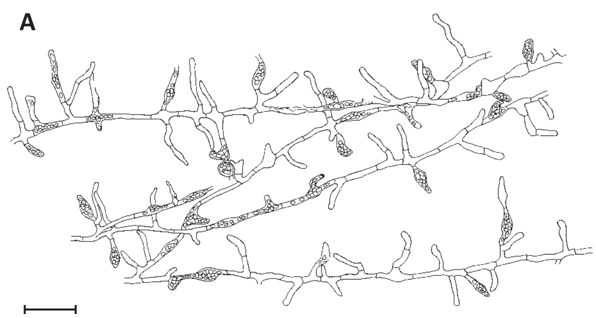
C: *Ulvella heteroclada*. Apical acrochaete-hair on upright broad filament. Scale 25 µm.

## *Ulvella inflata*

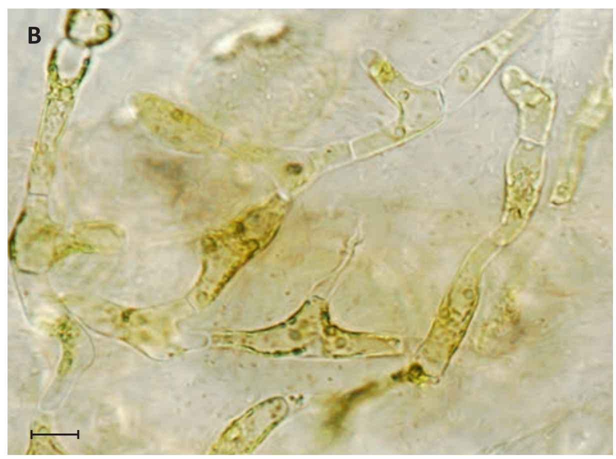
### (A.Ercegovic) R.Nielsen, C.J.O'Kelly & B.Wysor

**Appearance:** Microscopic endophytic filaments.
**Structure:** Creeping uniseriate filaments with scattered and opposite branches. Short few-celled branches are typical, they arise from main axes with approximately perpendicular branch angles. The first cell wall in a branch is typically at some distance from the branching point. Cells are cylindrical, relatively long and narrow, 2-4 µm in width and 10-15 times as long as wide. Vegetative cells contain a parietal plate-shaped plastid with 1-3 (-4) pyrenoids. Acrochaete-hairs may occur on scattered intercalary cells.

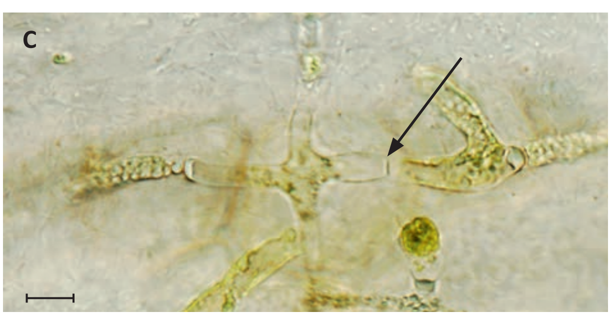
**Reproduction:** Vegetative reproduction by zoospores. Sporangia develop from vegetative cells, which swell slightly in the middle. Sporangia contain many zoospores at maturity. Zoospores are released through a papilla or short exit-tube to the surface of the host. An empty spore-wall and germination-tube occur on young germlings in culture.
**Seasonal variation:** Collected in June-October, sporangia recorded in June and October.
**Habitat:** In the outer cell wall between surface cells of Juicy Whorl Weed (*Chylocladia verticillata*), probably host specific. Collected in 0.5-3 m depth.
**References:** Ercegovic (1957, *Pseudodictyon inflatum*), Lein et al. (1999, *Acrochaete inflata*), Nielsen et al. in Brodie et al. (2007, *A. inflata*), Nielsen et al. (2013).




A: *Ulvella inflata.* Filaments with scattered and opposite branches, intercalary sporangia. In outer cell wall of Juicy Whorl Weed (*Chylocladia verticillata*), tile works, Helligsø, drift, 27.10.1973. Scale 50 µm.




B: *Ulvella inflata.* Vegetative filaments with scattered branches. Cells with 1-4 pyrenoids. Scale 10 µm. B-D: In outer cell wall of Juicy Whorl Weed (*Chylocladia verticillata*), Nissum Bredning, 3.5 m, 18.6.2007.



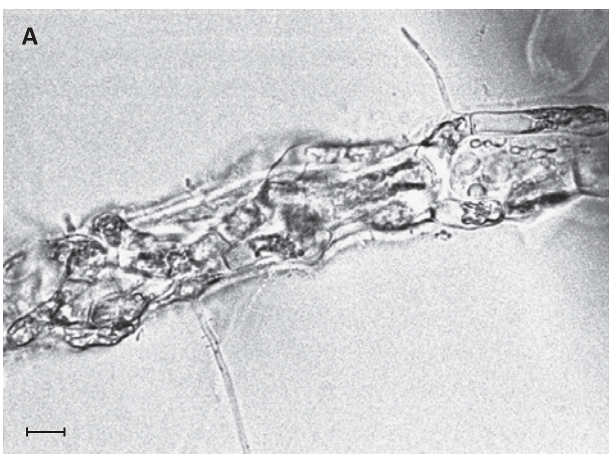

C: *Ulvella inflata.* Opposite branches, with first cross wall in branch at some distance from the branching point (arrow). Scale 10 µm.


D: *Ulvella inflata.* Sporangia (arrow) from transformed vegetative cells. Scale 10 µm.

## *Ulvella leptochaete*

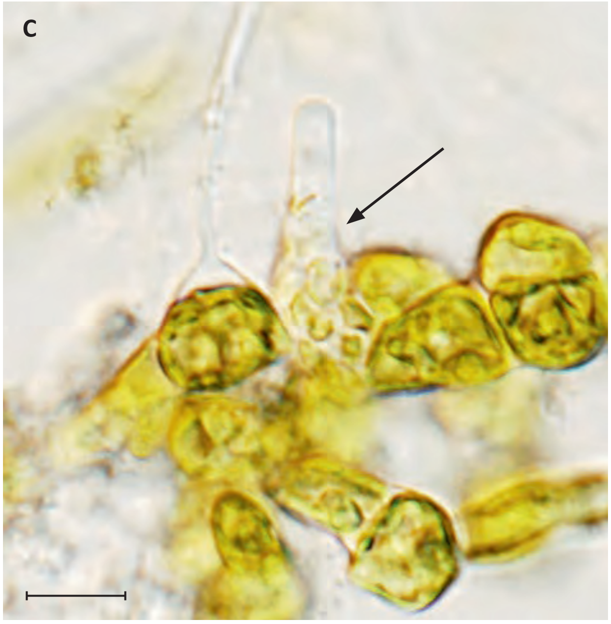
**(Huber) R.Nielsen, C.J.O'Kelly & B.Wysor**

**Appearance:** Microscopic, epiphytic filaments.
**Structure:** Filaments with scattered branches and small pseudoparenchyma. Vegetative cells have a parietal plate-shaped plastid with 1-3 pyrenoids. Culture studies necessary for reliable identification.
**Culture studies:** Young thalli consist of uniseriate filaments with scattered branches. They have cylindrical cells, 7.5-10.5 µm wide and 2.5-8 times as long as wide. Central cells in older algae are rounded, 13-22 µm in diameter, and are closely connected into a clumped pseudoparenchyma. Vegetative cells, each contains a parietal plastid with 1-3 (-4) pyrenoids. Acrochaete-hairs occur on intercalary cells and some are unusual in having 1-3 (-6) hair-like extensions from the basal rounded part. Vegetative reproduction by zoospores, sexual reproduction likely with small pale swarmers supposed to be male gametes, but copulation not observed. Sporangia develop from the rounded cells and become bottle-shaped with a conical top or exit-tube. The spore remains part of the young alga after the germination process.
**Seasonal variation:** Recorded in March, August, October-November, but only a few of the records confirmed by culture studies.
**Habitat:** Epiphytic on various larger algae, 0.5-1 m depth.
**Comment:** Culture studies are necessary to confirm development of the characteristic and unusual acrochaete-hair with more hair-like extensions from the rounded base. This feature is not reported on the alga in nature.
**References:** Huber (1892, *Endoderma leptochaete*), Kylin (1949, *Ectochaete leptochaete*), Nielsen (1983, *Acrochaete leptochaete*), Nielsen et al. in Brodie et al. (2007, *A. leptochaete*), Nielsen et al. (2013).



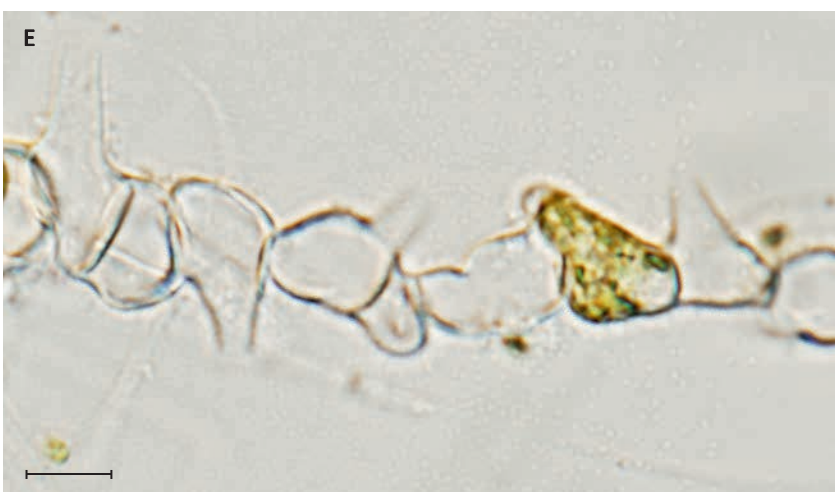

A: *Ulvella leptochaete.* Epiphytic filaments with acrochaete-hair. On Stalked Tree Weed (*Dasya baillouviana*), Margretheholms Havn, Copenhagen, 0.5 m, 20.7.2004. Scale 10 µm.


B: *Ulvella leptochaete.* Clumped pseudoparenchyma with radiating uniseriate branched filaments, narrow hairs. Scale 20 µm. B-E: Algae in culture, initiated from the alga, shown in fig. A.




C: *Ulvella leptochaete.* Intercalary cell with acrochaete-hair and a bottle-shaped sporangium (arrow). Scale 10 µm.


D: *Ulvella leptochaete.* Cell with characteristic and unusual acrochaete-hair, several (6) hair-like extensions from the basal swelling. Scale 10 µm.



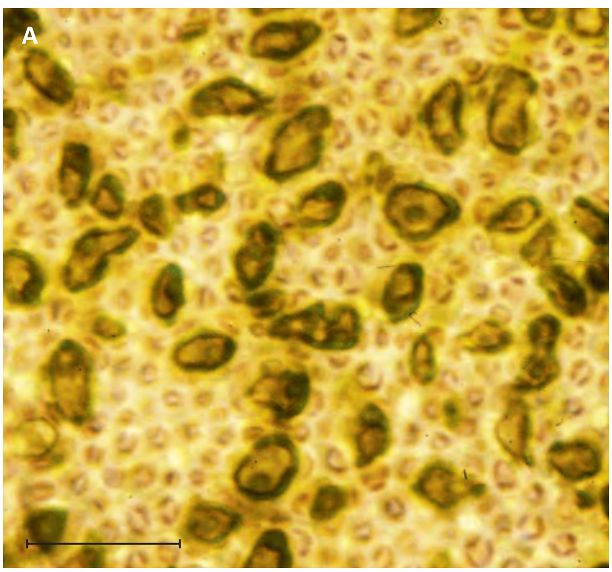

E: *Ulvella leptochaete.* Branch with empty bottle-shaped sporangia. Scale 10 µm.

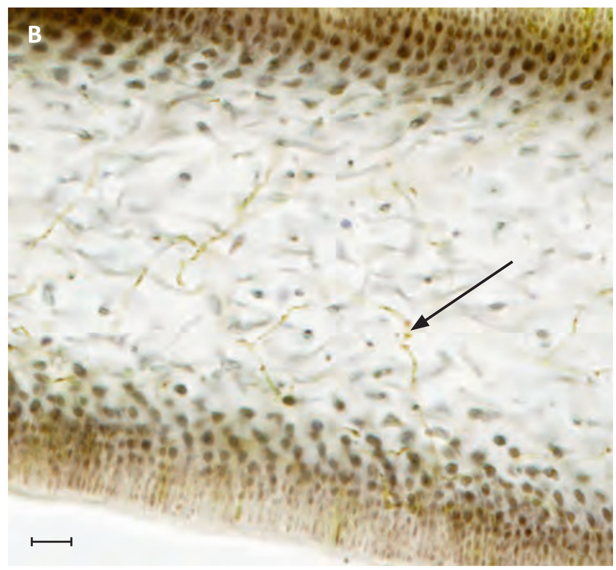
# *Ulvella operculata*

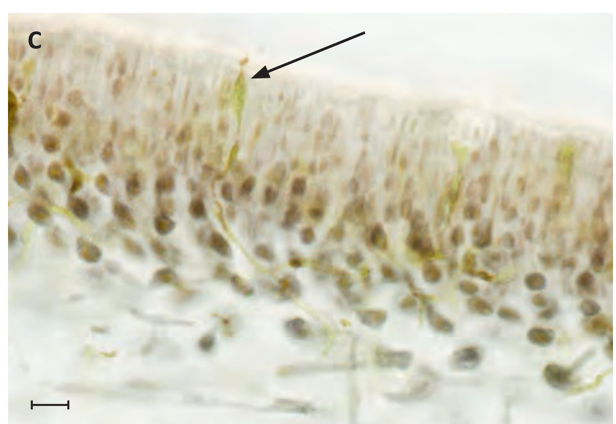
**(Correa & R.Nielsen) R.Nielsen, C.J.O'Kelly & B.Wysor**

**Appearance:** Microscopic, endophytic filaments.
**Structure:** Narrow filaments with scattered branches, which grow within the cortex and medulla of the host alga. Filaments in the medulla are narrow and bent, sparsely branched, with cells, 2-7.5 µm in width and 4-20 times as long as wide. Apical cells occur between the cortical cells of the host, and are elongate ellipsoid, 14-18 µm in width and approximately 28 µm long. Vegetative cells contain a parietal plastid with 1-3 pyrenoids. Acrochaete-hairs occur on apical cells.

**Reproduction:** Vegetative reproduction by zoospores. Sporangia develop from apical cells between surface cells of the host. Sporangia are the same size and shape as in the vegetative condition, but the upper part often becomes brown. Swarmers are released through a pore at the apex of the sporangium with a small brown lid. An empty spore-wall and germination-tube is visible on young thalli in culture.
**Seasonal variation:** Present all year, collected in February, March, May-September and December.
**Habitat:** Endophytic filaments in medulla and among surface cells of Irish Moss (*Chondrus crispus*), probably host specific. Collected in 0.5-9 m depth.
**References:** Correa et al. (1988, *Acrochaete operculata*), Gunnarsson & Nielsen (2016), Nielsen et al. in Brodie et al. (2007, *A. operculata*), Nielsen et al. (2013).




A: *Ulvella operculata*. Apical cells between cortical cells of host, in surface view. Bay of harbour, Hirsholm, 0.75 m, 28.12.1985. Scale 25 µm. A-C: In Irish Moss (*Chondrus crispus*).

B: *Ulvella operculata*. Slender filaments between medullary cells of host alga (arrow) and elongate ellipsoid cells between cortical cells, transverse section. Scale 20 µm. B-C: Bay of harbour, Hirsholm, 0.5 m, 19.2.1985.

C: *Ulvella operculata*. Ellipsoid cells between cortical cells of host (arrow), transverse section. Scale 10 µm.

# *Ulvella pachypes*

**R.Nielsen**

**Appearance:** Microscopic branched filaments with acrochaete-hairs. Only known from culture.

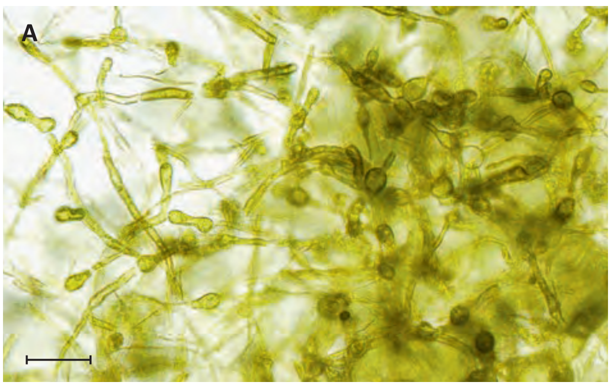
**Culture studies:** Filaments with scattered branches of cylindrical cells, 4.5-5 µm in width and 2-4 times as long as wide. Older cells become rounded or irregular in shape, 12.5-22 µm in diameter. Vegetative cells contain a parietal plastid with 1 (-2) relatively large pyrenoids. Acrochaete-hairs develop on scattered intercalary cells, and are distinct as the rounded base is relatively tall, 5-5.5 µm in width and 7-8 µm in height.

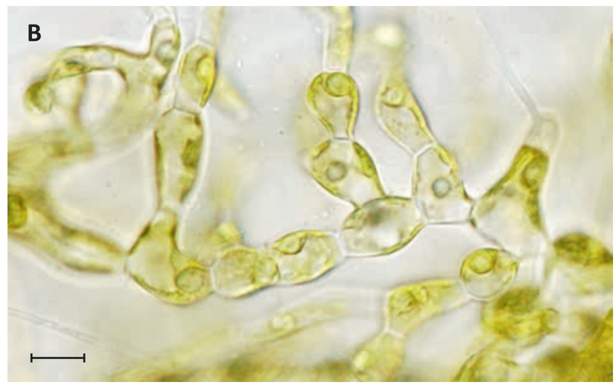
**Reproduction:** Vegetative reproduction by zoospores. Sporangia develop from rounded cells and become bottle-shaped with a long neck. Germinated spores remain part of young thalli.

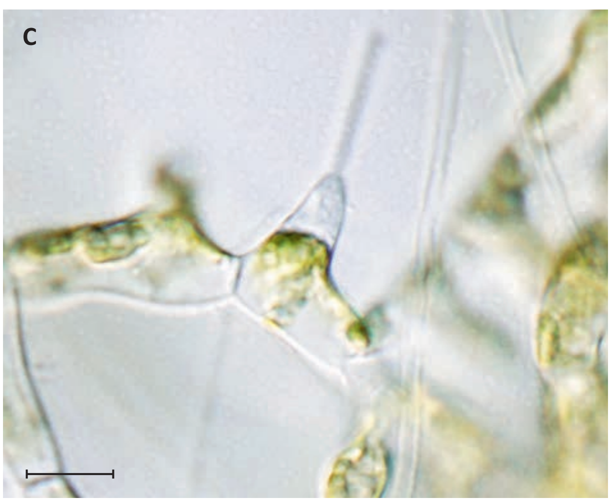
**Habitat:** Obtained in a crude culture, where it occurred on a small stone among other microscopic algae, 11 m depth.

**Seasonal variation:** Collected in August, only known from one collection.

**References:** Nielsen et al. (2013).





A: *Ulvella pachypes.* Openly branched filaments with long cylindrical cells and older rounded cells. Scale 20 µm.

A-D: Culture initiated from alga on a small stone, Endelave, 11 m, 23.8.1988.

C: *Ulvella pachypes.* Young acrochaete-hair with long rounded base on an intercalary cell. Scale 10 µm.

B: *Ulvella pachypes.* Filaments with short lenticular cells, each with one large pyrenoid. Scale 10 µm.

D: *Ulvella pachypes.* Bottle-shaped sporangium with long neck. Scale 10 µm.

# *Ulvella parasitica*

**(Oltmanns) R.Nielsen, C.J.O'Kelly & B.Wysor**

**Appearance:** Microscopic filaments, branched as a net among surface cells of host-alga.

**Culture studies:** Dense, pseudoparenchymatous alga. Central area cushion-shaped, consisting of short, rounded cells, 19-23 µm in diameter with a gradual transition to peripheral filaments of cylindrical cells, 7.5-8 µm in width and 3-6 times as long as wide. Vegetative cells contain a parietal lobed and slightly perforated plastid with 1-3 pyrenoids. Acrochaete-hairs occur on the upper part of rounded cells.

**Reproduction:** Vegetative reproduction by zoospores. Sporangia develop from rounded cells which become bottle-shaped with an exit-pore in the narrow end.

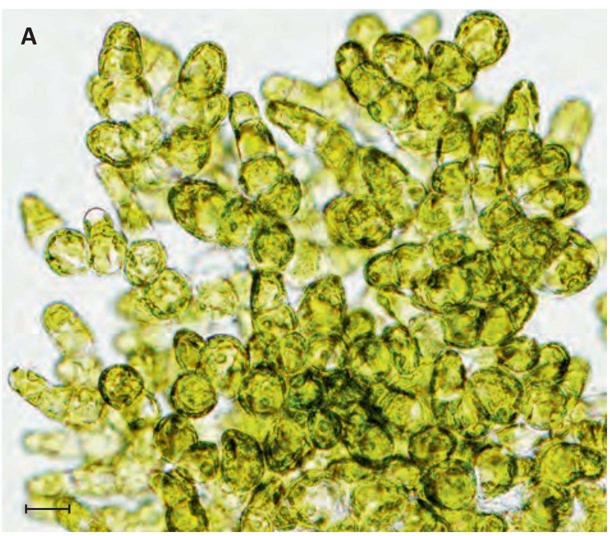
**Seasonal variation:** Probably present all year, collected in September.

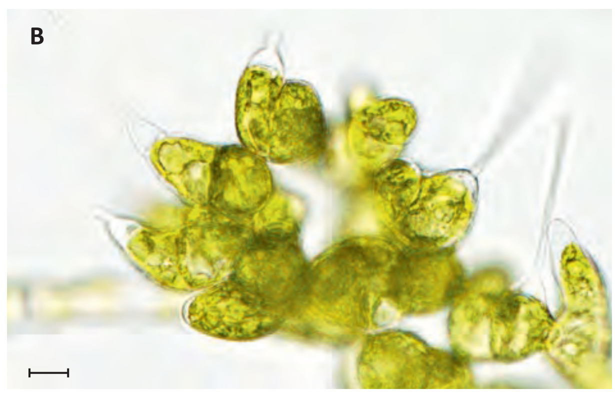
**Habitat:** Endophytic filaments among surface cells of Serrated Wrack (*Fucus serratus*), 0.5-5 m depth.

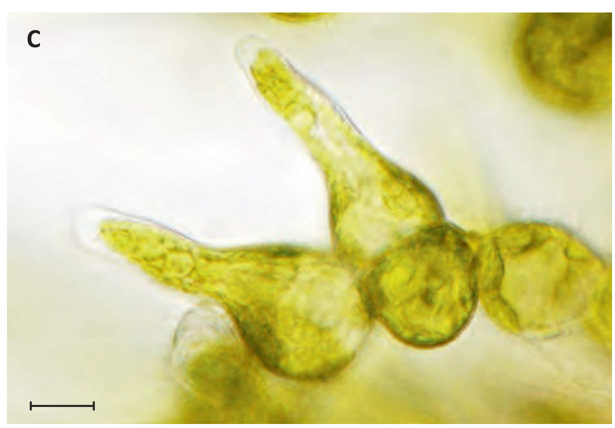
**Resembles:** Similar to *U. repens* but *U. parasitica* does not have heterotrichous growth and sporangia are bottle-shaped, not elongate cylindrical. Morphology in culture reminiscent of *U. reticulata* (Printz) R.Nielsen, C.J.O'Kelly & B.Wysor, but this has larger cells with more pyrenoids and is endophytic in Sugar Kelp (*Saccharina latissima*). *Ulvella reticulata* is not recorded in Danish waters.

**Comment:** Culture studies are necessary for reliable identification, because the similarity with *U. repens* in field collected material. The two were previously considered a single species (Nielsen 1979).

**References:** Gunnarsson & Nielsen (2016), Nielsen (1979, *Acrochaete*), Nielsen et al. (2013), Oltmanns (1894, *A. parasitica*).




A: *Ulvella parasitica*. Pseudoparenchyma of rounded cells, each with 1-3 pyrenoids. Scale 20 µm. A-C: The alga in culture initiated from among surface cells of Serrated Wrack (*Fucus serratus*). Nordre Rønner, Læsø, 1 m, 6.9.1972.

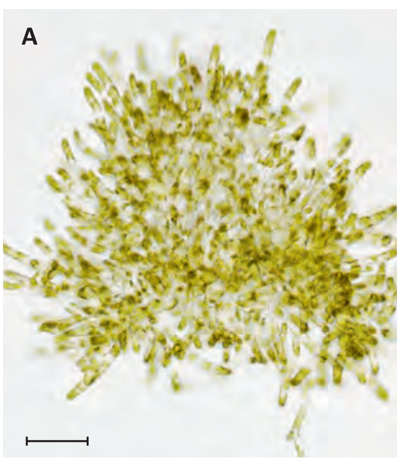
B: *Ulvella parasitica*. Rounded vegetative cells with young and older acrochaete-hairs. Scale 10 µm.

C: *Ulvella parasitica*. Young bottle-shaped sporangia. Scale 10 µm.

# *Ulvella pseudorepens*

**R.Nielsen**

**Appearance:** Microscopic, endophytic filaments. Reliable identification dependent on culture studies.
**Culture studies:** Heterotrichous alga with narrow creeping filaments at the base of relatively wide upright filaments. Tufts of upright filaments, approximately spherical and consist of cylindrical cells, 11-15 µm in width and 3-6 times as long as wide. These filaments arise from large, rounded cells, 25-40 µm in diameter which form the central part of the alga. Vegetative cells contain a parietal, lobed and slightly perforated plastid with 3-7 small pyrenoids. Acrochaete-hairs occur on apical cells of the wide filaments or on upright protuberances from other cells of the wide filaments.
**Reproduction:** Vegetative reproduction by zoospores. Sporangia develop from apical cells in the wide filaments and from upright protuberances on other cells in the wide filaments. Sporangia are elongate cylindrical.
**Habitat:** Endophytic filaments between paraphyses in Bootlace Weed (*Chorda filum*).
**Seasonal variation:** Collected in October.
**Resembles:** *Ulvella repens* also grows between paraphyses in Bootlace Weed (*C. filum*) and looks similar but has only 1-3 pyrenoids in vegetative cells.
**Comment:** Species identification only confirmed by molecular studies in two collections, studied in culture (Nielsen et al., 2013). Records of *U. repens* in the database, the algal herbarium, Natural History Museum of Denmark, probably include misidentified *U. pseudorepens,* therefore the distribution map comprises both these species.
**References:** Gunnarsson & Nielsen (2016), Nielsen et al. (2013).




A: *Ulvella pseudorepens.* Tuft of relatively thick upright filaments. Scale 50 µm. A-C: Algae in culture, initiated from an alga on Bootlace Weed (*Chorda filum*). Lyngså Strand, drift, 7.10.1976.



B: *Ulvella pseudorepens.* Upright filaments arise from rounded cells. Parietal plastid, lobed and perforated with several small pyrenoids (arrow). Scale 10 µm.

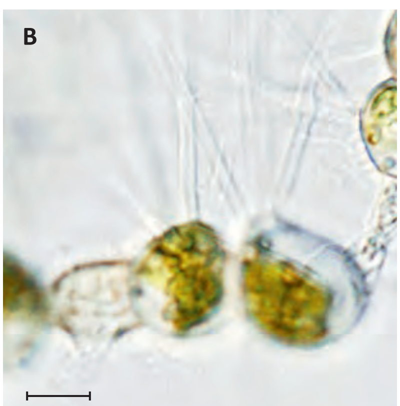
C: *Ulvella pseudorepens.* Acrochaete-hair, apical on upright filament. Scale 10 µm.

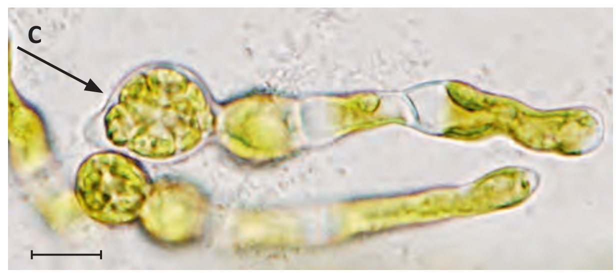
## *Ulvella ramulosa*

### (L.Moewus) R.Nielsen, C.J.O'Kelly & B.Wysor

**Appearance:** Microscopic, branched filaments. Reliable identification only possible by culture studies.
**Culture studies:** Few-celled filaments with scattered branches, marginal cells are cylindrical, 4.5-7 µm in width and 2-3 times as long as wide, with gradual transition to the central, approximately spherical cells, 10.5-14 µm in width. Vegetative cells have a parietal plastid with one pyrenoid. Acrochaete-hairs occur on the rounded cells and may have several hair-like extensions from the rounded basal part.

**Reproduction:** Vegetative reproduction by zoospores. Transformed rounded cells become ovoid sporangia with an exit-papilla in the narrow end. Germinated zoospores remain part of young thalli.
**Seasonal variation:** Collected in July.
**Habitat:** Epiphytic on Flax Brick Weed (*Chaetomorpha linum*).
**Resembles:** Acrochaete-hairs with one or several hair-like extensions also occur in *A. leptochaete*, but this has 1-3 pyrenoids per cell.
**References:** Gunnarsson & Nielsen (2016), Moewus (1949, *Ectochaete ramulosa*), Nielsen et al. (2013).




A: *Ulvella ramulosa*. Vegetative few-celled alga, each cell with a parietal plastid and one pyrenoid. Scale 10 µm. A-E: The alga in culture initiated from epiphytic filament on Flax Brick Weed (*Chaetomorpha linum*), Hirsholm, 7.7.1978.

B: *Ulvella ramulosa*. Acrochaete-hairs with 3 hair-like extensions. Scale 10 µm.

C: *Ulvella ramulosa*. Unbranched few-celled alga with mature sporangium (arrow). Scale 10 µm.

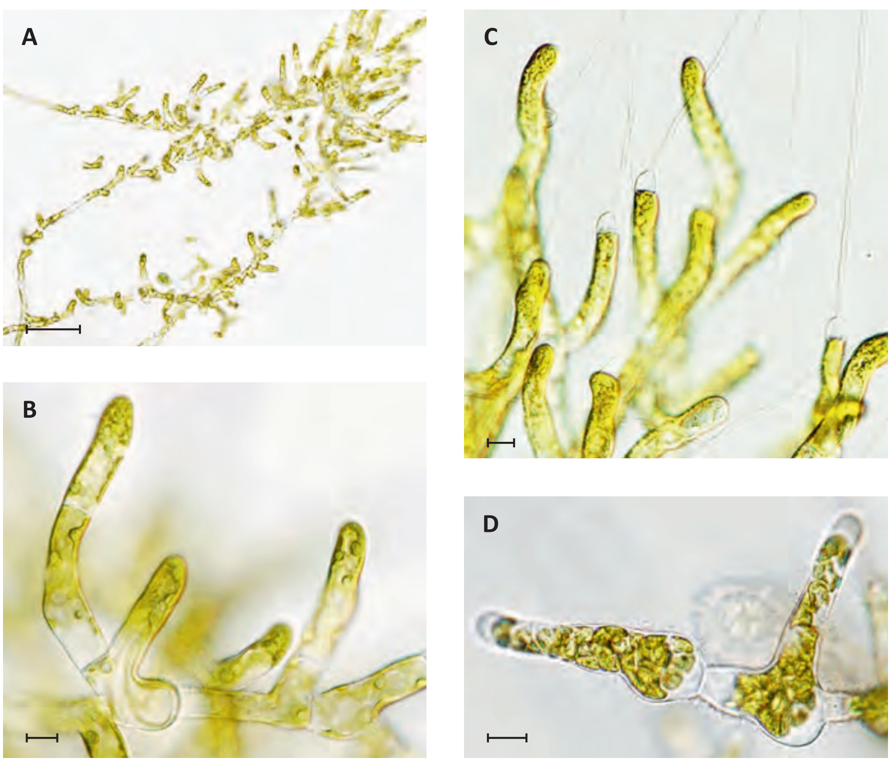
D: *Ulvella ramulosa*. Branched alga with 1 mature (arrow) and 2 empty sporangia. Scale 10 µm.

E: *Ulvella ramulosa*. Germinated zoospore (arrow) remains part of young alga. Scale 10 µm.

# *Ulvella repens*

**(Pringsheim) R.Nielsen, C.J.O'Kelly & B.Wysor**

**Appearance**: Microscopic, endophytic filaments.
**Structure:** Creeping uniseriate filaments, 5-6 µm in width with few-celled upright branches, 10-15 µm in width. Vegetative cells have a parietal plastid with 1 large or 2-3 minor pyrenoids. Acrochaete-hairs are apical on upright filaments.
**Culture studies:** Tufts of upright filaments, 17-20 µm in width with slender creeping filaments, 7.5-10 µm in width at base (heterotrichous). The parietal plastid is perforated with 1-4 (5) pyrenoids. Apical acrochaete-hair on upright wide filaments, and on upright protuberances from cells in the creeping filaments.
**Reproduction:** Sporangia develop from apical cells of wide filaments and become elongate cylindrical, and from upright protuberances of other cells in these filaments and become L-shaped. Zoospores with 4 flagella and swarmers with 2 flagella are observed, the biflagellate swarmers small and pale or larger and green, probably anisogametes. Germinated spores remain part of young thalli.
**Seasonal variation:** Probably present all year, on species of Wrack (*Fucus*) and in summer and autumn on Bootlace Weed (*C. filum*).
**Habitat:** Creeping filaments between paraphyses of Bootlace Weed (*Chorda filum*) and among surface cells of Wrack (*Fucus*), 0.5-15 m depth.
**Resembles:** Culture studies necessary to confirm the identity as it might be confused with the similarly looking *U. pseudorepens,* which also grows between paraphyses of Bootlace Weed (*Chorda filum*), and *U. parasitica*, which grows between surface cells on species of Wrack (*Fucus*). *Ulvella parasitica* is coarser than the other two and does not have heterotrichous growth. The number of pyrenoids are different in the other two being 3-7 pyrenoids per cell in *U. pseudorepens* and 1-4 (5) pyrenoids per cell in *U. repens*.
**Comment:** See comment for *U. pseudorepens*.
**References**: Nielsen et al. (2013), Pringsheim (1862, *Acrochaete repens*).




A: *Ulvella repens.* Creeping filaments with upright, few-celled branches. Scale 100 µm. A-D: The alga in culture initiated from alga on Bladder Wrack (*Fucus vesiculosus*), Hirsholm, 0.5 m, 26.2.1975.

B: *Ulvella repens.* Upright vegetative cells. Scale 20 µm.

C: *Ulvella repens.* Many upright filaments with apical acrochaete-hair. Scale 10 µm.

D: *Ulvella repens.* Mature sporangia, one of them apical and elongate, the other L-shaped. Scale 10 µm.

## *Ulvella scutata*

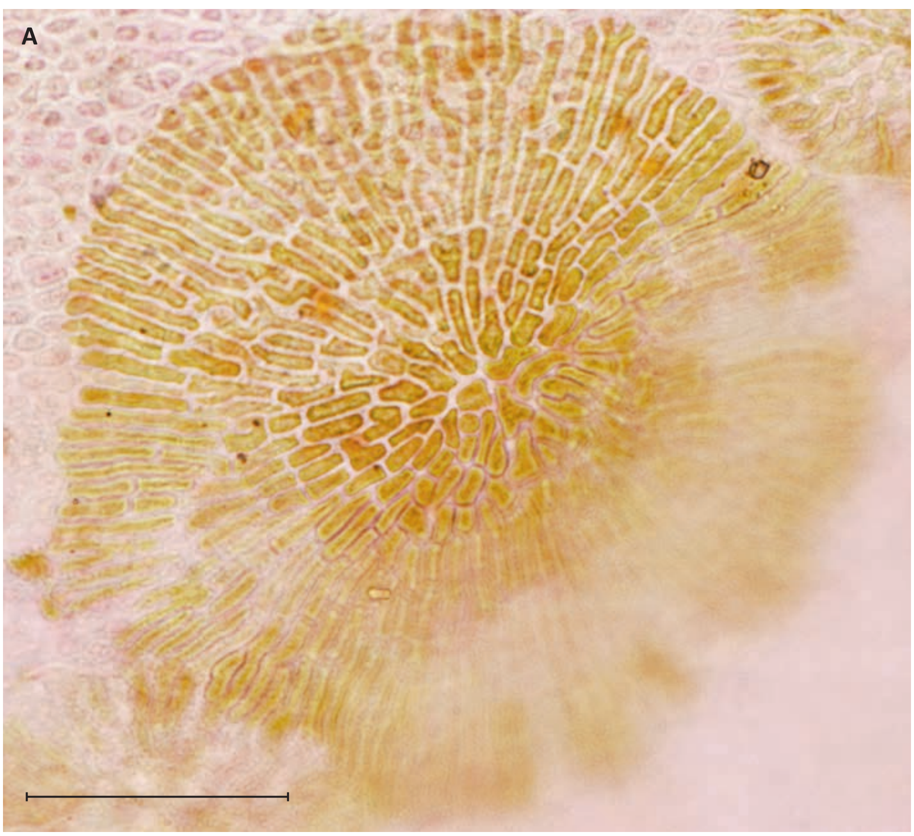
### (Reinke) R.Nielsen, C.J.O'Kelly & B.Wysor

**Appearance:** Microscopic, disc-shaped epiphytes.
**Structure:** Disc-shaped almost circular monostromatic pseudoparenchyma, 100-150 µm in diameter. The disc consists of radiating filaments with furcate marginal cells. Central cells are rounded or slightly angular with a gradual transition to the cylindrical marginal cells, which are 2-3 times as long as wide. Vegetative cells each contains a parietal plate-shaped plastid with one pyrenoid. Delicate tiny hairs may occur on the central cells.
**Reproduction:** Sporangia develop from all vegetative cells, starting at the centre and continuing to the marginal cells. Sporangia are the same size and shape as in the vegetative condition and develop a small exit-papilla. Sporangia contain biflagellate swarmers at maturity. Some swarmers are small and pale, others in different sporangia of the same individual are larger and green, and probably anisogametes. In culture studies the next generation are irregularly lumpy thalli, producing quadriflagellate zoospores. Disc-shaped thalli with sporangia which contained quadriflagellate zoospores are reported from Japan, but such are not observed in the alga from Danish waters.
**Seasonal variation:** Present all year, collected in January, March-December.
**Habitat:** Epiphytic on various algae such as Pitcher Siphon Weed (*Polysiphonia stricta*), Purple Felt Weed (*Rhodochorton purpureum*) and on leaves of Eelgrass (*Zostera marina*), also common on shells of living Blue Mussel (*Mytilus edulis*).
**Resembles:** Disc-shaped *U. lens* P.Crouan & H.Crouan and *U. setchellii* also have furcate marginal cells but differ from *U. scutata* by being polystromatic in central part. Marginal cells of *U. setchellii* are 3-6 times as long as wide, whereas only 2-3 times as long as wide in *U. scutata*. *Ulvella lens* is not recorded from Danish waters.
**References:** Gunnarsson & Nielsen (2016), Nielsen in Brodie et al. (2007, *Pringsheimiella scutata*), Nielsen & Pedersen (1977, *P. scutata*), Nielsen et al. (2013), Reinke (1888b, 1889a, b, *Pringsheimia scutata*).


A: *Ulvella scutata*. Monostromatic disc with furcate marginal cells. On Pitcher Siphon Weed (*Polysiphonia stricta*), Lysegrund, 10.5 m, 19.1.1997. Scale 20 µm.

## *Ulvella setchellii*
**P.J.L.Dangeard**

**Appearance:** Disc-shaped epiphytes, up to 2 mm in diameter.
**Structure:** Circular to slightly irregular pseudoparenchyma of confluent radiating filaments with furcate marginal cells. Young individuals are monostromatic. In older individuals the central area consists of a few cell layers of rounded cells, 5-8 µm in diameter. The marginal part is monostromatic and consists of relatively long cylindrical cells, 3-5 µm in width and 3-6 times as long as wide. Vegetative cells each contains a parietal plastid with one pyrenoid. Hair-like extensions may occur on the central cells of the alga studied in culture.
**Reproduction:** Sporangia develop from the central, rounded cells, and develop a conical exit-tube, but are otherwise similar to the vegetative cells in shape and size. Vegetative reproduction by zoospores with 4 flagella, observed in culture studies.
**Seasonal variation:** Present all year. Collected in January-June, August and December.
**Habitat:** Common on old blades of Sandy Leaf Bearer (*Phyllophora crispa*), 11-19 m depth.
**Resembles:** *U. scutata* is also disc-shaped with furcate marginal cells, but monostromatic throughout and marginal cells only 2-3 times as long as wide.
**References:** Dangeard (1931), Nielsen (1977), Nielsen in Brodie et al. (2007), Nielsen et al. (2013).

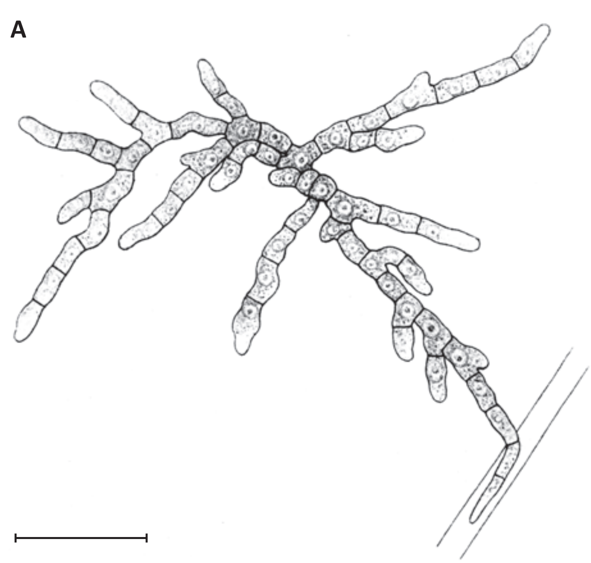



A: *Ulvella setchellii*. Disc-shaped alga with elongate peripheral cells and furcate marginal cells. On Sandy Leaf Bearer (*Phyllophora crispa*), Kims Top, 19 m, 4.2.1996. Scale 200 µm.

# *Ulvella viridis*

**(Reinke) R.Nielsen, C.J.O'Kelly & B.Wysor**

**Appearance:** Microscopic, branched epi- or endophytic filaments.
**Structure:** Radiating mutually free filaments with scattered branches. Vegetative cells, each with one pyrenoid. Several species look similar, therefore careful culture studies are necessary for reliable identification, preferably supported by molecular studies.
**Culture studies:** Larger thalli are lumpy pseudoparenchyma, sometimes with a basal layer attached to the substratum. Central cells are irregularly rounded, 5-15 (-20) µm in width. Uniseriate filaments with scattered branches arise from the central cells, they consist of cylindrical cells, 3-5 µm in width and 2-3 (-10) times as long as wide. Vegetative cells, each contains a parietal plastid with 1 (-2) pyrenoids. Acrochaete-hairs occur on scattered intercalary cells.
**Reproduction:** Sporangia develop from rounded intercalary cells, which become bottle-shaped with a conical top or exit-tube.
**Seasonal variation**: Thalli resembling *U. viridis* present all year.
**Habitat:** Epi- and endophytic filaments with scattered branches on larger algae.
**Comment:** It is common to observe branched filaments which fit the description of *U. viridis* on and between surface cells of various larger algae. Such thalli were previously referred to *U. viridis* by Nielsen (1979, 2005a as *Acrochaete viridis* (Reinke) R. Nielsen). Molecular studies have revealed that several different species look similar in the field. In Danish waters, such creeping filaments are common in cell walls of Sea Oak (*Phycodrys rubens*). These have cylindrical vegetative cells with one pyrenoid and sporangia formed from intercalary vegetative cells. Similar algae observed in America, in Sea Oak (*P. rubens*) were found to be different from *U. viridis* (Nielsen et al., 2013), but the identity was not determined. DNA sequence data of algae from Sea Oak (*P. rubens*) in Danish waters, were not obtained by Nielsen et al. (2013) but the Danish individuals are probably similar to those in the American studies.
**References:** Gunnarsson & Nielsen (2016), Nielsen (1979, 2005a, *Acrochaete viridis*), Nielsen et al. in Brodie et al. (2007, *A. viridis*), Nielsen et al. (2013), Reinke (1879, *Entocladia viridis*).



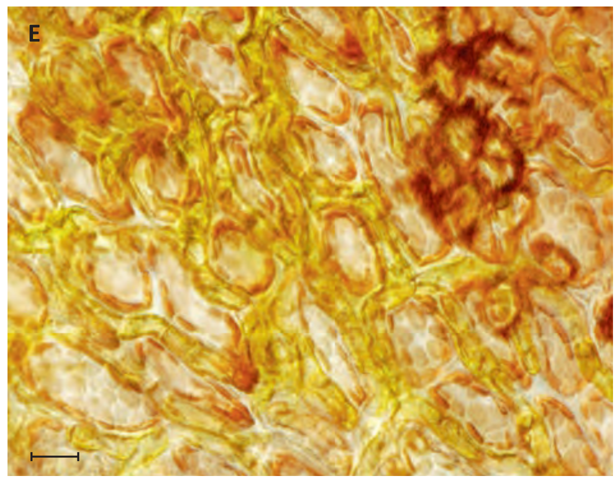


A: *Ulvella viridis.* Epiphytic on *Derbesia* with a few cells in cell wall of the host alga. Original illustration of alga from Naples, after Reinke (1879). Scale 50 µm.

B: *Ulvella viridis.* Young alga of filaments with scattered branches of cylindrical cells. Scale 20 µm. B-D: Alga in culture initiated from alga collected at type locality in Naples.


C: *Ulvella viridis*. Acrochaete-hair on intercalary rounded cell (arrow). Scale 10 µm.


D: *Ulvella viridis*. Empty intercalary sporangia with exit-tubes. Scale 10 µm.

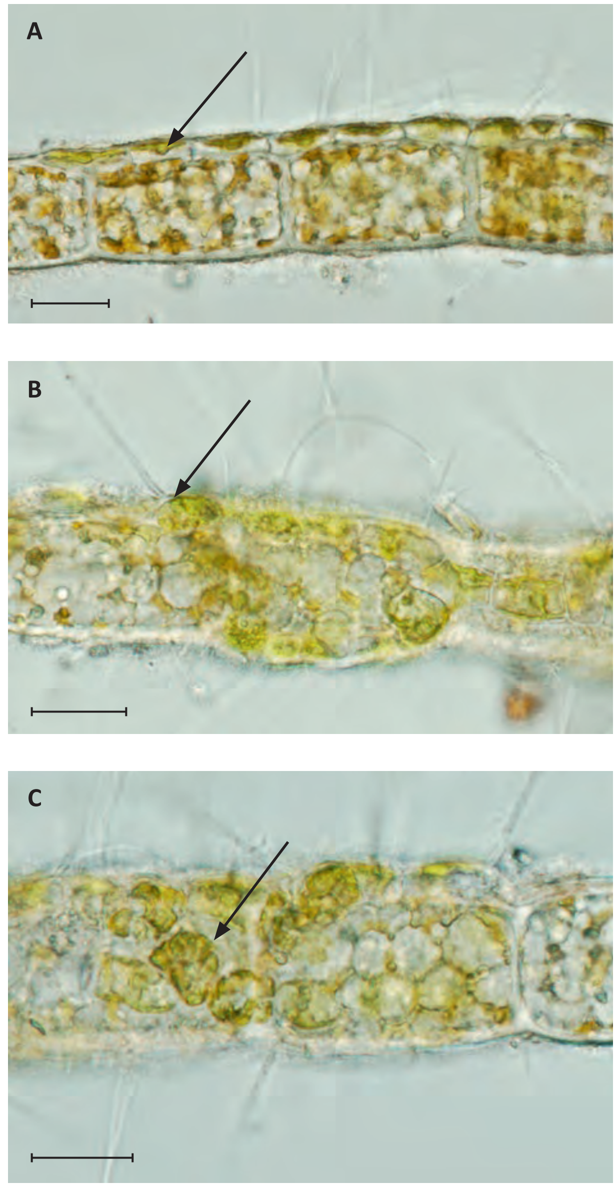



E: Branched filaments in wall of Brittle Fern-Weed (*Osmundea oederi*), which might be *U. viridis*. Hirsholm, drift, 14.4.2015. Scale 10 µm.

# *Ulvella wittrockii*

## (Wille) R.Nielsen, C.J.O'Kelly & B.Wysor

**Appearance:** Microscopic, epi- and endophytic branched filaments in outer cell walls of host alga.
**Structure**: Short, branched filaments of cylindrical or slightly rounded cells. Cylindrical cells, 4-5 µm in width and (1-) 2-3 times as long as wide, rounded cells up to 10 µm in diameter. Vegetative cells each contains a parietal plastid with one pyrenoid. Acrochaete-hairs occur on scattered intercalary cells.
**Reproduction:** All cells may transform into sporangia, slightly wider than in the vegetative condition and develop a small exit-papilla. Swarmers may have 2, 3 or 4 flagella, although 3 flagella are very exceptional but well documented. Germinated spores remain part of developing new individuals.
**Seasonal variation:** Present all year, collected in April-November.
**Habitat:** In outer cell walls of filamentous brown algae, such as Cotton Wool Weeds (*Ectocarpus* sp.), Tiny Wrack Bush (*Elachista fucicola*) and Pylaie's Brown Filaments *(Pylaiella littoralis*).
**Resembles:** Easy to confuse with other *Ulvella*-species with one pyrenoid per cell, although likely to be *U. wittrockii* when endophytic in filamentous brown algae. This can be confirmed by observation of zoospores with 3 flagella, a unique feature for the species.
**References:** Gunnarsson & Nielsen (2016), Kornmann (1993, *Acrochaete wittrockii*), Kylin (1938, *Ectochaete wittrockii*), Nielsen (1983, *A. wittrockii*), Nielsen et al. in Brodie et al. (2007, *A. wittrockii*), Nielsen et al. (2013), Wille (1880, *Entocladia wittrockii*).




A: *Ulvella wittrockii.* Filament of cylindrical vegetative cells, one pyrenoid per cell (arrow). Scale 10 µm. A-C: In cell wall of Pylaie's Brown Filaments (*Pylaiella littoralis*). Nakkehoved Fyr, 0.5 m, 6.7.2006.

B: *Ulvella wittrockii.* Branched filaments, acrochaete-hair with colourless, short, rounded base (arrow). Scale 10 µm.

C: *Ulvella wittrockii.* Intercalary, mature sporangium (arrow). Scale 10 µm.

# Identification key to genera of Chlorophyta – Green algae

## In a few cases identification go to species

| | | |
|---|---|---|
| 1a. | Macroscopic algae | 2 |
| 1b. | Microscopic algae or algae < few millimetres | 22 |
| 2a. | Blade, ribbon, tube or thread-like parenchyma | 45 |
| 2b. | Thallus of a different shape and not parenchymatous | 3 |
| 3a. | Thallus of mutually free filaments, branched or unbranched | 4 |
| 3b. | Thallus more complex | 21 |
| 4a. | Branched filaments | 5 |
| 4b. | Unbranched filaments | 15 |
| 5a. | Siphonous filaments (without cross walls) | 6 |
| 5b. | Cellular filaments | 11 |
| 6a. | Distinct main axis with branches | *Bryopsis* |
| 6b. | Irregular branching, no distinct difference between branches | 7 |
| 7a. | Small obovoid, lateral sporangia with many spores | *Derbesia* |
| 7b. | No sporangia, or sporangia with one big zoospore | 8 |
| 8a. | On soil in salt marshes. Cross walls only in association with reproductive structures | *Vaucheria* (Tribophyceae, see Christensen, 1987) |
| 8b. | Sublittoral | 9 |
| 9a. | Plastids disc shaped. Thick cross walls at branching points | *Derbesia* |
| 9b. | Plastids spindle-shaped | 10 |
| 10a. | Plastids with pyrenoids | Juvenile *Bryopsis* |
| 10b. | Plastids without pyrenoids | Juvenile *Codium* |
| 11a.[5] | Branches restricted to short rhizoidal protrusions from single cells | 12 |
| 11b. | Bush-like thallus of branched filaments | 13 |
| 12a. | Rhizoids are scattered and occur individually. Reticulate plastid | *Rhizoclonium* |
| 12b. | Rhizoids typically on two neighbour-cells, so they occur in pairs. Central stellate plastid | *Rosenvingiella* |
| 13a. | Branches mutually free, reticulate, spongy plastid | *Cladophora* |
| 13b. | Branches more or less matted by narrow hyphae-like filaments, reticulate cylindrical plastid | 14 |

| | | |
|---|---|---|
| 14a. | Branches > 40 μm in width. Cells with several nuclei | *Acrosiphonia* |
| 14b. | Branches < 30 μm in width. Cells with one nucleus | *Spongomorpha* |
| 15a.(4) | Filaments form entangled masses | 16 |
| 15b. | Filaments are mutually free | 17 |
| 16a. | Central plastid with one pyrenoid. On stone and bulwark in salt-dust zone | *Rosenvingiella* |
| 16b. | Reticulate, spongy plastid with several pyrenoids. Common on soil in salt marshes and may occur as a thin cover on stones in the wave-splash and salt-dust zones and as unattached filaments between various algae in the sublittoral | *Rhizoclonium* |
| 17a. | Unattached filaments typically very curled, forming mats in shallow water at sheltered localities, densely connected into an elongate ball-shape or twisted around other algae in the sublittoral | *Chaetomorpha linum*, *C. ligustica* |
| 17b. | Attached filaments | 18 |
| 18a. | Parietal plate- or belt-shaped plastid | 19 |
| 18b. | Reticulate, spongy plastid or a perforated cylinder-shaped plastid, many pyrenoids | 20 |
| 19a. | On stone or epiphytic, in the littoral or upper part of the sublittoral. Cells with one or a few pyrenoids | *Ulothrix* |
| 19b. | Epiphytic on crustose algae in the sublittoral. Few-celled slightly curved uniseriate filaments 4-14 μm in width. Cells without pyrenoids | *Okellya* |
| 20a. | Closely packed thalli in the littoral and upper part of the sublittoral, frequent in spring. Attached with rhizoids from the lowest or the lower cells of filaments | *Urospora* |
| 20b. | Individually or in fascicles of a few filaments. Basal cells elongate terminating in attachment discs | *Chaetomorpha* |
| 21a.(3) | Terete branches, approximately 0.5 cm in width. Syntagma of siphonous filaments | *Codium* |
| 21b. | Main branches with short branches in whorls | Charophyceae (see Schubert & Blindow, 2004) |
| 22a.(1) | Grow into calcified material (shells, stones, worm tubes, calcified red algae) | 23 |
| 22b. | Does not grow into calcified material | 27 |
| 23a. | Unicellular algae | sporophyte of *Gomontia* or *Monostroma* |
| 23b. | Branched filaments | 24 |

| | | |
|---|---|---|
| 24a. | Siphonous filaments (without cross walls) | *Ostreobium* |
| 24b. | Cellular filaments | 25 |
| 25a. | Thick often lamellated cross walls, no hairs | *Eugomontia* |
| 25b. | Cross walls not unusual wide, with hairs | 26 |
| 26a. | Spiral twisted hairs, filaments, 8-12 μm in width | *Phaeophila* |
| 26b. | Straight, narrow hairs, filaments, 3-7.5 μm in width | *Ruthnielsenia* |
| 27a.(22) | Unicellular alga | 28 |
| 27b. | Alga of several cells | 30 |
| 28a. | Cells small, ellipsoid, 1.5-5 μm in width and 3.5-8 μm in height, in great number forming blue-green spots or covers on echinoderms or at the mantle-line of bivalves | *Coccomyxa* (Chlamydomonadales, see Mortensen & Rosenvinge, 1933) |
| 28b. | Cells large, ellipsoid, 15-100 μm in width | 29 |
| 29a. | Cells with a colourless stipe. In dense mats, forming a velvet-like cover on stone in the wave-splash zone | *Codiolum*-phase of *Urospora* |
| 29b. | Endophytes | *Codiolum*-phase of *Acrosiphonia*, *Monostroma*, *Spongomorpha*, *Ulothrix* |
| 30a. | Small monostromatic parenchyma or filamentous with parenchymatous sections. Central stellate plastid. Wave-splash and salt-dust zone | *Prasiola* |
| 30b. | Not parenchymatous. Parietal plastid | 31 |
| 31a. | Small, branched bush-like alga of uniseriate filaments, up to 3 mm in height. Distinct basal cell | *Lychaete* |
| 31b. | Disc, crust or filamentous without a distinct basal cell | 32 |
| 32a. | Large irregular cells, 25-125 μm in width, typically at some distance from each other and connected by narrow colourless filaments | *Blastophysa* |
| 32b. | No colourless connecting filaments between cells | 33 |
| 33a. | Approximately circular discs | 34 |
| 33b. | Branched filaments, sometimes confluent to pseudoparenchyma | 38 |
| 34a. | Disc-shaped, margin regular with furcate cells | *Ulvella scutata*, *U. setchellii* |
| 34b. | Disc with mutually free filaments of 1-2 cells at margin | 35 |
| 35a. | Vegetative cells typically ovoid with coarse straight hairs | *Ochlochaete* |
| 35b. | Without hairs | 36 |

| | | |
|---|---|---|
| 36a. | Approximately circular monostromatic disc with cylindrical cells at margin, 3-4 µm in width and 1.5-3 times as long as wide | 37 |
| 36b. | Polystromatic pseudoparenchyma of irregular shape. Epiphytic on *Fucus* spp. | *Pseudendoclonium fucicola* |
| 37a. | Central cells develop into large club-shaped sporangia, with many swarmers at maturity | *Syncoryne* |
| 37b. | Central cells develop into sporangia, only slightly larger than vegetative cells and contain 4 swarmers at maturity | *Neostromatella* |
| 38a. | With hairs | 30 |
| 38b. | Without hairs | 41 |
| 39a. | Hairs straight, part of ordinary vegetative cells with 1 (-3) pyrenoids | *Ochlochaete* |
| 39b. | Basal part of hairs rounded, onion-shaped and smaller than ordinary vegetative cells | 40 |
| 40a. | Basal part of hairs with a small plastid | *Bolbocoleon* |
| 40b. | Basal part of hairs colourless, without plastid | *Ulvella* |
| 41a. | Endozoic | 42 |
| 41b. | Epi- or endophytic, on stone or other solid substrata | 44 |
| 42a. | In periostracum of Flat Periwinkle (*Littorina obtusata*) | *Tellamia* |
| 42b. | In chitin wall of bryozoans and hydroids | 43 |
| 43a. | In the hydroid *Dynamena pumila* | *Pseudendoclonium dynamenae* |
| 43b. | In bryozoans (*Alcyonidium*, *Flustra* and *Securiflustra*) | *Epicladia philipsii, E. flustrae* |
| 44a. | Few celled algae in wood such as poles of bulwark, and on stone in the salt-dust zone | *Pseudendoclonium submarinum* |
| 44b. | In epidermis cells of decaying, drift leaves of Eelgrass (*Zostera marina*) | *Epicladia perforans* |
| 45a.[2] | Blades, few mm and up to 1 cm, consist of thick-walled cells in rows, each cell with a central stellate plastid with one pyrenoid. Wave-splash and the salt-dust zone | *Prasiola* |
| 45b. | Mainly larger fronds, each cell with a parietal plastid | 46 |
| 46a. | Parenchymatous threads of 2 parallel cell rows | *Percursaria* |
| 46b. | Parenchymatous with more than 2 parallel cell rows | 47 |
| 47a. | Monostromatic blade | 48 |
| 47b. | Blade of 2 cell layers or tubular thallus of one cell layer, with or without branches and in part compressed | 51 |

| | | |
|---|---|---|
| 48a. | Base tubular, marginal cells of blade distinctly larger than other cells. Vegetative cells, each with 1-4 pyrenoids. Thallus becomes olive-brown to nearly black when decayed or dry | *Ulvaria* |
| 48b. | Most vegetative cells with one pyrenoid. Thallus remain green when dry | 49 |
| 49a. | Young algae are monostromatic bladder-shaped membranes, which split, become cone-shaped and latter irregularly split in several elongate lobes. Cells just above the base are elongate with several pyrenoids. Present in October-April (June) | *Monostroma* |
| 49b. | Blade lanceolate- or tongue-shaped, attach by a felty mass of rhizoids. Dry individuals have a shiny surface | 50 |
| 50a. | Blade elongate, may have a few lobes, margin very wavy to give a frilly appearance. Present in spring | *Protomonostroma* |
| 50b. | Blade rounded, attach to substratum by rhizoids from cells in a large area of the lower part. Present all year | *Gayralia* |
| 51a. | Tubular parenchyma, few centimetres in height, of relatively small cells, 5-7 µm in width, with thick walls. Plastid with a central pyrenoid | *Blidingia* |
| 51b. | Larger thallus with cells > 7 µm in width. Parietal plastid with one or several pyrenoids | 52 |
| 52a. | Tubular olive-green to brownish unbranched parenchyma. Cells in very regular transverse and longitudinal rows. New cells are in groups of 2 or 4 cells in a mutual outer cell wall | *Capsosiphon* |
| 52b. | Clear green, blade or tubular parenchyma. Cells in rows or irregularly arranged | *Ulva* |

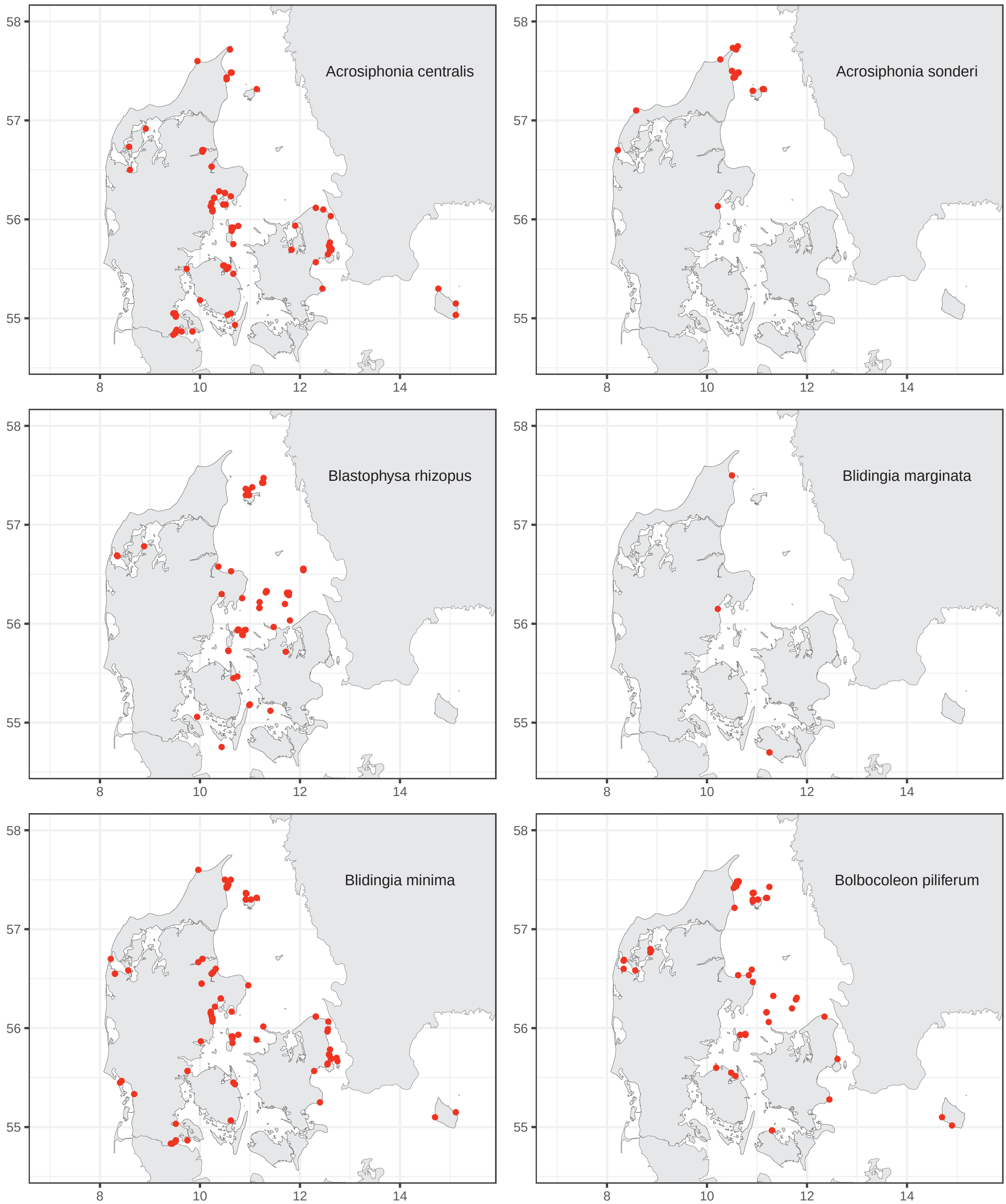
# Collection localities for Chlorophyta – Green algae

Maps with collection localities for the algae are based on information in the database of the algal herbarium, Natural History Museum of Denmark, which contains registration of approximately 60.000 Danish seaweeds. The dots in the maps show where the algae were collected and comprise attached and drift individuals.

For each species, a map contains information of both generations for species with heteromorphic life histories.

There is no map for *Acrosiphonia arcta*, which is only recorded as drift in Danish waters. Maps are also absent for species only collected at a single or a few localities. These include *Cladophora hutchinsiae, Ulva curvata, U. intestinaloides, Ulvella pachypes, U. ramulosa* and *Urospora neglecta*.

*Cladophora flexuosa* and *C. sericea* are easily confused, therefore collection localities for both species occur on one map. Similarly, there is only a single map for *Ulvella pseudorepens* and *U. repens*, which occur with the same algal host, and reliable identification is only possible after culture studies.


Acrosiphonia centralis
Acrosiphonia sonderi
Blastophysa rhizopus
Blidingia marginata
Blidingia minima
Bolbocoleon piliferum
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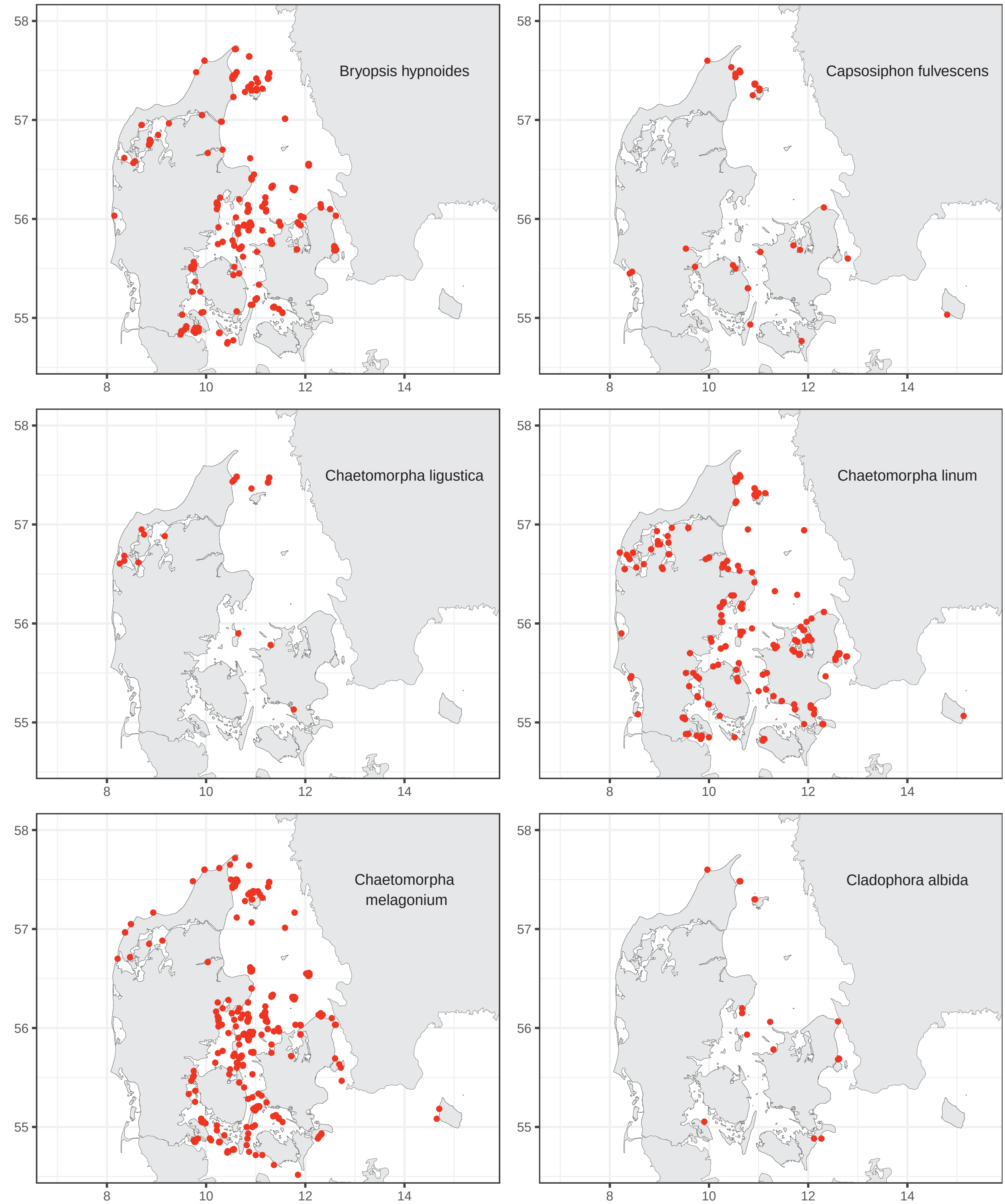
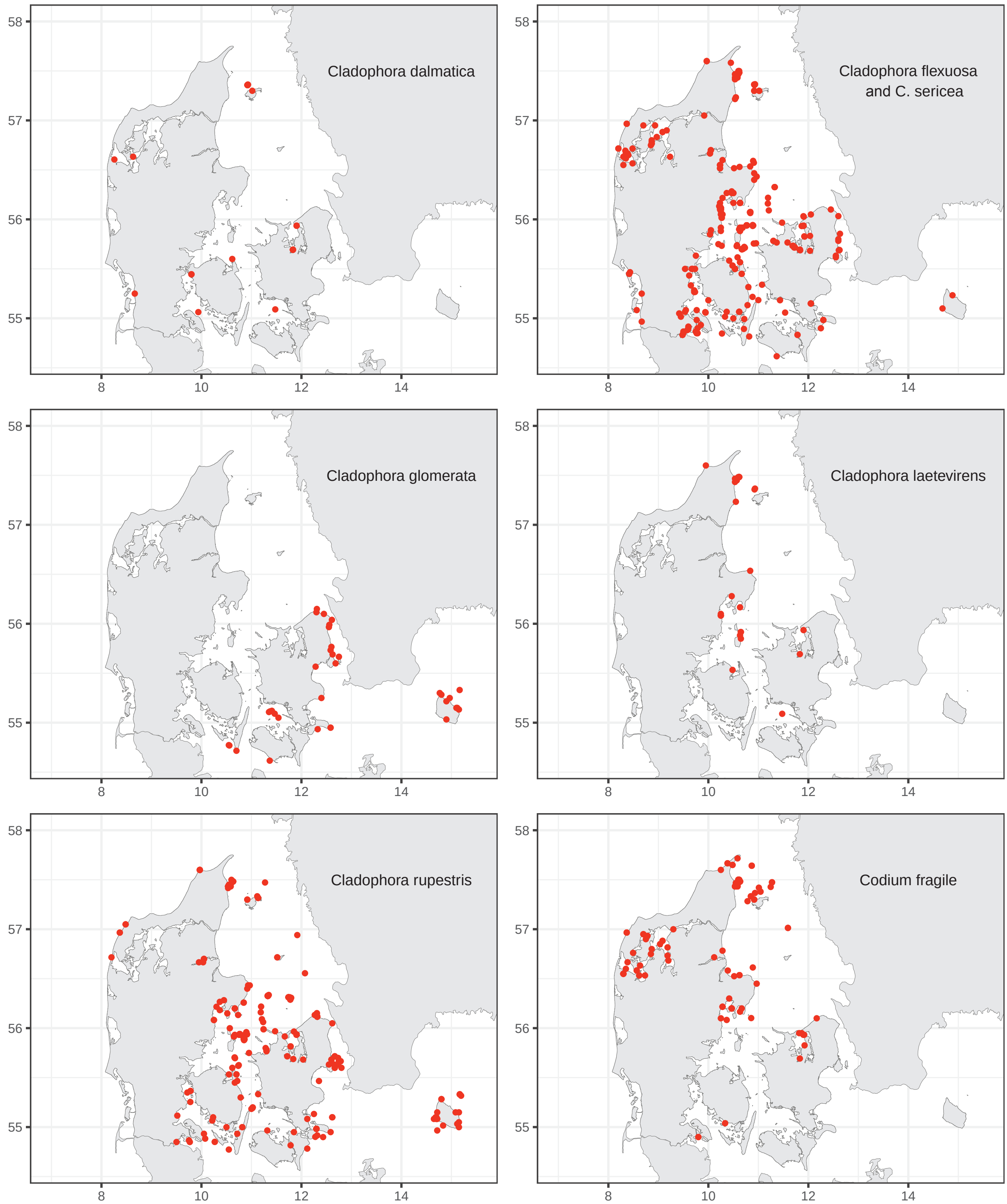

Bryopsis hypnoides
Capsosiphon fulvescens
Chaetomorpha ligustica
Chaetomorpha linum
Chaetomorpha melagonium
Cladophora albida


Cladophora dalmatica
Cladophora flexuosa
and C. sericea
Cladophora glomerata
Cladophora laetevirens
Cladophora rupestris
Codium fragile
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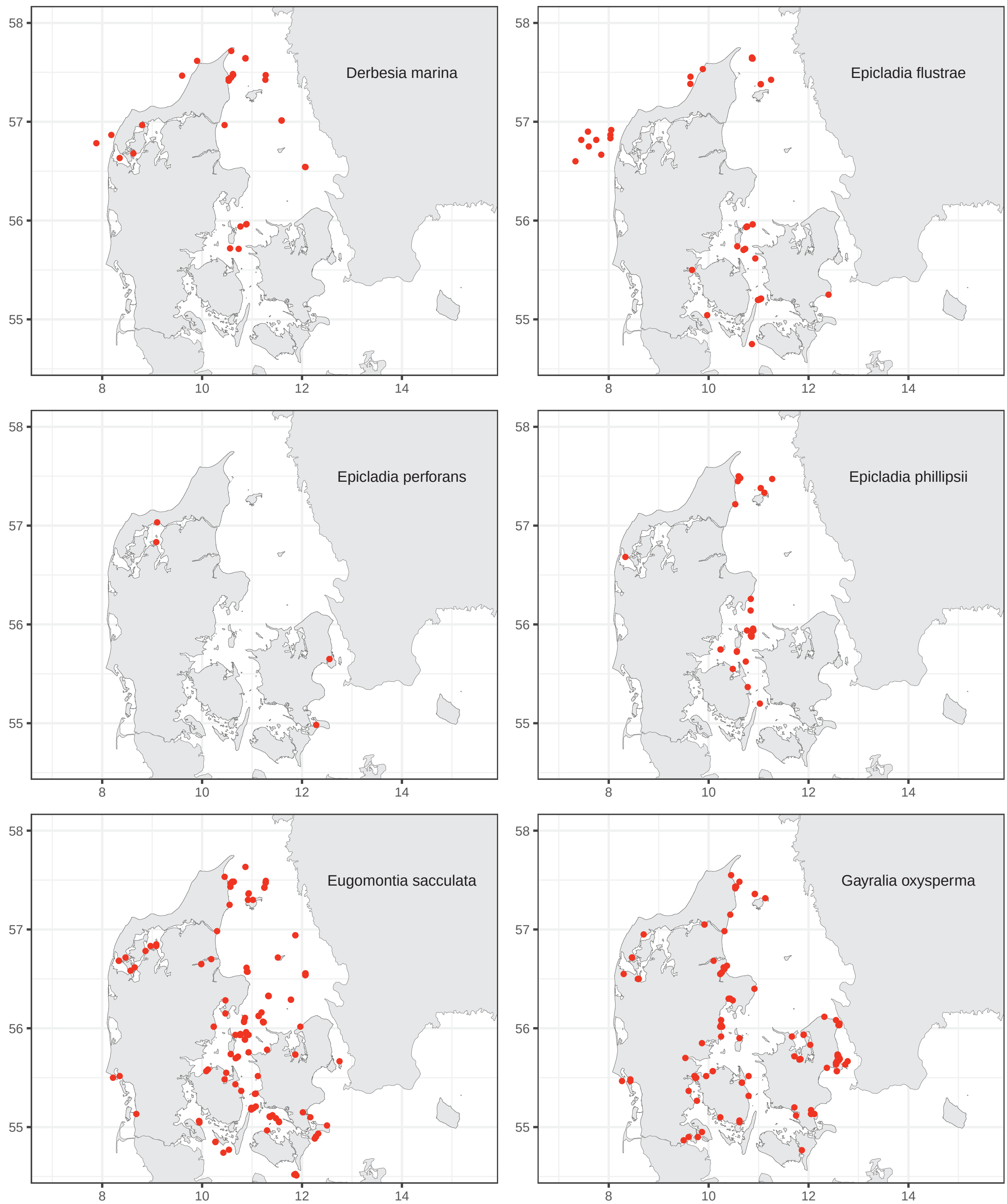
Derbesia marina
Epicladia flustrae
Epicladia perforans
Epicladia phillipsii
Eugomontia sacculata
Gayralia oxysperma
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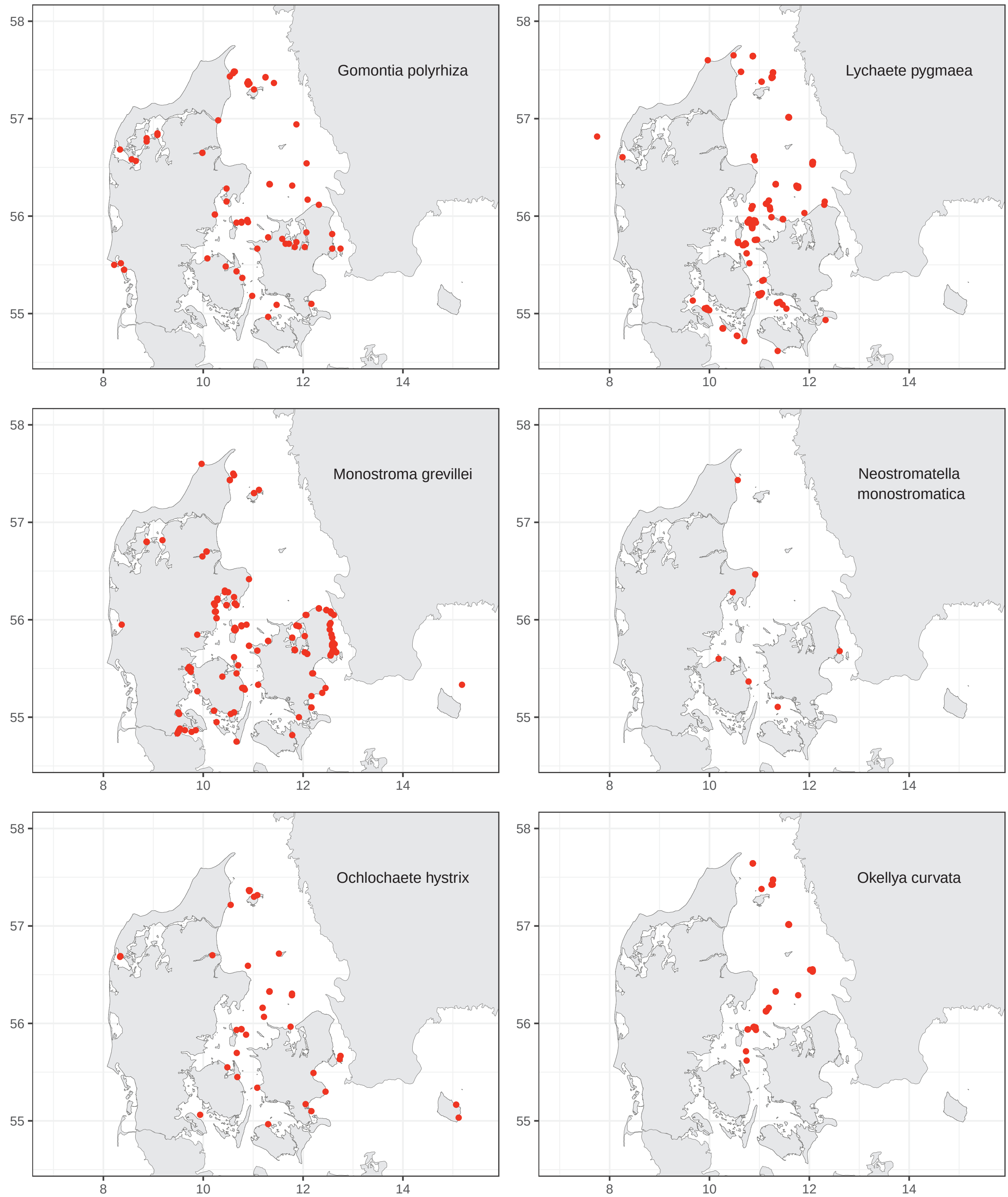
Gomontia polyrhiza
Lychaete pygmaea
Monostroma grevillei
Neostromatella monostromatica
Ochlochaete hystrix
Okellya curvata
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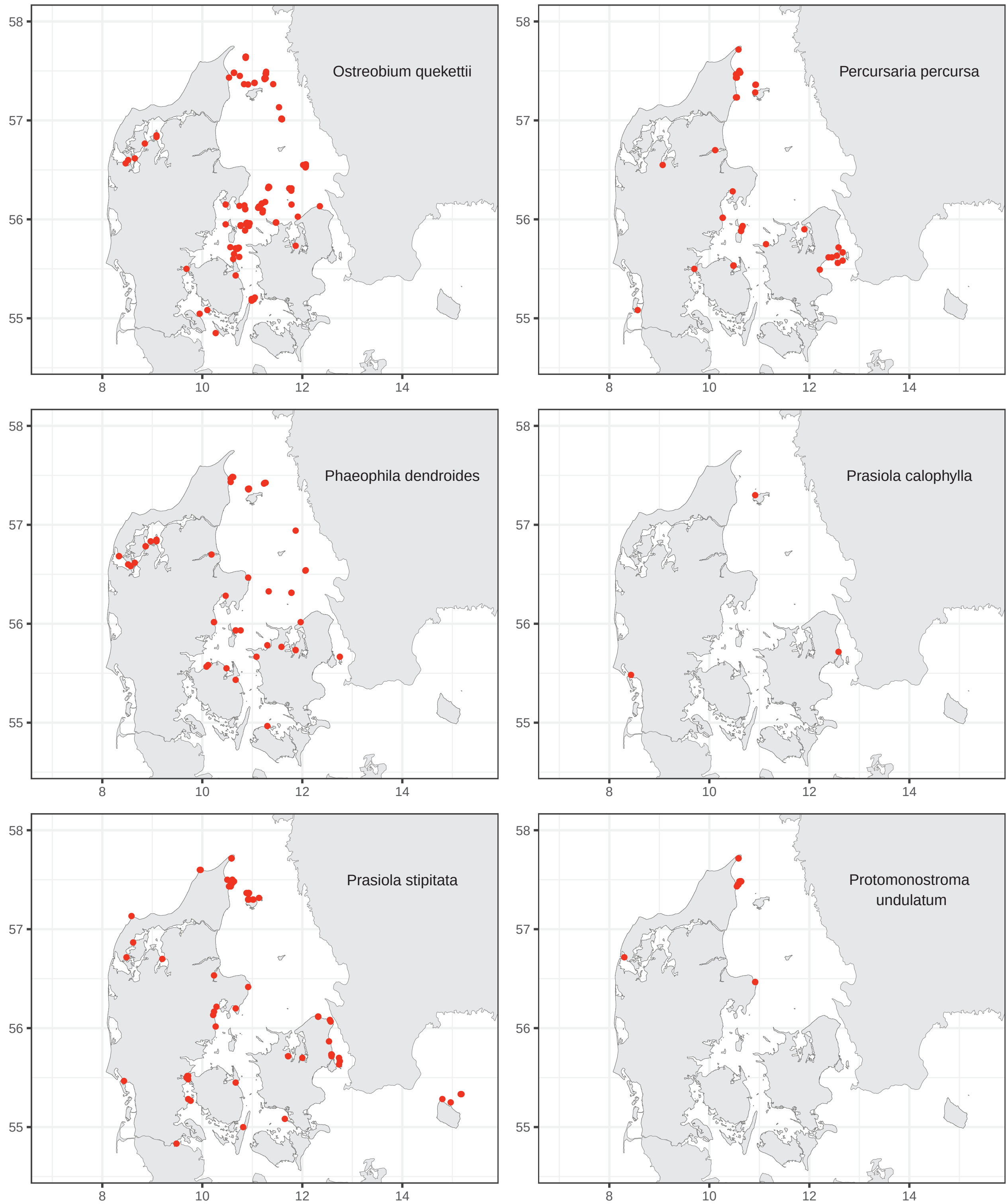
Ostreobium quekettii
Percursaria percursa
Phaeophila dendroides
Prasiola calophylla
Prasiola stipitata
Protomonostroma undulatum
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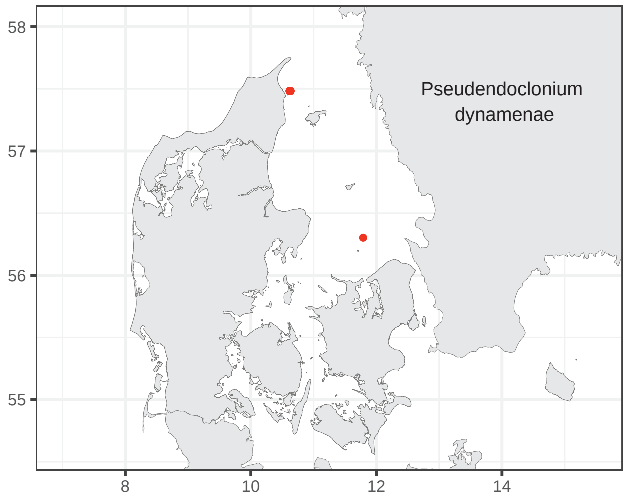
Pseudendoclonium
dynamenae
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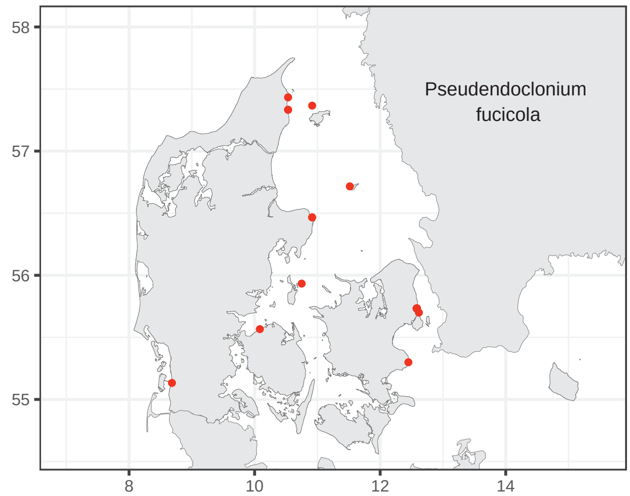
Pseudendoclonium
fucicola
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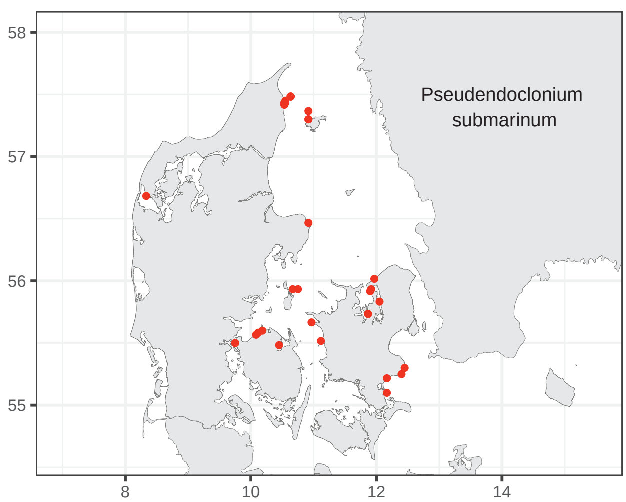
Pseudendoclonium
submarinum
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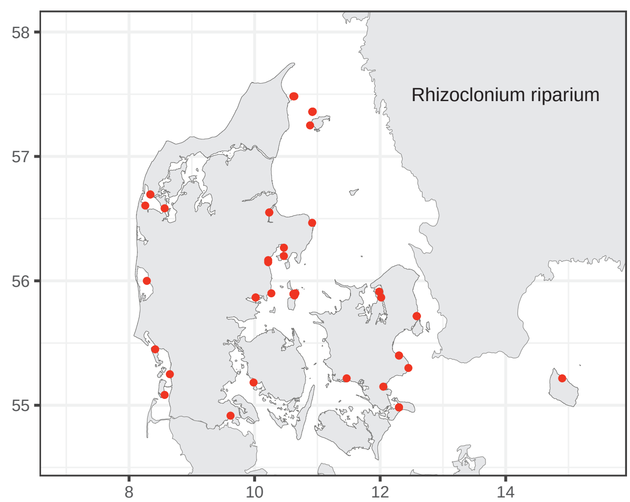
Rhizoclonium riparium
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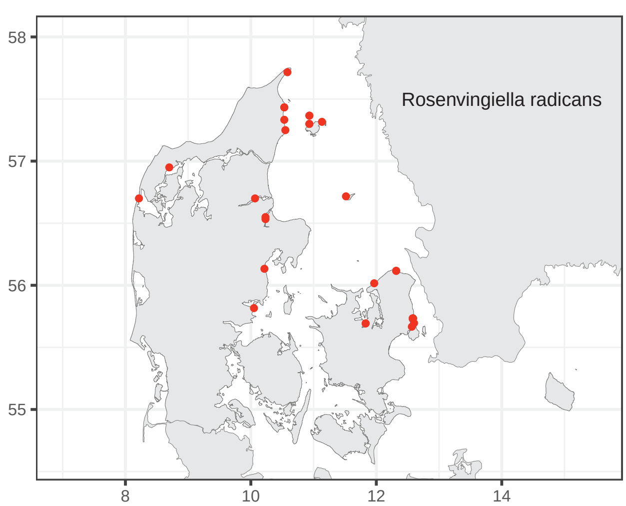
Rosenvingiella radicans
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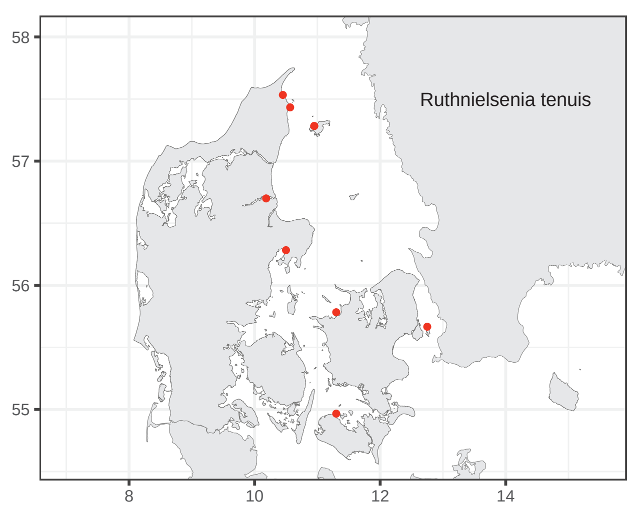
Ruthnielsenia tenuis
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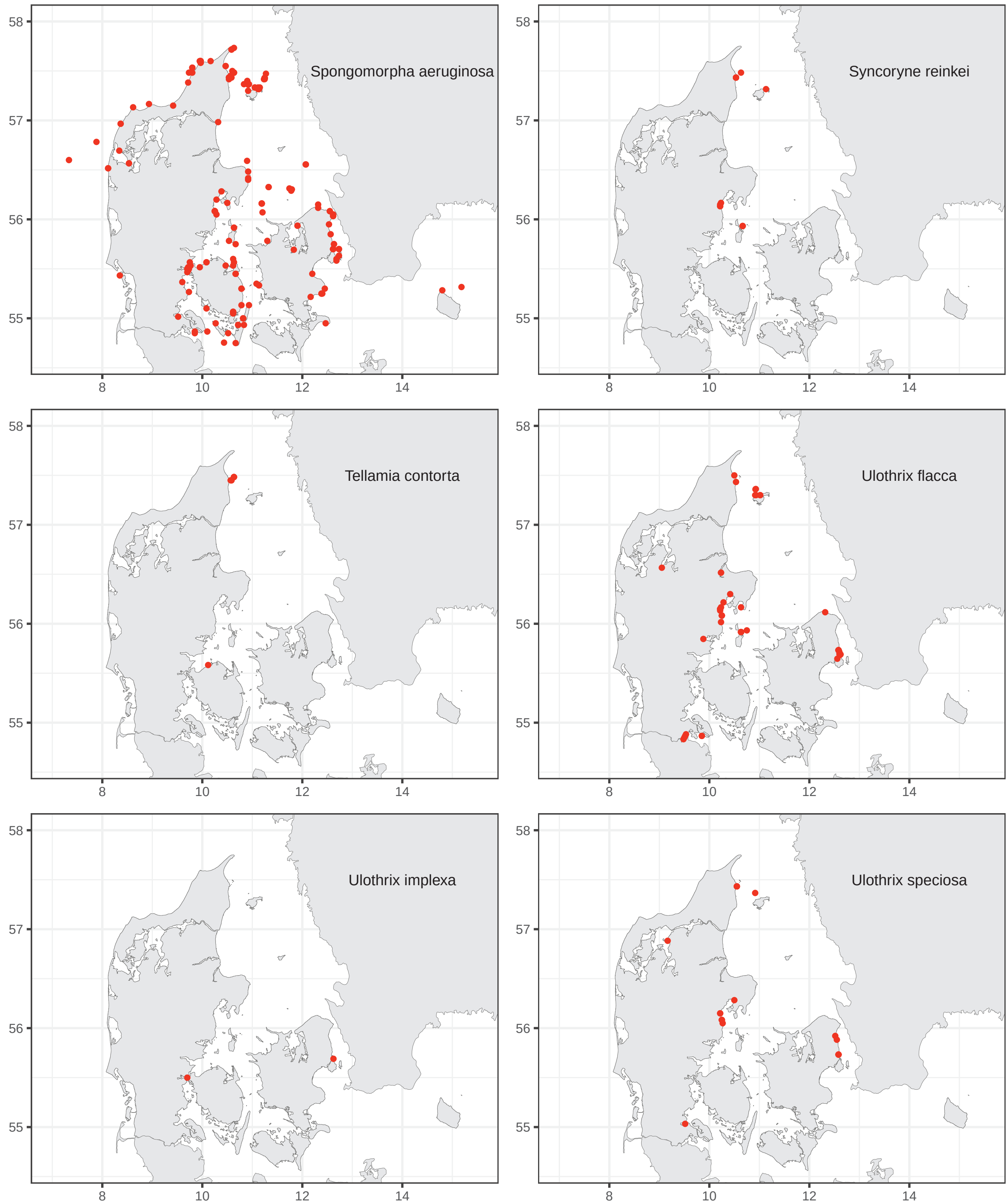
Spongomorpha aeruginosa
Syncoryne reinkei
Tellamia contorta
Ulothrix flacca
Ulothrix implexa
Ulothrix speciosa
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Ulothrix subflaccida
Ulva clathrata
Ulva compressa
Ulva fenestrata
Ulva flexuosa
Ulva intestinalis
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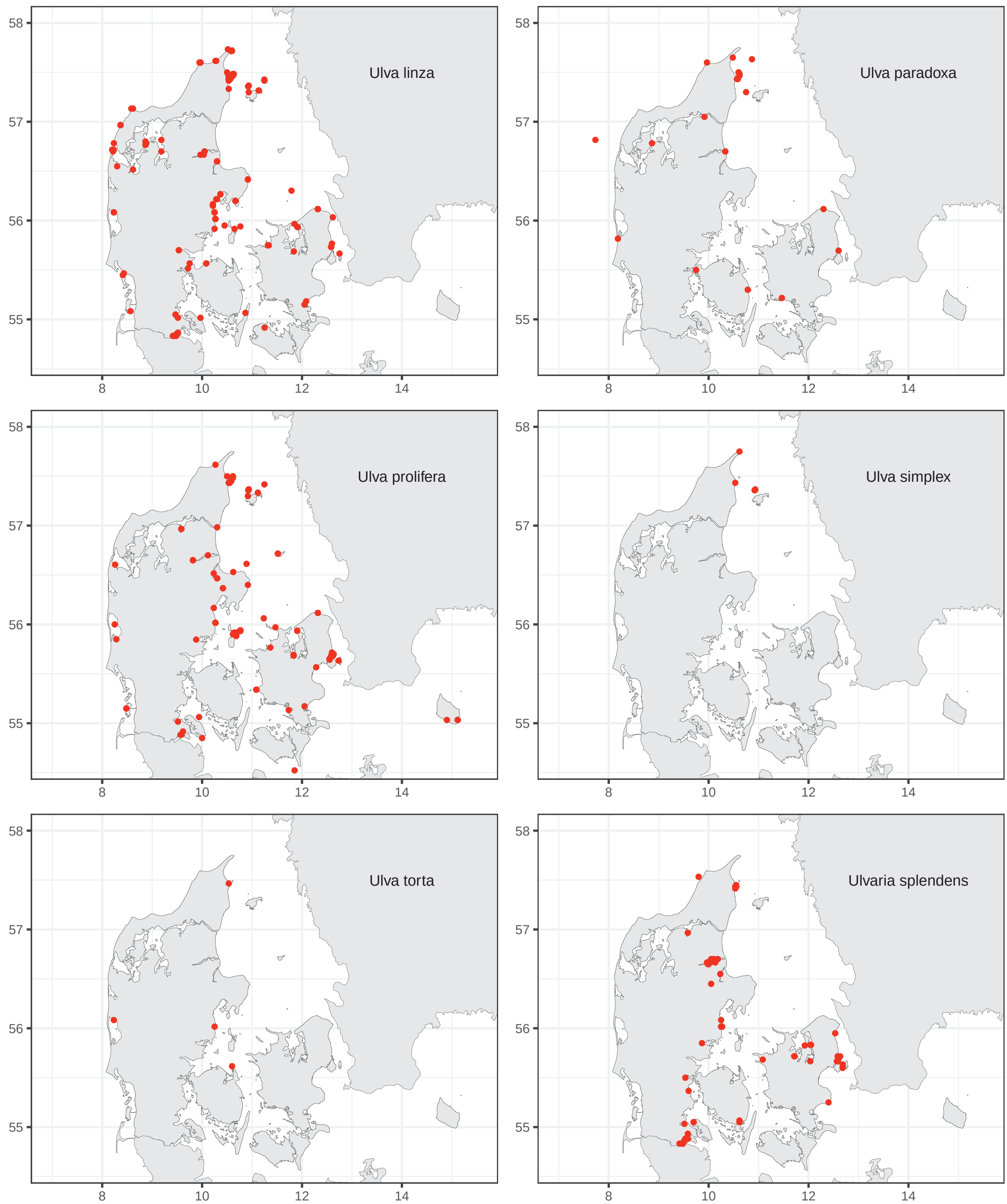
Ulva linza
Ulva paradoxa
Ulva prolifera
Ulva simplex
Ulva torta
Ulvaria splendens
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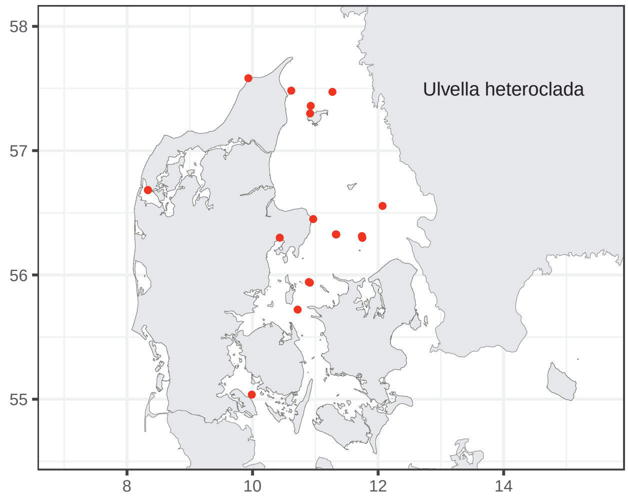
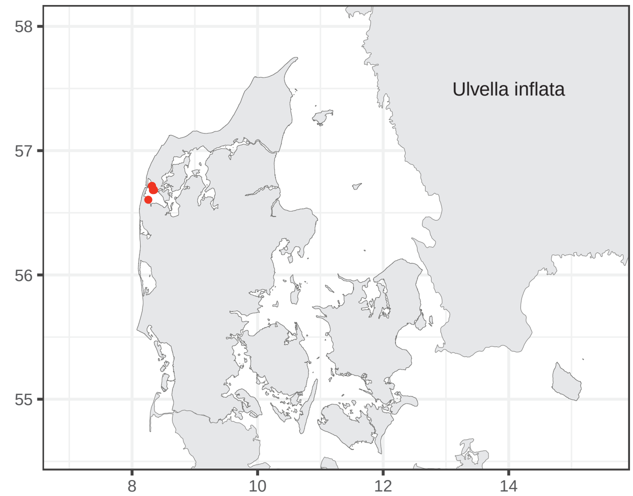
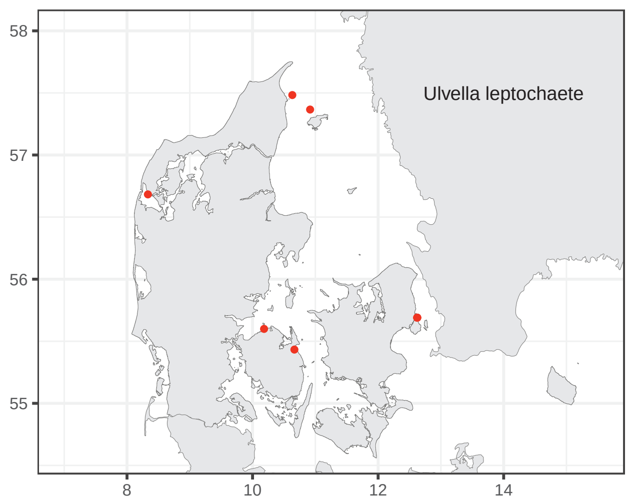
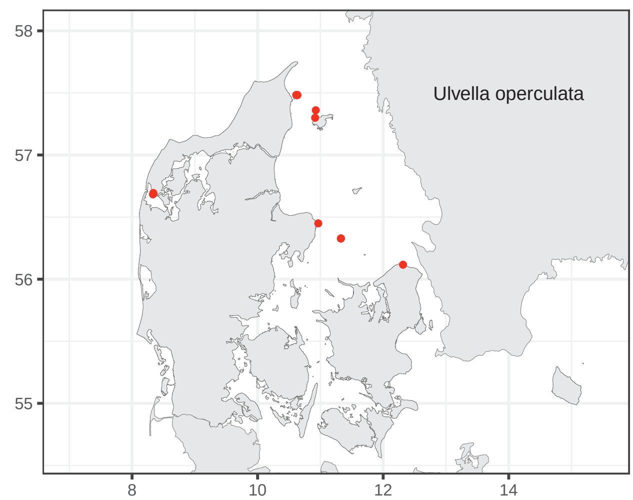
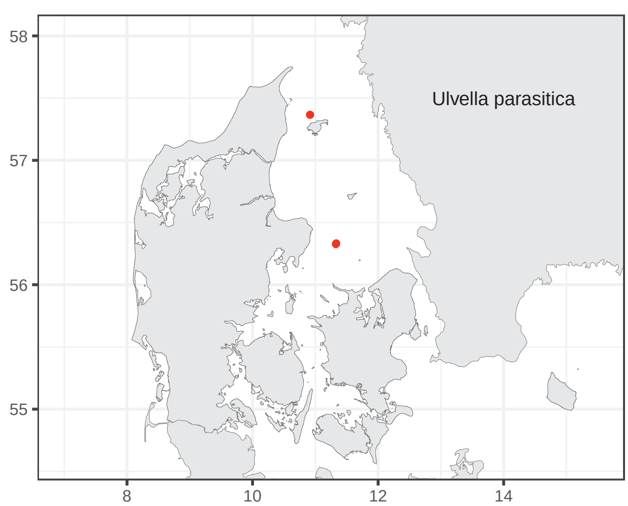
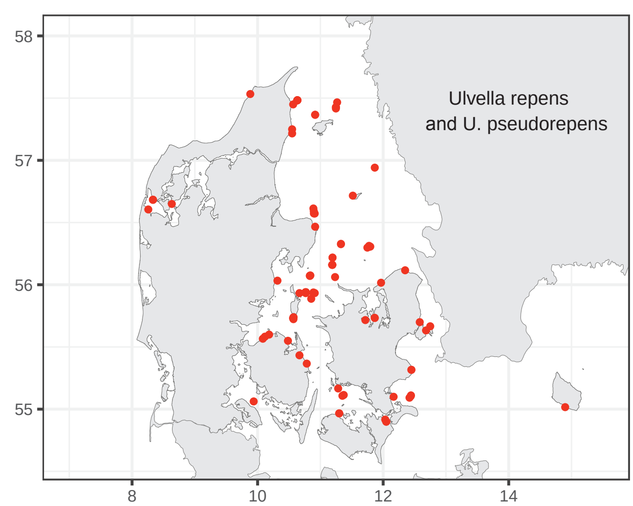

Ulvella heteroclada

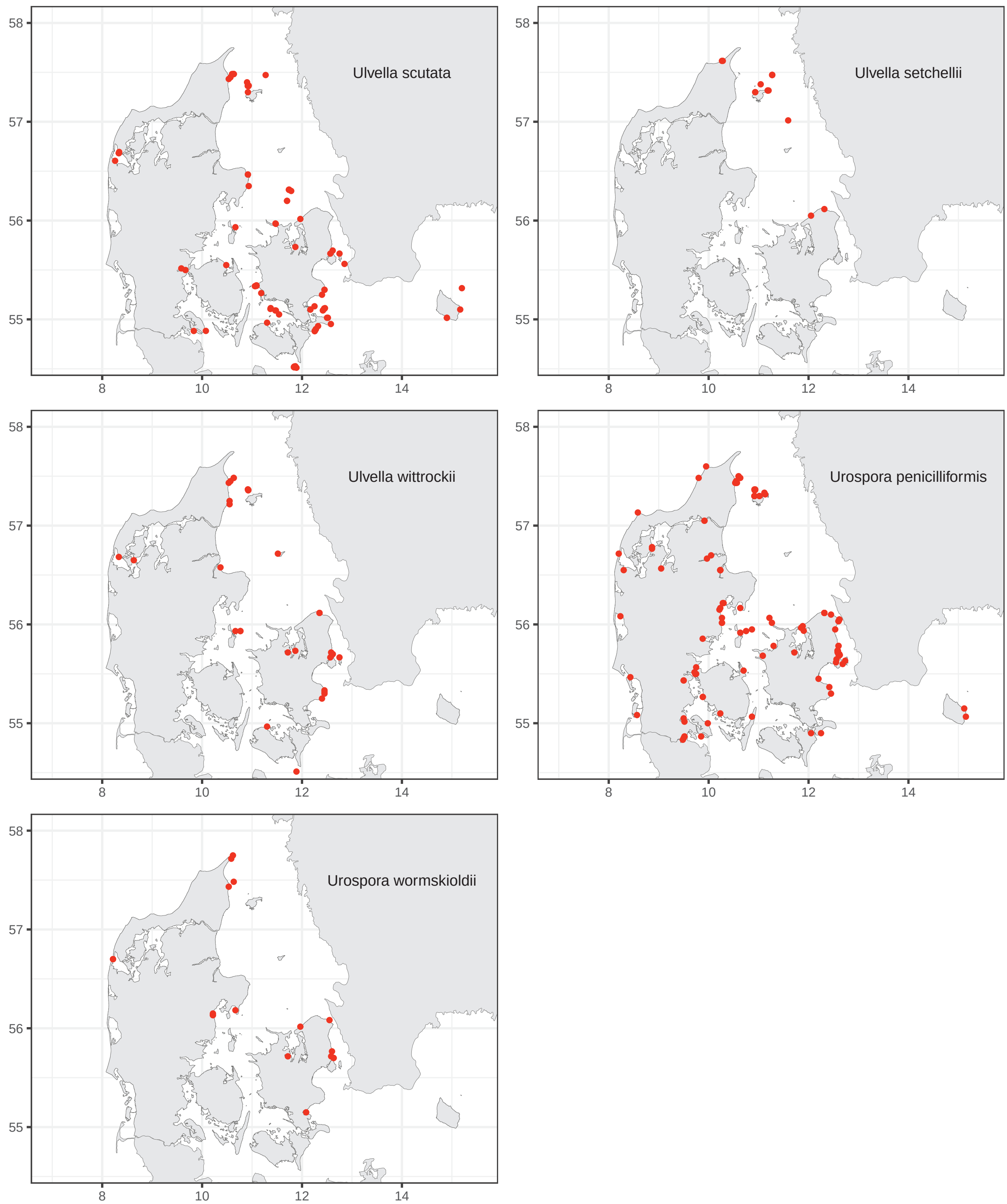

Ulvella inflata


Ulvella leptochaete


Ulvella operculata


Ulvella parasitica


Ulvella repens
and U. pseudorepens


Ulvella scutata
Ulvella setchellii
Ulvella wittrockii
Urospora penicilliformis
Urospora wormskioldii
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# Glossary of scientific terms

**Abaxial.** The side or face of a lateral branch away from the main axes or branch. Branches or sporangia placed on outside of branches.
**Acrochaete-hair**. Colourless hair-like extension from a small colourless bulbous base separated by a wall from the carrying vegetative cell below.
**Acropetal growth.** Growth and formation of branches occur at the apex (*Cladophora*).
**Acute.** Tapering sharply to a point or a narrow angle.
**Adaxial.** The side against the main axes. Branches or sporangia placed on inside of branches.
**Air-bladder**. Air filled balloon-like sac.
**Agamospore.** Formed by mitotic divisions in a vegetative cell, and when released germinate to conchocelis (Bangiaceae).
**Agar.** Pectin-like product from the walls of red algae e.g. *Gracilaria*. Agar is used as a gelling agent in the food industry and as a stabilizer in growth media used for microbiological research.
**Akinete.** Asexual resting spore formed by transformation of a vegetative cell in which the cell content condenses and is surrounded by a thick wall. (*Chroodactylon* and *Stylonema*).
**Alternate.** Individual branches or sporangia arranged in two rows and regularly turned to one or the other side. Also used for alternation between different phases in a life history.
**Androphor.** Special stalk cell for antheridia (*Kylinia*).
**Anisogametes**. Gametes dissimilar in shape, size or behaviour.
**Antheridium.** Cell where the male gametes develop.
**Anticlinal.** Perpendicular to the surface, a term used for cell divisions (Sphacelariales).
**Apex.** The tip or youngest part of a branch or thallus.
**Apical.** Relating to the apex or top.
**Apical cell.** Cell at the apex of an axis or a frond.
**Apical growth.** Growth mainly by divisions of the apical cell.
**Aplanospore.** Vegetative spore without flagella formed in sporangia.
**Archeospore.** Spore that develops from a vegetative cell, and when released germinates to a new erect thallus (Bangiaceae).
**Ascending filament.** Prostrate filament that curves upward.
**Asexual.** Vegetative reproduction not involving sexual copulation.
**Ascocyst.** Special hyaline or darkly stained cell with fucosan (brown algae).
**Assimilator.** Special filament of vegetative cells with plastids (Chordariaceae).
**Attenuate.** Tapering gradually.
**Auxiliary cell.** Special cell in the female gametophyte of some red algae, contributes to multiply the gonimoblasts.
**Axial filament.** Central filament of branch or thallus.

**Bifurcate.** Equally divided into two branches or forks (dichotomous branching).
**Biseriate.** Arranged in two rows or series.
**Bisporangium.** Sporangium with two spores.
**Blade**. Flat (leaf-like) part of thallus.
**Bolbocoleon-hair.** Small onion-shaped cell with a hair-like colourless extension between ordinary vegetative cells.
**Brown algal hair.** See true brown algal hair.
**Byssus.** Thin filaments on blue mussels, at first sticky, later becoming a tuft of horny threads.

**Caecostomata.** Small cavities just beneath the surface of *Fucus distichus*. Best seen in light falling through the thallus.
**Carragenan.** Pectin-like product extracted from the cell walls of e.g. *Chondrus crispus* and used as a gelling agent particularly in the food industry (E 407).
**Cap-shaped plastid.** Plastid placed in the upper part of the cell, looking like a small cap (*Ulva*).

**Carpogonial branch.** Special branch in the female gametophyte, whose terminal cell is the carpogonium.
**Carpogonium.** Female reproductive cell (red algae).
**Carposporangium.** Sporangium on the carposporophyte, each forming one carpospore (red algae).
**Carpospore.** Diploid spore released from carposporangium on the carposporophyte (red algae).
**Carposporophyte.** Diploid cell structure formed from the zygote on the female gametophyte (red algae).
**Cartilaginous.** Texture tough, like cartilage.
**Cell fusion.** Cells of different cell rows fused together.
**Coaxial.** Monomerous thallus with cells uniform in length and the end-cell walls form curving rows in a transverse direction to the filaments (Corallinaceae).
**Complanate.** Flattened or branched in one plane.
**Conceptacle.** Jar-shaped cavity with reproductive structures.
**Conceptacle plate.** Cell layer that covers the conceptacle in calcified crusts (Corallinaceae).
**Connecting filament**. Filament connecting a carpogonium and an auxiliary cell.
**Copulation.** Fusion of gametes.
**Cortex**. Outermost cell layers of thallus, usually small and pigmented.
**Cruciate**. Cross-shaped. Division in a tetrasporangium in which the first and the following walls are perpendicular to each other.
**Crustose.** Crust-like, closely adherent outwardly radiating thallus. Monostromatic or multilayered.
**Cryptostoma** (pl. **cryptostomata**). Small cavity with brown algal hairs (*Fucus*).
**Cyst.** Vegetative cell transformed into a spore surrounded by a thick wall (*Prasiola*).

**Dentate.** With tooth-like projections.
**Determinavit (det.).** Identified by.
**Dichotomy.** Bifurcate branching.
**Dichotomous branching.** Division of an apical cell, that develops into two equal branches. (*Dictyota* and *Fucus*). See also pseudodichotomous.
**Diffuse growth.** Growth by division of scattered cells.
**Dimerous thallus.** Consists of prostrate filaments along the substrate from which upright filaments originate (Corallinaceae).
**Dioecious.** Male and female reproductive structures on different individuals.
**Diploid.** With a double set of chromosomes (2n) in each nucleus.
**Direct life history.** Without change of generations.
**Disc.** Almost circular, closely adherent pseudoparenchyma.
**Discoid.** Disc-shaped.
**Distal.** Away from the base of the thallus, the upper part.
**Distichous**. Arranged in two rows along axis.
**Distromatic.** Composed of two cell layers.

**Egg.** Non-motile female gamete, usually larger than the male.
**Emulsifier.** Product that assists the formation and stabilization of other substances, e.g. cream.
**Endogenous.** Originates inside an axis, e.g. a branch which develops from a cell of a central filament (*Leptosiphonia*).
**Endophytic.** Growing within another alga or plant.
**Endozoic.** Growing within an animal.
**Entire.** Margin without divisions, indentations, lobes or proliferations.
**Epidermis.** Surface layer, in an alga of several cell layers.
**Epilithic.** Growing on stone (pebble or rock).
**Epiphytic.** Growing on the surface of an alga or plant.
**Epithallial cell.** Cell of the surface layer (Corallinaceae).
**Epithet.** Latin name that indicates a species, for instance '*vesiculosus*' in *Fucus vesiculosus*.
**Epizoic.** Growing on the surface of an animal.
**Eutrophic.** Nutrient rich.
**Eyespot.** Orange-red spot in swarmers, composed of carotenoid, and often occurs close to a flagellum.

**False branching.** A type of branching of a uniseriate filament within a sheath. After rupture of the filament, the part below the place of rupture grows through the sheath and continues as a branch. The part above the rupture continues as before (Stylonemataceae).
**False hair**. Pale apex of filament tip with relatively narrow cells elongating toward the apex and containing a few plastids.

**Fasciculate.** Forming a dense bundle of filaments.
**Fertile**. With reproductive structures.
**Filament.** A branched or unbranched thread-like row of uniseriate or multiseriate cells.
**Flagellum** (pl. **flagella).** Thin thread-like appendage used for locomotion.
**Frond**. Part of thallus above the attachment structure.
**Furcate.** Forked.
**Furcellaran**. Pectin-like product extracted from the cell walls of e.g. *Furcellaria lumbricalis*. Furcellaran, also known as danagar, has a thickening effect and is used in the food industry.
**Fucosan.** Component of cells with tannin, often in small vesicles around the nuclei, and occurs in ascocysts (brown algae).
**Fucoxanthin.** Brown pigment in plastids of brown algae.
**Fusion.** Two or more cells combine.

**Gelatinous.** Slimy and jelly-like.
**Gametangium.** Cell producing one or more gametes.
**Gamete.** Sexual cell.
**Gametophyte.** Sexual individual.
**Geniculate.** Articulated (Corallinaceae).
**Germination disc.** Germination pattern where the first cells form a small quadrangular monostromatic plate (e.g. Corallinaceae).
**Germ tube.** A thin tube on a germling.
**Gland cell.** Colourless cell with refracting content (red algae).
**Gonimoblast.** Dense diploid cell structure that produces carpospores on female gametophytes (red algae). Mentioned as cystocarp by some authors (red algae).
**Gonimocarp.** Gonimoblast surrounded by pericarp. Mentioned as cystocarp by some authors (red algae).
**Growth by stretching.** Takes place without cell divisions when the cells increase in length.
**Growth zone.** Area with many cell divisions, observed as many short cells (= meristem).

**Hair.** Long narrow filament on the surface or at the apex of the frond, consisting of one or several cells.
**Hairy flagellum.** Flagellum with thin appendices and winding movements. In brown algal swarmers directed forwards.
**Haploid.** A single set of chromosomes (n) in each nucleus.
**Hapteron** (pl. **haptera**). Short branch to attach the alga (*Furcellaria*, Laminariales).
**Heteromorphic.** Life history with different generations of dissimilar morphology.
**Heterotrichous.** Different looking parts e. g. prostrate and upright filaments.
**Holdfast.** Structure attaching thallus to the substratum.
**Hyaline.** Colourless, transparent.
**Hypha** (pl. **hyphae**). A thin pale filament.

**Illegitimate name.** A name not in agreement with the rules of botanical nomenclature.
**Inflated.** Distended by air.
**Intercalary.** Occurring in any position within a thallus other than apex or base.
**Inverse egg shape.** Egg-shaped with the broad part above the middle (obovate).
**Involucral branches.** Small branches surrounding a gonimoblast (red algae).
**Isodiametric.** Cells with diameters or axes of equal length.
**Isogametes.** Gametes that look alike, have identical shape and size and behave similarly.
**Isomorphic.** Life history with different generations of similar morphology.

**Lamellated.** Layered.
**Lanceolate.** Narrow and tapering in both ends.
**Lateral.** Axes or sporangia formed as branches to a main axis or another lateral axis.
**Legit (leg.).** Collected by.
**Lenticular**. Lens-shaped.
**Linear.** Long and narrow with parallel sides.
**Littoral zone.** Part of shore covered by water at high water and dry at low water. Some authors also include the zones beaten by waves, spray or salt dust.
**Lobe.** Extension or patch.

**Macrothallus** (pl. **macrothalli**). The largest phase in a life history with an alternative microthallus phase.
**Maerl.** Loose-lying corallines (free-living rhodoliths), often covering large areas on the sea bottom (Corallinaceae).
**Margin.** Edge of thallus.
**Medulla.** The innermost part of thallus, often of colourless tissue.
**Membranous**. Cells forming a delicate thin sheet, appearing like a membrane
**Meiosis.** Division of nuclei that halves the number of chromosomes.
**Meristem.** Growth zone.
**Microthallus** (pl. **microthalli**). The smallest phase in a life history with an alternative, larger, macrothallus phase.
**Midrib.** Conspicuous thickened central axis of a thallus.
**Mitosis.** Division of nuclei after which the chromosome number is unchanged.
**Monoecious**. Male and female reproductive structures on the same individual.
**Monomerous.** Thallus composed of prostrate filaments that bend upward to become perpendicular to the substratum (Corallinaceae).
**Monophyletic.** Group of organisms with the same ancestor.
**Monopodial.** Growth form in which the branches develop below the apical cell and the main axis is maintained as the line of growth.
**Monosporangium.** Sporangium in which a single spore is formed.
**Monostromatic.** Composed of single layer of cells.
**Multiaxial syntagma.** Syntagma with several central filaments and several apical cells.
**Multinucleate**. Cell with several nuclei.
**Multiporate conceptacle.** Roof of conceptacle with many pores (Corallinaceae).

**Negatively phototatic.** Moving away from the light source.
**Nemathecium.** Thickened area or special branch with reproductive structures.
**Neutral spore.** Spore formed by mitotic division in a vegetative cell and germinating into an upright thallus (Bangiaceae).
**Nomenclature.** Rules of scientific naming.

**Obovate**. Broadest part above the middle = inverse egg-shape.
**Ochlochaete-hair.** Colourless, coarse straight hair from the wall of a vegetative cell, very characteristic when they arise from the narrow end of ovoid cells.
**Octosporangium.** Sporangium producing eight spores.
**Octospore.** One of the spores formed in an octosporangium.
**Oogamous reproduction.** Fusion between non-motile female egg cell and male gamete.
**Oogonium.** Cell producing egg cells.
**Opposite.** Two from the same position, opposite to each other, e.g. branches or sporangia.
**Organelle.** Specialised structure within a cell (e.g. nucleus, plastid), surrounded by a membrane and involved with a particular function in the cell.

**Palisade cells.** Dense and relatively tall narrow cells (Corallinaceae).
**Paraphysis.** Short asexual filament or cell between sporangia (*Rhodophysema*, brown algae).
**Parasite.** Growing on another organism from which nutrients are obtained.
**Parasporangium.** Irregular sporangium with more than four spores of the same nuclear phase as the parent thallus.
**Paraspore.** Spore formed in a parasporangium.
**Parenchyma.** Compact tissue with cell divisions in more than one plane.
**Parietal.** Lying at the edge of the cell wall; usually used with reference to the position of the plastid.
**Perennial.** Lasting for three or more years.
**Pedicel.** Stalk of a reproductive structure.
**Pericarp.** Haploid tissue of the gonimocarp formed from the female gametangial thallus, which surrounds a gonimoblast, often flask-shaped (red algae).
**Pericentral cell.** Cell that develops directly from the central cell in a uniaxial syntagma, often several cells surrounding the central cell.

**Periclinal.** Parallel to the surface.

**Pericyst.** Special refracting cell containing fucosan (brown algae).

**Phaeophila-hair.** Spirally-twisted colourless hair from the wall of a vegetative cell occasionally separated from the cell by a thick wall at the base.

**Phaeostroma-hair.** Brown algal hair with a characteristic long cell just below the growth zone.

**Phycocyanin.** Blue coloured pigment that assists in photosynthesis in plastids of red algae.

**Phycoerythrin.** Red coloured pigment that assists in photosynthesis in plastids of red algae.

**Phyllospore.** Spore produced from blade phase where ploidy level and the development are unknown (Bangiaceae).

**Pit connection.** Small pore between adjacent cells, closed with a pit plug in the cell wall of red algae. Both primary and secondary pit connections.

**Pit plug.** Consists of protein surrounded by membranes, the number of which is specific for different systematic groups.

**Plastid.** Cell organelle containing photosynthetic pigments.

**Plurilocular sporangia.** Develop from a cell that divides into several compartments, each with a single swarmer. The swarmers escape individually through a pore from each compartment, although this may be into the middle of the sporangium and the swarmers released in a single stream (brown algae).

**Polyphyletic**. Taxonomic group containing several different lines of descent.

**Polysiphonous**. Each axial cell surrounded with a particular number of periaxial cells.

**Polystromatic.** Thallus consists of several cell layers.

**Positively phototactic.** Movement towards the light source.

**Primary pit connection.** Pit connection between a neighbouring cell in the same filament (red algae).

**Propagule.** Structure that detaches from a parent alga and gives rise to a new individual.

**Prostrate.** Trailing or lying closely along the substratum.

**Protuberances.** Small outgrowths from a crustose thallus (Corallinaceae).

**Proximal.** Towards the base of the thallus.

**Pseudodichotomous.** The dichotomy caused by displacement of a branch, e.g. *Cladophora*, or where two branches have different length, e.g. *Ceramium*, where a lateral branch forms from the cell immediately below the apical cell and develop like the main axes.

**Pseudoparenchyma.** Syntagma in which the filaments are so close together that the thallus appears like parenchyma.

**Pyrenoid.** Protein containing organelle occurring within or adjacent to a plastid. Storage products often deposit around pyrenoids.

**Pyriform**. Pear-shaped.

**Receptacle.** Branch or apical part of thallus with reproductive structures (Fucales).

**Red algal hair.** Unicellular colourless hair, with the cytoplasm concentrated at the apex.

**Resin.** Plastic-like embedding material used for sectioning material with a microtome.

**Reticulate.** Net-like. Appearing like a net.

**Rhizoid.** Cell or filament involved in attachment. Term used also for short outgrowths from cells in *Rhizoclonium* and *Rosenvingiella*.

**Rhodoliths.** Free-living, nodules of branched, calcified red algae (Corallinaceae); see also maerl.

**Rule of priority.** Nomenclatural rule stating that the oldest name used for a taxonomic entity must be accepted.

**Scattered branches.** Branches irregular in position.

**Secund.** Arranged on one side only of a branch.

**Secondary pit connection.** Pit connection between neighbouring cells of different (dense) filaments. Formed after cell fusion of a cell in one of the filaments and a small cell cut off from a cell in the other filament (red algae).

**Serrate.** Saw-like edge of thallus.

**Sessile.** Borne directly on thallus, without a stalk.

**Segment.** A repeated uniform section of a branch. Frequent in monopodial syntagmas.

**Sheath.** An outer wall layer.

**Siphonous thallus.** Tubular without internal cell walls.

**Smooth flagellum.** Flagellum without appendages,

with stiff movements. In brown algal swarmers directed backwards.
**Sorus** (pl. **sori**). An aggregation of reproductive structures forming a patch on thallus.
**Spermatangium.** Cell in which the spermatia form after mitotic divisions (Bangiaceae).
**Spermatium.** Reproductive colourless male cell without flagella (red algae).
**Spermatozoid.** Reproductive male cell with flagella (brown and green algae).
**Spongy plastid.** Composed of many small plates or ribbons that border each other and fill the cell; only some of the plates contain pyrenoids.
**Sporangium** (pl. **sporangia**). Cell producing one or more spores.
**Sporophyll.** Special blade with sporangia (*Alaria*).
**Sporophyte.** Thallus which bears sporangia.
**Squash preparation.** Slide preparation squeezed to separate filaments, sporangia, or other structures from each other. Made by arranging the algal material between a glass slide and coverslip, placing this preparation upside down on a piece of filter paper and pressing it gently.
**Stellate plastid.** Star-shaped plastid with several short or longer extensions from a central area.
**Stephanocont swarmer.** Swarmer with several flagella in a whorl around the cell.
**Stichidium.** Special small branch with antheridia or tetrasporangia (Dasyaceae).
**Stolon.** Prostrate branch that appears similar to an upright branch.
**Sublittoral.** Zone of the sea, always covered by water.
**Substratum** (pl. **substrata**). Structure on which an alga is growing.
**Swarmer.** Motile reproductive cell of uncertain function.
**Sympodial growth.** The apical cell of an axis grows into a hair, a small branch, or a sporangium while the apical growth of the axis continues from a cell below the former apical cell.
**Synonym.** Two or more names for the same taxon.
**Syntagma.** Thallus composed of cohering filaments. See comments for uniaxial and multiaxial syntagma.
**Taxon.** Taxonomic unit at any level of classification.
**Terete.** Circular in transverse section.
**Tetrahedral.** Tetrasporangium with spores arranged in four lateral planes as in a tetrahedron.
**Tetrasporangium** (pl. **tetrasporangia**). Sporangium in which four spores are formed. Tetrasporangia of red algal tetrasporophytes form tetraspores after meiotic divisions. They can be zonate (transversely divided), cruciate or tetrahedral. They germinate and grow into male and female gametophytes.
**Tetraspore.** Spore formed in a tetrasporangium.
**Tetrasporophyte.** The diploid generation (2n) in the life history of red algae.
**Thallus** (pl. **thalli**). A term used for the whole organism, i.e. individual alga.
**Trichoblasts.** Simple or branched filaments of cylindrical cells with or without plastids. They may be unbranched, dichotomous or have opposite branches.
**Trichogyne.** Elongate extension of a carpogonium that receives the spermatium (red algae).
**Trichothallic.** Growth form with an intercalary zone near the tip of a branch forming a distal hair or hair like shoot and on the inner side contributes to the growth of the alga (brown algae).
**Trichotomous branching.** Three branches that look alike from a branching point.
**True brown algal hair**. Narrow uniseriate filament with basal meristem and cells elongating towards apex, no plastids. A basal sheath or collar may be present.
**Trumpet cell.** Elongate cell in medulla of Laminariales, the original thickness of the cell only maintained at the cross walls while the remaining part of the cell is very narrow apart from thick longitudinal walls.
**Tubular**. Hollow cylindrical shape.
**Type locality.** Original collection locality for a species.

**Unbranched.** Without branches.
**Undulate.** With a wavy surface.
**Uniaxial syntagma.** Syntagma constructed of a central filament with branches; a single apical cell.
**Unilateral.** To one side.
**Unilocular sporangium.** Sporangium with one compartment.

**Uniseriate.** In a single row.
**Upright filaments.** Filaments that are perpendicular to the substratum.
**Utricle.** Bladder-like apical portion of a siphonous filament or tube, e.g. forming the surface of *Codium*.

**Vacuole.** Part of a cell, normally consisting of fluid, surrounded by a membrane.

**Zonate.** Divided by parallel walls.
**Zoospore.** Asexual swarmer.
**Zygote.** The cell formed after fusion of two sexual cells.
**Zygotosporangium.** Cell formed after sexual reproduction (Bangiaceae).
**Zygotospore.** Form after mitotic divisions in a zygotosporangium (Bangiaceae).

# Species last collected more than 75 years ago

Several species that have been recorded for the Danish seaweed flora are only known from collections made 75-100 years ago. They need to be looked for and their presence in Danish waters documented by new collections.

| **Red algae (Rhodophyta)** | **Last collection** |
|---|---|
| *Acrochaetium balticum* | Bornholm, South of Broens Rev, 8 m, 6.8.1894. |
| *Acrochaetium cytophagum* | Harbour of Elsinore, 0.5 m, 10.9.1894. |
| *Acrochaetium dumontiae* | Harbour of Gilleleje, 0.5 m, 14.5.1905. |
| *Acrochaetium immersum* | Harbour of Skagen, 0.5 m, 25.7.1921. |
| *Choreonema thuretii** | The Northern Kattegat before 1917 (Rosenvinge, 1917) |
| *Colaconema attenuatum* | Nissum Bredning 5 m, 26.8.1893. |
| *Helminthocladia calvadosii* | Stone reef east of Hirtshals, 1 m, 13.7.1914. |
| *Polysiphonia orthocarpa* | Fur, Knudshoved, Lisehøj, 2 m, 24.7.1920. |
| *Tsengia bairdii* | Little Belt, at Lyngsodde, 17 m, 23.7.1915. |

| **Brown algae (Phaeophyceae)** | **Last collection** |
|---|---|
| *Asperococcus ensiformis* | Nordøst revet, Hirsholmene, 8 m, 4.8.1922. |
| *Endodictyon infestans* | The North Sea, 12.5 m, 8.8.1905. |
| *Halopteris scoparia* | Læsø Trindel, 15 m, 13.7.1892. |
| *Pogotrichum setiforme* | Harbour jetty of Aggersund, 6.5.1895 |
| *Sphacelaria plumula* | Lønstrup, Mellemgrund, 10-8 m, 2.8.1904. |
| *Sphacelaria reticulata* | Hofmansgave 1867, probably extinct. |
| *Sphacelaria tribuloides* | Aalbæk Bugt, Hulsig Stene, 25.7.1933. |
| *Stilopsis lejolisii* | Nissum Bredning, Mullerne, 5 m, 26.7.1905. |
| *Streblonema fasciculatum* | Korsør, 8.11.1892. |
| *Trachynema mortensenii* | Vodstrup Hage, 15.5.1895. |
| *Ulonema rhizophorum* | Bastholm, 15.6.1922. |

| **Green algae (Chlorophyta)** | **Last collection** |
|---|---|
| *Cladophora hutchinsiae* | Mors, Maleklit, 7.8.1943. |
| *Prasiola furfuracea* | Type locality: Hofmansgave, |
| *Urospora neglecta* | Elsinor, 1.5.1892. |

**Choreonema thuretii* (Bornet) F. Schmitz belongs in the coralline red algae but it is not dealt with elsewhere in the book.

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# Index

Accepted names of species recorded in Danish waters and covered in this book and names of higher rank than species are in **bold letters**. Page numbers in **bold** refer to volume 2.